

Research Letter

Mineral Licks Attract Neotropical Seed-Dispersing Bats

**Christian C. Voigt,¹ Dina K. N. Dechmann,^{1,2} Jamie Bender,³ Benjamin J. Rinehart,³
Robert H. Michener,⁴ and Thomas H. Kunz³**

¹ Leibniz Institute for Zoo- and Wildlife Research, Alfred-Kowalke Street 17, 10315 Berlin, Germany

² Smithsonian Tropical Research Institute, P.O. Box 0843-03092, Balboa, Ancon, Panama

³ Department of Biology, Center for Ecology and Conservation Biology, Boston University, Boston, MA 02215, USA

⁴ Department of Biology, Stable Isotope Laboratory, Boston University, Boston, MA 02215, USA

Correspondence should be addressed to Christian C. Voigt, voigt@izw-berlin.de

Received 4 September 2007; Accepted 10 October 2007

Recommended by B. A. Hawkins

Unlike most terrestrial mammals, female bats must supply their offspring with all required nutrients until pups achieve virtually adult size, at which time they are able to fly and become independent. Access to nutrients may be especially challenging for reproductively active females in mineral-poor landscapes such as tropical rainforests. We hypothesized that pregnant and lactating females from tropical landscapes acquire essential nutrients from locally-available mineral licks. We captured ten times as many bats at mineral licks than at control sites in a lowland rainforest in eastern Ecuador. Among bats captured at mineral licks, the sex ratio was heavily biased toward females, and a significantly higher portion of females captured at these sites, compared to control sites, were reproductively active (pregnant and lactating). Enrichment of ^{15}N in relation to ^{14}N in wing tissue indicated that bats captured at mineral licks were mostly fruit-eating species. Given the high visitation rates of reproductive active females at mineral licks, it is likely that mineral licks are important for fruit-eating female bats as a mineral source during late pregnancy and lactation. By sustaining high population densities of fruit-eating bats that disperse seeds, mineral licks may have an indirect influence on local plant species richness.

Copyright © 2007 Christian C. Voigt et al. This is an open access article distributed under the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

1. INTRODUCTION

For decades, ecologists have been puzzled by the paradox of high tropical biodiversity occurring on generally nutrient/mineral poor soils [1]. Minerals are important not only for plant growth and reproduction, but also for animals on which many tropical plants depend for seed dispersal. The limited distribution and availability of minerals in tropical forests, in combination with sensory limitations of animals trying to find them, may be a constraint on reproduction and geographic distribution because offspring production and population viability are ultimately linked to adequate nutrient sources [2, 3]. In most terrestrial mammals, juveniles begin to consume solid food while still being suckled, typically long before they achieve adult size. In contrast, juvenile bats cannot acquire water or nutrients except from the mother's milk until they are able to fly and they cannot fly until they are nearly adult size [4, 5]. Thus, all nutrients required for the production of an adult-size skeleton must come from the

mother through milk [6, 7]. Given that bat diets are generally poor in calcium and other minerals [8–10], females face a physiological dilemma: to allocate some of their own limited nutrient stores for production of offspring, or to expend additional energy and seek nutrient sources where they may be available [5, 11]. The dilemma may be particularly pronounced in tropical rainforests which usually occur in mineral-poor landscapes.

Anecdotal observations from the Amazonian rainforest suggest that bats visit the same water holes as do tapirs and other large mammals, where they also may consume the mineral-rich water [12]. However, heretofore, the function of water or soil consumption at mineral licks has remained unclear in bats. We postulate that mineral licks—small open muddy areas in tropical forested landscapes often with running water—are an important mineral source for fruit-eating bats, especially females during reproduction. To test this hypothesis, we set mist-nets at mineral licks and control sites in the rainforest of eastern Ecuador. In addition, we determined

the trophic level of captured bats by taking small wing biopsies and analyzing these for nitrogen isotopes to test the hypothesis that fruit-eating species are more active at mineral licks than elsewhere in the forest. Because enrichment of ^{15}N in relation to ^{14}N increases in animal tissue with increasing trophic level [13], we predicted that bats captured at mineral licks would show lower levels of ^{15}N enrichment, compared to species that feed at higher trophic levels (i.e., on insects and vertebrates) in the same forested landscapes.

