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SHORT COMMUNICATION

Ecological and isotopic discrimination of syntopic rodents in a neotropical rain forest of French Guiana

Jean-François Mauffrey[1] and François Catzeflis

Laboratoire de Paléontologie, Paléobiologie et Phylogénie, Institut des Sciences de l'Evolution de Montpellier, UMR 5554 CNRS, Université Montpellier II, cc 64, Place Eugène Bataillon, 34095 Montpellier cedex 5, France
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Stable isotopes are commonly used in ecological studies to infer food resources (Ambrose & DeNiro 1986, Bocherens *et al*. 1990, 1991, 1994; Yoshinaga *et al*. 1991) since isotopic composition is conserved during the feeding process. Moreover, for herbivorous (*sensu lato*) species, it is often possible to identify the main resource because different photosynthetic pathways generate different values of carbon isotope ratios (Park & Epstein 1961, Sternberg *et al*. 1984). This allows the characterization of broad biota such as savannas or forest and discrimination of grazers from sympatric folivorous species (DeNiro & Epstein 1978).

Additionally, in a closed tropical forest, the $^{13}C/^{12}C$ ratio of leaves exhibits a gradient from the canopy to the floor, named the canopy effect (Hanba *et al*. 1997, Medina & Minchin 1980, Schleser & Jayasekera 1985, Van der Merwe & Medina 1989, 1991). Emission of excess ^{12}C from the soil (Medina & Minchin 1980) or the photosynthetic process in shade conditions (Ehleringer *et al*. 1986, 1987; Yakir & Israeli 1995) may account for such a phenomenon. This difference in stable carbon isotope ratios between open and closed forests allowed Schoeninger *et al*. (1997) to separate several species of New World monkeys in relation to their habitat utilization: gaps and edges vs. inner closed forest.

Based on these premises, we investigated the efficiency of stable isotope ratios for discriminating species of rodents sharing the same ecologically restricted area, in a neotropical rain forest. Although stable isotopes are commonly used to describe variation in diet for a single species (Ben-David *et al*. 1997, 1999; Keeling & Nelson 2001), characterization of aquatic food webs and communities (Pinnegar & Polunin 2000) or soil invertebrates (Ponsard & Arditi 2000), they have never been used to document a vertebrate community sampled in the same restricted area. At the Les Nouragues Biological Station in French Guiana, a guild of small rodents (< 1 kg) comprising six genera and at least nine species was studied by the capture–mark–recapture method. Animals from various forest strata were sampled, from the ground level (*Proechimys* and *Oryzomys*) to the top of trees (*Oecomys*, *Rhipidomys* and *Echimys*). The aim of this study was to evaluate the efficiency of stable isotope ratios in discriminating the three most abundant members of the guild, (1) by their food resources and (2) by their habitat usage (terrestrial vs. arboreal species).

The animals were caught during July and August 1998 at Les Nouragues (CNRS-UPS 656, French Guiana, 4°05′ N, 52°40′ W). The studied area, around 7500 m^2, belongs to a primary forest and was sampled with 11 stations using the main trees of the area as supports. Terrestrial trapping was performed with 11 pairs of live-traps placed at the base of these trees, each station being separated by 15–20 m. Above these traps, completing the terrestrial sampling, arboreal trapping was done in the volume of the corresponding 11 trees. In each tree, wire-mesh BTS traps (33 × 11 × 10 cm) were set at different heights: one at 3 m, one at 15 m, and from 2–5 traps at 25–35 m; nine other BTS traps were dispersed in the canopy at 25–35 m. Each terrestrial station was composed of two traps, a Sherman (23 × 8 × 9 cm) and a BTS. The traps were baited every 2 d with peanut butter spread on a nut. The complete trapping effort represented 1815 trap-nights; 275 terrestrial trap-nights and 1540 arboreal ones. Animals caught were

[1] Email: jeff@isem.univ-montp2.fr

individually marked and released at the same place, except at the end of the sampling protocol when all caught specimens were removed for isotope analysis. All animals preserved as vouchers will be deposited at Museum National d'Histoire Naturelle (MNHN, Paris).

