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Trophic relationships in a neotropical bat community: a preliminary study using carbon and nitrogen isotopic signatures

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Abstract: We used stable isotope techniques to determine the nitrogen and carbon isotopic composition of 21 species of neotropical bats (17 phyllostomids, two mormopids, one molossid and one emballonurid) representing a diverse array of feeding habits (e.g., frugivory, nectarivory, insectivory, carnivory, and sanguinivory) as well as the isotopic composition of plants and insects presumably ingested by the bats. We found trophic enrichment of both $^{13}$C and $^{15}$N, although $^{15}$N enrichment was lower than expected between frugivorous and insectivorous bats. Our data indicate that most species of frugivorous bats examined have a mixed diet of fruits and insects and only Centurio senex, Artibeus lituratus and Dermanura watsonii appear to be exclusively frugivorous. One species of insectivorous bat, Tadarida evansi, apparently relies on fruit as part of its diet. Although preliminary, our results indicate that stable isotope methods can be used to quantify the importance of different dietary classes in the diets of bats.

Résumé: Des techniques isotopiques ont été utilisées afin de déterminer la composition isotopique en carbone et azote de 21 espèces de chauves-souris néotropicales (17 phyllostomides, 2 mormopides, un molosside et un emballonurid) présentant un tableau diversifié de leurs tendances alimentaires (fructivore, nectarivore, insectivore, carnivore, et sanguinaire) ainsi que la composition isotopique des plantes et des insectes vraisemblablement ingérées par les chauves-souris. Nous avons trouvé un enrichissement trophique aussi bien en azote ($^{15}$N) que carbone ($^{13}$C) bien que la richesse en azote était plus basse que prévue entre les chauves-souris à tendance fructivore et insectivore. Nos données indiquent que la plupart des espèces de chauves-souris fructivores qui ont été examinées ont un régime alimentaire mélangé de fruits et d’insectes et seules Centurio senex, Artibeus lituratus et Dermanura watsonii semblent être exclusivement fructivores. Une des espèces de chauve-souris insectivores, Tadarida evansi, intègre apparemment les fruits dans son régime alimentaire. Quoique préliminaires, nos résultats montrent que les méthodes isotopiques relatives peuvent être utilisées pour quantifier l’importance des différentes types d’alimentation dans les régimes alimentaires des chauves-souris.

Resumen: Se utilizaron técnicas de isótopos estables para determinar la composición isotópica de nitrógeno y carbono de 21 especies de murciélagos neotropicales (17 folístomidos, dos mormopídeos, un molosido y un emballonurido) con diversos hábitos alimenticios (frugívoros, nectarívoros, insectívoros, carnívoros y sanguinívoros), así como la composición isotópica de plantas e insectos inadvertidamente por los murciélagos. Encontramos enriquecimiento trófico tanto de $^{13}$C como de $^{15}$N, aunque este último fue más bajo que lo esperado entre los murciélagos frugívoros e insectívoros. Nuestros datos indican que la mayoría de las especies de murciélagos frugívoros examinados tienen una dieta mixta de frutas e insecto y solamente Centurio senex, Artibeus lituratus y Dermanura watsonii parecen ser exclusivamente frugívoros. Una especie de murciélagos insectívoros, Tadarida evansi, aparentemente toma frutas como parte de su dieta. Aunque preliminar, nuestros resultados indican que los métodos de isótopos estables pueden ser utilizados para cuantificar la importancia de diferentes tipos de dietas en los murciélagos.

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TROPHIC STRUCTURE IN A BAT COMMUNITY

Resumo: Para determinar a composição isotópica de azoto e carbone de 21 espécies de morcegos neotropicais (17 phyllostomídeos, dois mormópídeos, um molossídeo e um emballonurido) com hábitos alimentares diversos (frugívoros, nectarívoros, insectívoros, carnívoros e sanguinívoros), bem como a composição isotópica das plantas e insetos presumivelmente ingeridos pelos morcegos usaram-se técnicas de isótopos estáveis. Encontrou-se um enriquecimento trófico quero no $^{13}$C que no $^{15}$N se bem que o enriquecimento em $^{15}$N tenha sido menor do que o antecipado entre os morcegos frutívoros e os insectívoros. Os resultados obtidos indicam que muitas das espécies de morcegos frutívoros examinadas têm uma dieta mista de frutos e insetos e só a Centurio senex, Aristeus littoratus e Dermamur watsonii parecem ser exclusivamente frutívoros. Uma das espécies de morcegos insectívoros, Tomatia evans está, aparentemente, depende dos frutos como parte da sua dieta. Os resultados, embora preliminares, indicam que uso de métodos com recurso aos isótopos estáveis podem ser utilizados para quantificar a importância das diferentes classes de dieta dos morcegos.