2. METHODS

Our study was conducted during the dry season at the Tiputini Biodiversity Station (TBS) ($0^{\circ}38.31'\text{S}$, $76^{\circ}8.92'\text{W}$) between 26 January and 23 February 1998, on 4 January 1999, and between 14 March and 13 April 2007. Habitats at TBS are terra firme forest, varzea forest, palm swamps, small oxbow lakes, and streams at elevation of 190–270 m as [14]. Scattered mineral licks dot the landscape. Monthly rainfall throughout the year varies between 50 and 650 mm (TBS weather station) with two rainy seasons, the first is from May to July, and the other is from October through December.

We set ground-level mist nets (length 6 to 9 m; 70 denier/2 ply, 36 mm mesh, 5 shelves) (R. Vohwinkel, Veltbert, Germany) to catch bats at six mineral licks and at 15 arbitrarily selected control sites in the forest. Nets were monitored between 1800 and 2130 hours. Our netting effort at mineral licks included one night at four sites and two nights each at the two others. Because free-ranging fruit-eating bats generally do not survive more than 8 years, we consider our mist-netting efforts in 1998 and 2007 to be independent events for statistical purposes. We identified bats using available taxonomic keys [15, 16], recorded relative age (young and adult) and reproductive condition [17], then released animals at the site of capture as soon as possible after processing. In 1998, bats were banded on the forearm using numbered, plastic rings (A. C. Hughes, United Kingdom). In 2007, we collected two small wing-membrane biopsies from each bat for stable isotope analysis [18]. No marked bats were recaptured.

2.1. Stable isotope analysis

Wing samples were weighed on a microbalance (Sartorius AG, Göttingen, Germany) and then loaded into tin capsules. All samples were combusted and analyzed using a Fisons NA 1500 elemental analyser and a Finnigan continuous flow system, coupled to a Delta-S isotope ratio mass spectrometer at (Stable Isotope Laboratory, Boston University, MA, USA). Atmospheric nitrogen was used as the standard for the $^{15}\text{N}/^{14}\text{N}$ ratio and nitrogen isotope ratios are given in the $\delta^{15}\text{N}$ notation (‰). Precision of isotope measurements was better than $\pm 0.01\text{‰}$. We used the following equation to calculate $\delta^{15}\text{N}$

$$\delta^{15}\text{N} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) * 1000, \quad (1)$$

where R_{sample} and R_{standard} represent the $^{15}\text{N}/^{14}\text{N}$ ratios of the sample and standard, respectively.

2.2. Statistics

To control for different levels of mist-netting efforts between mineral licks and control sites, we calculated the average number of bats captured at each site (expressed as number of bats per meter of net per mist-net hours). We performed a Mann-Whitney U tests to compare captures at mineral licks and control sites and Fisher's exact test to test for differences in sex ratios, ratios of reproductive active and nonreproductive females, and ratios of different subfamilies between mineral licks and at control sites. A Bonferroni correction was applied to each test since the same capture data was used for several tests [19].

3. RESULTS

We captured 389 bats comprising of 31 species. Among these, 339 bats were captured in nets set at mineral licks and 50 at control sites (Table 1). We netted nearly 10 times more bats per meter net hour at mineral licks than control sites (Mann-Whitney U-Test: $U = 11$, $n_1 = 15$, $n_2 = 8$, $P = .0009$). The median number of bats captured per meter net hour equaled 0.58 (mean ± 1 SD: 1.17 ± 1.7) at mineral licks and 0.06 (0.08 ± 0.07) at control sites. We captured 254 females and 85 males at mineral licks and 24 females and 26 males at control sites. The sex ratio of bats at mineral licks was heavily biased toward females compared to control sites (Fisher's exact test: $P = .0002$). We also captured significantly more reproductively active females (late pregnancy and lactation) than nonreproductive females at licks (Fisher's exact test: $P < .0001$). Most bats that we captured at mineral licks were members of the phyllostomid subfamily Stenodermatinae (Fisher's exact test: $P < .0001$). In addition, stenodermatine bats (i.e., typically fruit-eating species) captured at mineral licks had significantly lower $\delta^{15}\text{N}$ than the nonstenodermatine bats at the control sites which consume a more insect dominated diet (Figure 1: Mann-Witney U-Test: $U' = 162$, $n_1 = 17$, $n_2 = 10$, $P < .0001$).