Long bones (femur, tibia and ulna) were cleaned from their flesh and whole bone powder was obtained by crushing them. Half of this powder was purified into bone collagen using five baths in 4% hydrochloric acid solution complemented by a slight sonication (Branson sonifier) during each bath in order to remove phosphates and carbonates. Fatty acids were removed in a methanol–chloroform–water (2:1:0.8) solution (following Van der Merwe & Medina 1991). The samples were rinsed (two distilled-water baths) and then oven dried (200 °C, 5 h). A small quantity of pure collagen (850–1150 μg) was burnt at 850 °C in a CN Analyser and the resulting gases were analysed in a Finnigan-Thermoquest Delta S mass spectrometer at the Service Central d'Analyses (Vernaison, CNRS). The results are reported relative to the PDB isotope standard for the carbon and AIR for the nitrogen using the notation:

$$\delta X = (R_{sample} / R_{standard} - 1) \times 1000$$

where X may be ^{13}C or ^{15}N and R_{sample} and $R_{standard}$ are the $^{13}C/^{12}C$ (respectively $^{15}N/^{14}N$) ratios of the sample and the standard, respectively. Internal replicate analyses (replications of standard measurement on L-valine) are reproducible to 0.1‰ and 0.2‰ for carbon and nitrogen, respectively. Since the bones of Sigmodontinae (*Oecomys rutilus* Anthony and *Rhipidomys nitela* Thomas) rodents yielded little collagen, the measurements of nitrogen isotopes were performed on hairs freshly sampled from the shoulder of live rodents and preserved in a silica gel water-free atmosphere. Each hair-tuft has been cut to eliminate basal corpuscles. A significant linear regression plotting $\delta^{13}C_{hair}$ and $\delta^{13}C_{collagen}$ ($r^2 = 0.67$, $P = 0.002$, $n = 17$) permits estimation of $\delta^{13}C_{collagen}$ for *Echimys chrysurus* (Zimmermann).

Among the five species of Sigmodontinae (*Oecomys rutilus*, *O. auyantepui* Tate, *Rhipidomys nitela*) and Echimyidae (*Proechimys cuvieri* Petter and *Echimys chrysurus*) rodents trapped, only three are considered here, since their sample size was sufficient for analysis: two small murids (*R. nitela*, *O. rutilus*) and a rat-like caviomorph (*P. cuvieri*). This restricted α-diversity is a part of the forest rodent diversity at Les Nouragues including six additional taxa, *Mesomys hispidus* (Desmarest) and *Proechimys cayennensis* (Desmarest) for Echimyidae, *Oecomys bicolor* (Tomes), *Oryzomys megacephalus* (Fischer) for Sigmodontinae, *Sciurus aestuans* (Linné) and *Sciurillus pusillus* (Desmarest) for Sciuridae. Results on captures are presented in Table 1. Since only six out of seven *Oecomys rutilus* have been recaptured at the end of the study we performed the carbon isotopic analysis on these six individuals only.

All of the five *Proechimys cuvieri* (Echimyidae) were trapped at the ground level. Additional individuals have been caught in neighbouring areas (15 *Proechimys* for 19 captures) and all of them were trapped at ground level confirming an exclusively terrestrial habit for this species. *Oecomys rutilus* and *Rhipidomys nitela* are small arboreal Sigmodontinae rodents (15–70 g). In the area studied, all of them were caught in arboreal traps from 3 to 35 m high (see Figure 1). Both of them present anatomical adaptations for an arboreal life in relation to their space occupancy. *Rhipidomys nitela* hind feet are short and broad with a relatively long fifth digit and large inter-digital pads, its tail (T) is much longer than head and body (HB) length (T/HB = 1.34 ± 0.08, n = 54) and its whiskers are dense and quite long. Relative to *Rhipidomys*, *Oecomys rutilus* has less-marked adaptations for an arboreal life: feet are short and broad with a relatively medium-sized fifth digit and pads, whiskers are dense but not very long, and tail longer than head and body length but not to the same extent as *Rhipidomys* (T/HB = 1.16 ± 0.08, n = 18). According to the trap height it seems possible to distinguish the three species based on their habitat use. There appears to be a vertical segregation from the ground (*Proechimys cuvieri*) to the canopy (*Rhipidomys nitela*) via the intermediate stratum (*Oecomys rutilus*) which is mainly composed of the small trees and the trunks of the big trees (Figure 1).

The isotopic signal variability of whole-bone powder and pure collagen fractions are compared to evaluate their relative use for providing accurate signals: since collagen extraction from rodent bones yielded little material, we investigated the reliability of whole-bone material (Cormie & Schwarcz 1996), easy to collect and in sufficient quantity for multiple analyses, vs. bone collagen, to segregate the different species. This pattern of variability

Table 1. Capture–recapture results in terms of number of individuals, and characterization of trap height for the three most frequently trapped species. H. min. (max.): minimum (maximum) height of capture.