Key Words: carnivorous bats, feeding habits, frugivorous bats, nectarivorous bats, insectivorous bats, stable isotopes, trophic levels, vampire bats.

Introduction

Dietary studies in bats have traditionally relied on the examination of feces, pellets, fur, and stomach contents (Alvarez & Gonzalez Quintero 1970; Thomas 1988; Whitaker 1988). More recently, stable isotope techniques have been used in bats to determine trophic patterns as well as migratory movements (DeMarais et al. 1980; Fleming et al. 1993; Herrera et al. 1993). While these techniques do not provide detailed information about the identity of food consumed by animals, they allow long-term examination of dietary trends. For example, the examination of the isotopic composition of muscle tissue reflects the diet of the animal 1-2 months before the tissue was collected (Tieszen et al. 1983). Carbon and nitrogen are the most commonly used isotopes in animal studies and, because they show trophic fractionation, they can be used to separate trophic levels in animal communities (Hobson et al. 1994; Mizutani et al. 1992). In general, there is an enrichment of 1% in $^{13}$C and of 2-4% in $^{15}$N from one trophic level to the next (DeNiro & Epstein 1978; Ehleringer et al. 1986).

Here we examine the trophic structure of a neotropical bat community using both carbon and nitrogen stable isotope signatures. We focus on bats in the family Phyllostomidae because its members exhibit a broad array of feeding habits (e.g., nectarivory, frugivory, insectivory, carnivory, sanguinivory; Gardner 1977). Bats in this family have been traditionally separated into different trophic guilds although some frugivorous and nectarivorous species may consume insects and leaves to fulfill their nitrogen requirements (Kunz & Diaz 1995; Thomas 1984). On the other hand, some insectivorous phyllostomids also ingest fruits (Gardner 1977). The primary goal of this study was to determine the extent to which bats that are traditionally assigned to the above-mentioned categories rely on plant and/or animal sources to meet their nutritional requirements. We also examined bats in other families that are considered strictly insectivorous and plants and insects that are probably consumed by bats. We expected to find an enrichment in $^{13}$C and $^{15}$N of at least +1% and +3%, respectively, from lower to higher trophic levels if bats fit into distinct feeding categories and do not include a mixture of animal and plant items in their diet.

Materials and methods

Tissue samples were collected in April 1994 at the end of the dry season during a transect survey of the Calakmul Biosphere Reserve (19-18°N, 89-90°W) conducted by the Instituto de Ecología in the state of Campeche, Mexico. Pectoral muscle samples were collected from bat specimens originally sacrificed for a museum reference collection. We collected samples from one to three individuals of nine species of frugivorous and nectarivorous bats (Phyllostomidae: Centurio senex Gray, Aristeus littoratus Olfers, A. intermedius Allen, Vampyressa pusilla Wagner, Carollia brevicauda Schinz, C. perspicillata Linnaeus, Dermamur watsonii Saussure, Stenura lilium Geoffroy, Glossophaga soricina Fallas), 9 species of insectivorous bats (Phyllostomidae: Tonatia brasilensis
Peters, T. evolis Davis & Carter, Micronycteris schmidt- 
torun Sanborn, M. brachyotis Dobson, Minio bennettii 
Gray; Mormoopidae: Pteropus parrelli Gray, P. davyi 
Gray; Molossidae: Molossus rufus Miller; Emballonuridae 
: Peropyretes macrotis Wagner); one carnivorous species 
(Phyllostomidae: Vampyrus spectrum Linnaeus) and two 
species of vampires (Phyllostomidae: Diphylla ecaudata 
Spix and Desmodus rotundus Geoffroy). We also col- 
clected nocturnal insects and tissue (leaves or fruits if avail- 
able) from plants that are presumably ingested by bats. 
Because fractionation can occur in plant parts (Handley & 
Raven 1992), tissue actually ingested by the animals was 
collected whenever possible preferentially fruit, although 
there is evidence of leaf consumption in some frugivorous 
bats (Kunz & Díaz 1995). We collected one individual of 
one of unidentified species of insect in each of the orders 
Coleoptera, Lepidoptera, and Hemiptera along with one 
individual of eight species of plants (Leguminosae: Bauhinia 
isp. (leaf); Piperaceae: Piper amalago Linnaeus (leaf); 
Moraceae: Ficus sp. (fruit), Brosimum alicastrum Berg 
(leaf); Sapotaceae: Manilkara sapota van Royen (leaf), 
Chrysophyllum sp. (fruit), Pouteria campechiiana Baehni 
(leaf); Combretaceae: Bucida biceras Linnaeus (fruit).