4. DISCUSSION

Our results indicate that mineral licks are hot spots of nocturnal bat activity in tropical rainforests. Similar concentrations of bat activity have only been reported from autumn swarming sites at temperate latitudes, where males court females prior to hibernation [20]. In contrast to swarming sites, where sex ratios are either equal or biased in favor of males, there are significantly more females than males at mineral licks. Moreover, almost all females were either pregnant or lactating, consistent with the hypothesis that their presence is associated with nutrient demands associated with reproduction. Nitrogen isotope ratios of stenodermatine bats captured at mineral licks were significantly lower than that of nonstenodermatine bats, indicating a difference of one trophic level from species captured at control sites [13, 18]. Thus, our results strongly support the hypothesis that mineral licks are preferentially visited by female fruit-eating bats during late pregnancy and lactation. Such sites also are visited by larger mammals [21–23] and birds [24]. By visiting and ingesting

TABLE 1: Phyllostomid bats captured at mineral licks and control sites in the rainforest at the Tiputini Biodiversity Station in eastern Ecuador, sorted according to subfamilies, and ranked by number of captured individuals at mineral licks (Ind. = individuals, ♀ = females, ♂ = males).

Subfamily	n species	Ind.	Mineral licks		Ind.	Control sites	
			♀	♂		♀	♂
Stenodermatinae	18	322	250	72	14	5	9
Carollinae	4	15	2	13	24	12	12
Glossophaginae	4	2	2	0	5	3	2
Phyllostominae	4	0	0	0	7	4	3
Total	30	339	254	85	50	24	26

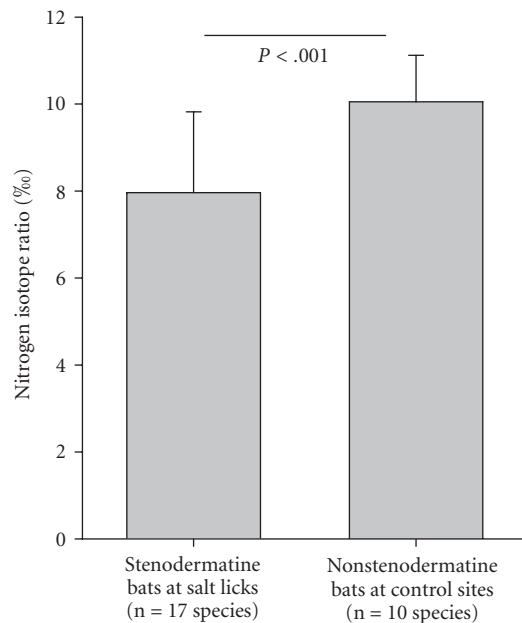


FIGURE 1: Nitrogen isotope ratios (mean ± 1 SD; δ¹⁵N; ‰) of stenodermatine bats captured at mineral licks and nonstenodermatine bats at control sites at the Tiputini Biodiversity Station in eastern Ecuador. Stenodermatine bats captured at mineral licks were significantly depleted in ¹⁵N relative to nonstenodermatine bats from control sites.

mineral-rich water in mineral licks, fruit-eating bats gain essential minerals to produce nutrient-rich milk that facilitates growth and development of embryos and pups. They may also benefit if the minerals buffer secondary plant compounds [25] often present in fruits and leaves that are ingested by females during periods of high energy demand during pregnancy and lactation.