Species	Number of individuals	Total number of captures	Mean height (m)	H. min. (m)	H. max. (m)
Proechimys cuvieri	5	5	0	0	0
Oecomys rutilus	7	18	16.4	3	35
Rhipidomys nitela	6	13	28.5	15	35

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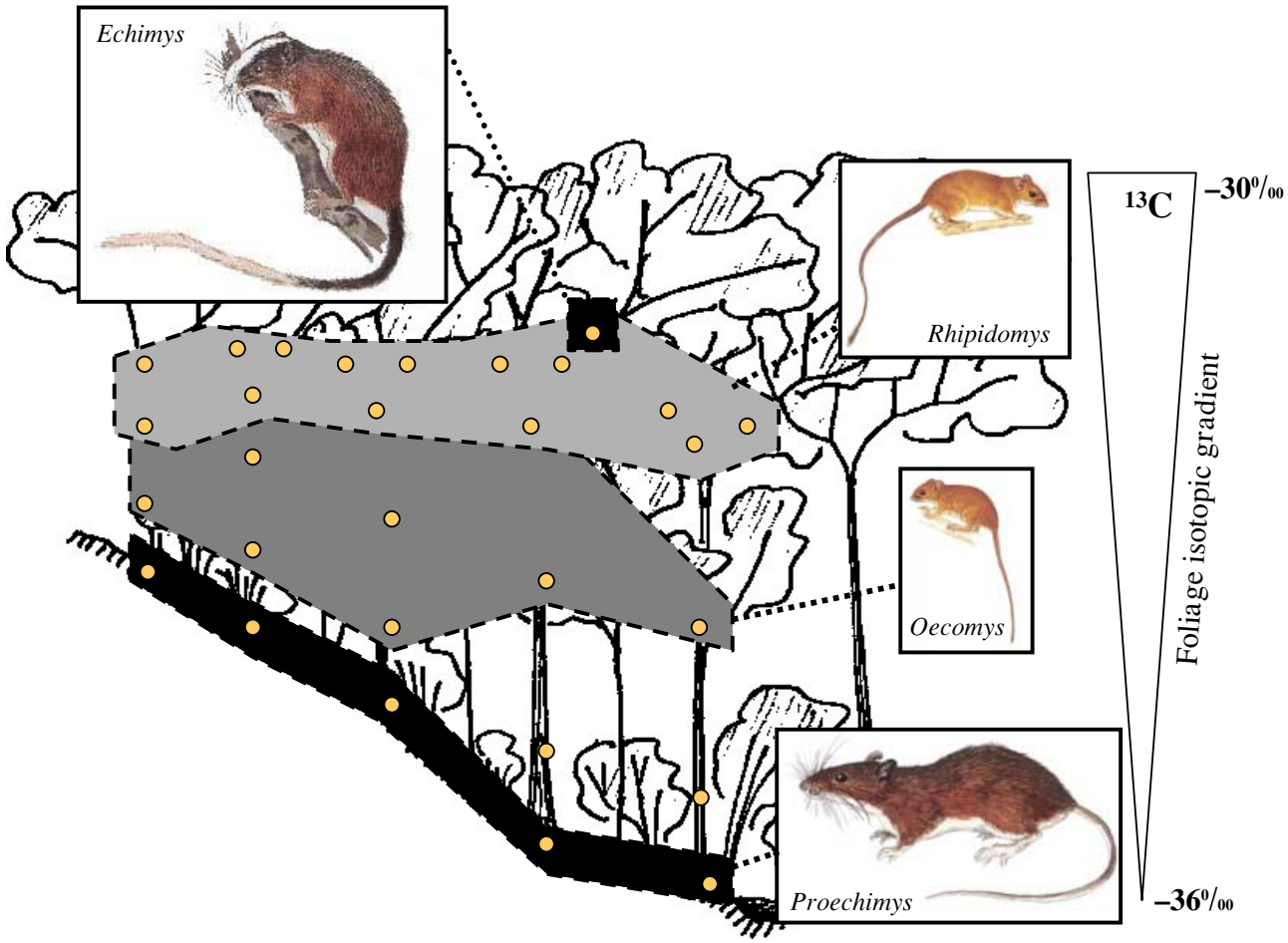

Figure 1. Transect illustration of the sampling area in the closed-canopy forest showing the main trees supporting the traps, and trap location (open circles) on each stratum of the forest. Shaded areas correspond to the cumulative trapping location of different individuals from the same species. The foliage isotopic gradient (so-called canopy effect) is represented on the right (Van der Merwe & Medina 1991). *Oecomys* and *Rhipidomys* illustrations from Reid (1997) (reproduced with permission from Oxford University Press), *Proechimys* and *Echimys* from Emmons & Feer (1997) (reproduced with permission from The University of Chicago Press).

in the isotopic signal according to the biochemical nature of the sample is shown in Table 2.