The nitrogen and carbon composition of pectoral muscle 
collected from individuals of the 21 species of bats 
was assessed using the methodology described by Sealy et 
al. (1987). In brief, 12-15 mg of ground muscle samples 
were combusted at 800°C in Vycor ampules with 1 g of 
cupric oxide, 1 g of copper and a small amount of silver 
foil (ca. 50 mg). Nitrogen and carbon were cryogenically 
purified from the combustion products in a vacuum sys-

\[
\delta ^{15}N = \left( \frac{^{15}N}{^{14}N}_{\text{sample}} \right) \left( \frac{^{15}N}{^{14}N}_{\text{standard}} - 1 \right) \times 1000, 
\]

A similar procedure was used with the insect and 
plant samples, except that we used 20 mg of plant tissue 
per sample. The standard for \( \delta ^{13}C \) values was the 
Peedee belemnite marine limestone (PDB), and it was 
atmospheric nitrogen for \( \delta ^{15}N \). Precision was ± 0.175% 
(S.D.) and ± 0.1% (S.D.) for nitrogen and carbon, 
respectively.

Statistical analysis

Mean \( \delta ^{13}C \) and \( \delta ^{15}N \) values were compared between 

trophic levels (i.e., plants vs. frugivorous bats, plants vs. 

ingsects, frugivorous bats vs. insectivorous bats, insects vs. 
insectivorous bats, insectivorous bats vs. carnivorous bats) 

using Mann-Whitney's U tests. When more than one indi-

vidual per species was analyzed, we used the mean value 

for the species. Bats were separated into trophic guilds for 

the analysis according to traditional classifications 

(Gardner 1977). We also conducted a linear regression 

analysis using mean \( \delta ^{13}C \) and \( \delta ^{15}N \) values of all the spe-

cies of bats and followed the above-mentioned procedure when 

one species was represented by more than one individual.

Results

Mean values of \( \delta ^{13}C \) and \( \delta ^{15}N \) increased (i.e., exhibited 
enrichment of \( ^{13}C \) and \( ^{15}N \)) from lower to higher trophic 

levels (Fig. 1). The enrichment in \( ^{13}C \) was +3.110 between 

plants and insects, +3.667 between plants and frugivorous 

bats, +1.716 between frugivorous and insectivorous bats, and 

+1.027 between insectivorous and carnivorous and 
insectivorous bats. The enrichment in \( ^{15}N \) was -0.400 

between plants and insects, +2.109 between plants and 

frugivorous bats, +0.750 between frugivorous and insectivorous 
bats, and +2.227 between insectivorous and carnivorous and 
insectivorous bats.

Carbon isotopic compositions were significantly dif-

ferent between plants and insects (U = 24, P = 0.018) and 

frugivorous bats (U = 72, P = 0.000), and between insec-

tivorous bats and insects (U = 27, P = 0.01) and 

frugivorous bats (U = 71, P = 0.000). Significant differences 
in nitrogen isotopic composition were found between 
insects and insectivorous bats (U = 27, P = 0.016), and be-

between insectivorous and carnivorous bats (U = 55, P = 

0.010).

There was significant positive correlation between \( \delta ^{13}C \) 

and \( \delta ^{15}N \) values when the values for all the species of bats 

were pooled (r = 0.478, F = 5.64, P = 0.028, d.f. = 1, 19, Y 

= 0.655x - 29.313; Fig. 2). There was a substantial overlap 

between isotope values of insectivorous and frugivorous 
bats, particularly in \( \delta ^{15}N \) values (Fig. 2).

Discussion

In general, both carbon and nitrogen \( \delta \) values dis-

criminated among different trophic levels in the species of
bats we studied, although some species did not fit their expected trophic level. The relationship between carbon and nitrogen isotopic signatures was significant although the correlation coefficient was not particularly high (r = 0.478); in some cases bats had low δ¹³C and high δ¹⁵N values (or otherwise) that prevented their categorization into a distinct trophic level (e.g., Desmodus rotundus, Tontonia evos, Stinarah lilliam, Caroliia breviceuda, C. perspicillata, Glossophaga soricina).

¹³C enrichment was higher between plants and primary consumers (insects and frugivorous bats) than between primary and secondary consumers (insectivorous bats) and between secondary and tertiary consumers (carnivorous and vampire bats). A similar pattern occurs in marine-terrestrial communities; carbon enrichment in primary consumers (e.g., euphausiids, mussels) is +3‰ relative to particulate organic matter but it decreases between higher levels (Hobson et al. 1994).