5. CONCLUSIONS

Among fruit-eating mammals, bats outnumber all other taxa in Neotropical mammal assemblages [26]. Fruit-eating bats usually feed on a mineral poor foods [21, 27], but sometimes supplement their diet with leaves that are more enriched than the average diet of bats [27, 28]. Fruit-eating bat populations may benefit from mineral licks in the rainforests, by achieving higher growth rates and producing more offspring than bats in rainforests without mineral licks. By helping to sus-

tain high population densities of fruit-eating bats, mineral licks would contribute indirectly to seed dispersal and as a consequence potentially to increased plant diversity. Future studies need to address whether geographic variation in the abundance of mineral licks may not only influence local population densities of fruit-eating bats, but also plant species diversity in so-called biodiversity hotspots [29, 30].

ACKNOWLEDGMENTS

The authors would like to thank Gabriela de Luna, Krista Capps, Alex Flecker, Jaime Guerra, and the staff and administration of the Tiputini Biodiversity Field Station. They also thank the authorities of Ecuador, especially those of Yasuni National Park, for granting permission to work at TBS. All protocols were approved by the Boston University Animal Care and Use Committee. This study was funded by Boston University Center for Ecology and Conservation and by the Deutsche Forschungsgemeinschaft (Grant no. Vo 890).

REFERENCES

- [1] J. Terborgh, *Diversity and the Tropical Rain Forest*, Scientific American Library Press, New York, NY, USA, 1992.
- [2] J. L. Gittleman and S. D. Thompson, "Energy allocation in mammalian reproduction," *American Zoologist*, vol. 28, no. 3, pp. 863–875, 1988.
- [3] A. Prentice, "Calcium in pregnancy and lactation," *Annual Review of Nutrition*, vol. 20, pp. 249–272, 2000.
- [4] U. M. Norberg and J. M. V. Rayner, "Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation," *Philosophical Transactions of the Royal Society of London. Series B*, vol. 316, no. 1179, pp. 335–427, 1987.
- [5] R. M. R. Barclay, "Constraints on reproduction by flying vertebrates: energy and calcium," *The American Naturalist*, vol. 144, no. 6, pp. 1021–1031, 1994.
- [6] E. H. Studier and T. H. Kunz, "Accretion of nitrogen and minerals in suckling bats, *Myotis velifer* and *Tadarida brasiliensis*," *Journal of Mammalogy*, vol. 76, no. 1, pp. 32–42, 1995.
- [7] G. G. Kwiecinski, L. Krook, and W. A. Wimsatt, "Annual skeletal changes in the little brown rat, *Myotis lucifugus lucifugus*, with particular reference to pregnancy and lactation," *American Journal of Anatomy*, vol. 178, no. 4, pp. 410–420, 1987.
- [8] J. O. Keeler and E. H. Studier, "Nutrition in pregnant big brown bats (*Eptesicus fuscus*) feeding on June beetles," *Journal of Mammalogy*, vol. 73, no. 2, pp. 426–430, 1992.
- [9] E. H. Studier and S. H. Seveck, "Live mass, water content, nitrogen and mineral levels in some insects from south-central

- lower Michigan," *Comparative Biochemistry and Physiology Part A*, vol. 103, no. 3, pp. 579–595, 1992.
- [10] R. M. R. Barclay, "Do plants pollinated by flying fox bats (Megachiroptera) provide an extra calcium reward in their nectar?" *Biotropica*, vol. 34, no. 1, pp. 168–171, 2002.
- [11] R. T. F. Bernard and A. Davison, "Does calcium constrain reproductive activity in insectivorous bats? Some empirical evidence for Schreibers' long-fingered bat (*Miniopterus schreibersii*)," *South African Journal of Zoology*, vol. 31, no. 4, pp. 218–220, 1996.
- [12] M. D. Tuttle, "Unusual drinking behavior of some stenodermatine bats," *Mammalia*, vol. 38, pp. 141–144, 1974.
- [13] M. J. Deniro and S. Epstein, "Influence of diet on the distribution of nitrogen isotopes in animals," *Geochimica et Cosmochimica Acta*, vol. 45, no. 3, pp. 341–351, 1981.
- [14] H. Kreft, N. Köster, W. Küper, J. Nieder, and W. Barthlott, "Diversity and biogeography of vascular epiphytes in Western Amazonia, Yasuní, Ecuador," *Journal of Biogeography*, vol. 31, no. 9, pp. 1463–1476, 2004.
- [15] L. Albuja, *Murciélagos del Ecuador*, Circetrónica Compañía Limitada Offset, Quito, Ecuador, 2nd edition, 1999.
- [16] D. Tirira, *Mamíferos del Ecuador*, Museo de Zoología, Quito, Ecuador, 2007, Publicación Especial 2.
- [17] P. A. Racey, "Reproductive assessment in bats," in *Ecological and Behavioral Methods for the Study of Bats*, T. H. Kunz, Ed., pp. 277–302, Smithsonian Institution Press, Washington, DC, USA, 1988.
- [18] C. C. Voigt and F. Matt, "Nitrogen stress causes unpredictable enrichments of ^{15}N in two nectar-feeding bat species," *Journal of Experimental Biology*, vol. 207, no. 10, pp. 1741–1748, 2004.
- [19] R. R. Sokal and F. J. Rohlf, *Biometry*, Freeman, New York, NY, USA, 1995.
- [20] K. N. Parsons, G. Jones, and F. Greenaway, "Swarming activity of temperate zone microchiropteran bats: effects of season, time of night and weather conditions," *Journal of Zoology*, vol. 261, no. 3, pp. 257–264, 2003.
- [21] S. R. Moe, "Mineral content and wildlife use of soil licks in southwestern Nepal," *Canadian Journal of Zoology*, vol. 71, no. 5, pp. 933–936, 1993.
- [22] G. Klaus, C. Klaus-Hügi, and B. Schmid, "Geophagy by large mammals at natural licks in the rain forest of the Dzanga National Park, Central African Republic," *Journal of Tropical Ecology*, vol. 14, no. 6, pp. 829–839, 1998.
- [23] A. Mills and A. Milewski, "Geophagy and nutrient supplementation in the Ngorongoro Conservation Area, Tanzania, with particular reference to selenium, cobalt and molybdenum," *Journal of Zoology*, vol. 271, no. 1, pp. 110–118, 2007.
- [24] N. B. Simmons and R. S. Voss, "The mammals of Paracou, French Guiana: a neotropical lowland rainforest fauna—part 1: bats," *Bulletin of the American Museum of Natural History*, no. 237, pp. 1–219, 1998.
- [25] J. D. Gilardi, S. S. Duffey, C. A. Munn, and L. A. Tell, "Biochemical functions of geophagy in parrots: detoxification of dietary toxins and cytoprotective effects," *Journal of Chemical Ecology*, vol. 25, no. 4, pp. 897–922, 1999.
- [26] D. J. Brightsmith and R. A. Muñoz-Najar, "Avian geophagy and soil characteristics in Southeastern Peru," *Biotropica*, vol. 36, no. 4, pp. 534–543, 2004.
- [27] J. Ruby, P. T. Nathan, J. Balasingh, and T. H. Kunz, "Chemical composition of fruits and leaves eaten by short-nosed fruit bat, *Cynopterus sphinx*," *Journal of Chemical Ecology*, vol. 26, no. 12, pp. 2825–2841, 2000.
- [28] S. L. Nelson, D. V. Masters, S. R. Humphrey, and T. H. Kunz, "Fruit choice and calcium block use by Tongan fruit bats in American Samoa," *Journal of Mammalogy*, vol. 86, no. 6, pp. 1205–1209, 2005.
- [29] N. Myers, "Threatened biotas: "hot spots" in tropical forests," *The Environmentalist*, vol. 8, no. 3, pp. 187–208, 1988.
- [30] N. Myers, "Biodiversity hot spots revisited," *BioScience*, vol. 53, no. 10, pp. 916–917, 2003.