Enrichment in ¹⁵N was less pronounced than that of ¹³C, especially between plants and insects and between frugivorous and insectivorous bats. Nitrogen composition in plants was highly variable (δ¹⁵N values ranged from -2.2 to 9.9‰) and was not significantly different from that of insects and frugivorous bats. Furthermore, ¹⁴N enrichment between plants and primary consumers was at the lower end of the expected range (DeNiro & Epstein 1978) and in the case of insects there was negative enrichment. Unless the insects in this study were feeding on items other than plants (rather unlikely for the insects included in the study), the expected values of plant ¹⁵N should be around 1.5 if there is a trophic enrichment of +3‰ (DeNiro & Epstein 1978) since the ¹⁵N average value for insects was 3.6. The limited number of species of plants included in this study is probably not fully representative of the nitrogen composition of the plant community in the area of study. In addition to this, because only one individual per species of plant was included in the analysis, we cannot estimate intraspecific variation in nitrogen composition. Similarly, the low sample size of insects in this study prevents any generalization for the isotopic composition of this group of animals.

Average ¹⁵N enrichment among bat trophic guilds was lower than expected, especially between frugivorous and insectivorous bats. This suggests that some species of bats are not strict fruit- or insect-eaters. For example, Tonatia evos had very low ¹⁵N values for an insectivore; members of the genus Tontonia feed on both insects and fruits (Gardner 1977), and our results support this. Several species of frugivorous bats (Stinarah lilliam, Caroliia breviceuda, C. perspicillata) had lower ¹³C values than...
insectivorous bats, but their $\delta^{15}N$ were not different than the mean value for insectivores. Similarly, Glossophaga soricina had low $\delta^{15}N$ values but high $\delta^{13}C$ values that suggest a mixed diet of fruits and insects. Based on the examination of stomach contents and feces (Fleming et al. 1972; Palmer et al. 1989; Willig et al. 1993), the diets of these species are mostly composed of fruit with the proportion of insects ranging from none (S. lilium) to low (C. brevicauda and C. perspicillata) and large (G. soricina) amounts of insects. In contrast, Artibeus lituratus Dermapurura watsonii and especially Centurio senex had low values of $\delta^{13}C$ and high $\delta^{15}N$ that suggest a diet of fruit. The diet of A. lituratus has been reported as consisting only of fruits (Palmer et al. 1989; Willig et al. 1993) or a mixture of fruits and insects (Fleming et al. 1972), and C. senex is considered by Gardner (1977) to be an obligate frugivore. A. intermedius had a nitrogen composition similar to C. senex and a carbon isotopic signature intermediate between the mean values for frugivorous and insectivorous bats. Some insectivorous species (Toniaria brasiliensis, and Pteronotus parrinelli) had $\delta^{15}N$ lower than the average for this group of bats although their $\delta^{13}C$ values were intermediate between insectivorous and frugivorous species. P. parrinelli feeds mostly on insects but there is evidence that indicates that this species includes small amounts of fruits in its diet (Fleming et al. 1992). Pollen has also been reported in the diet of another species of Pteronotus (P. quadridens Gundlach; Rodriguez-Duran & Lewis 1987). The remaining insectivorous species seem to feed exclusively on insects, although some of them (Miniopterus wynadottensis) and some individuals of Micronycteris schmidtorum had slightly higher $\delta^{15}N$ values than the carnivorous species (Vampyrum spectrum). The diet of V. spectrum consists of
small birds and mammals, insects and probably fruits (Gardner 1977) while M. bennettii and M. schmidtorum, although mostly insectivorous, may also include fruit in their diet (Gardner 1977). In general, the two species of vampire bats had nitrogen and carbon compositions that place them at the top of the trophic chain, except for the exceptionally low $\delta^{13}C$ value of Desmodus rotundus. We do not have an explanation for the carbon composition of D. rotundus.

In conclusion, isotopic examination of carbon and nitrogen composition offered a broad picture of the trophic structure in the bat community we studied. Our results show that it is rather difficult to place certain species of phyllostomid bats, especially frugivorous species, into distinct trophic guilds. Previous studies of feeding habits based on traditional methods support this view, but our study is the first attempt to quantify the relative importance of plant and animal items in the diet at a community level using stable isotope techniques. We consider this a preliminary study and hope to stimulate further use of stable isotopes in bat biology (also see Fleming 1995). In particular, future trophic studies should increase the number of species of plants and insects sampled and consider seasonal variations in the diet of the animals. Use of blood samples instead of collecting muscle tissue from dead animals would allow increased sample sizes without sacrificing animals. One of us (LGHM) is currently using blood to study food habits in bat communities.

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