The variability of $\delta^{13}C$ depends on the biochemical homogeneity of the tissue. Purified collagen $\delta^{13}C$ yields a significantly lower variability than whole bone $\delta^{13}C$ (Mann–Whitney U-test, $P = 0.01$, 0.05, 0.03 for *Proechimys*, *Oecomys* and *Rhipidomys*, respectively). This may be due to the presence in variable proportions of fatty components in whole-bone powder, a material known to have a depleted $\delta^{13}C$ signal (DeNiro & Epstein 1978). Moreover, the entire-bone powder contains both bone proteins (mostly collagen) and carbonates in the hydroxylapatite matrix. The first component reflects the dietary proteins while the second integrates the entire diet (Ambrose & Norr 1993, Lee-Thorp *et al.* 1989). This mixed composition explains the larger isotopic variability of bone powder. If the whole-bone signal does not allow discrimination between the different taxa because of its heterogeneous composition, collagen – which is a pure fraction – shows a discriminating distribution in its $\delta^{13}C$ among the rodent samples analysed.

The range of variation for carbon isotope from bone

Table 2. Mean and standard error for all bone powder and purified collagen fraction isotopic signals, for three rodent species inhabiting the same forest location except for *Proechimys cuvieri*, for which four animals were caught nearby (150 m distance).

Tissue		*Proechimys cuvieri* (n = 5)	*Oecomys rutilus* (n = 6)	*Rhipidomys nitela* (n = 6)
Bone powder $\delta^{13}C$	Mean	–25.1 ± 0.3	–24.7 ± 0.8	–24.4 ± 0.7
Bone collagen $\delta^{13}C$	Mean	–24.0 ± 0.0	–23.8 ± 0.5	–22.9 ± 0.3
$\Delta = \delta^{13}C_{collagen} - \delta^{13}C_{bone}$	Mean difference	1.1	0.9	1.5

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collagen lies between −24.2‰ to −22.3‰ and for the nitrogen signal between 5.6 and 9.1‰ (see Figure 3). For all the species examined, mean and standard deviation for carbon content in collagen and nitrogen content in hair are respectively 46.7 ± 1.8 (n = 17) and 14.8 ± 1.0 (n = 20) testifying biochemical purity in the extracted material.

Even in this relatively small range of variation, plotting mean and confidence interval for the three species (see Figure 2) shows a clear segregation. Statistical reliability of such an isotopic segregation is tested using non-parametric Mann–Whitney U-test for different species pairs. The $\delta^{13}C$ measurements of *Proechimys cuvieri* (n = 5) and *Rhipidomys nitela* (n = 6) show a highly significant (P = 0.01) difference between them. Thus carbon isotopic signal from bone collagen is accurate at discriminating these two species occupying different ecological niches. The same approach gives discriminating $\delta^{13}C$ values for *Oecomys rutilus* (n = 6) and *Rhipidomys nitela* (n = 6; P = 0.02), but not between *Oecomys rutilus* and *Proechimys cuvieri* (P = 0.83). The small rice rat *Oecomys rutilus* does not show a different signal from *Proechimys cuvieri* even though all individuals were trapped in the trees (at heights of 3–35 m). Nevertheless, this species was observed at a lower height than *Rhipidomys nitela* (mean trap height is 16.4 m for *Oecomys rutilus* and 28.5 m for *Rhipidomys nitela*). The specific segregation in nitrogen signals is significant between arboreal and terrestrial species (Mann–Whitney U-test, P = 0.04 both between *Proechimys* and *Rhipidomys* and between *Proechimys* and *Oecomys*) but not between the two arboreal ones (*Rhipidomys nitela* and *Oecomys rutilus*, Mann–Whitney U-test, P = 0.94). Additional data from another arboreal Echimyidae species, *Echimys chrysurus*, show a different pattern of distribution with strong positive nitrogen values and high $\delta^{13}C$. Finally, the $\delta^{15}N$ values discriminate *Proechimys* from *Oecomys* and *Rhipidomys* and the $\delta^{13}C$ values segregate *Rhipidomys* from *Proechimys* and *Oecomys*. The combination of both signals give reliable information on isotopic segregation for these different species.

A clear link between trap height, carbon isotopic segregation and habitat discrimination was found. The arboreal species (*Rhipidomys* and *Echimys*) showed higher $\delta^{13}C$ values than terrestrial ones such as *Proechimys*, even if the signal of the arboreal rice mice (*Oecomys rutilus*) did not significantly differ from *Proechimys* (Figure 2). These differences in $\delta^{13}C$ values between terrestrial and arboreal species are compatible with the vertical gradient, the so-called canopy effect, i.e. the carbon isotopic ratio decreases from the canopy to the ground (Figure 1; Hanba *et al*. 1997, Medina & Minchin 1980, Schleser & Jayasekera 1985, Van der Merwe & Medina 1989, 1991). These results might indicate an arboreal vs. terrestrial food intake (leaves or fruits vs. tubers, roots or

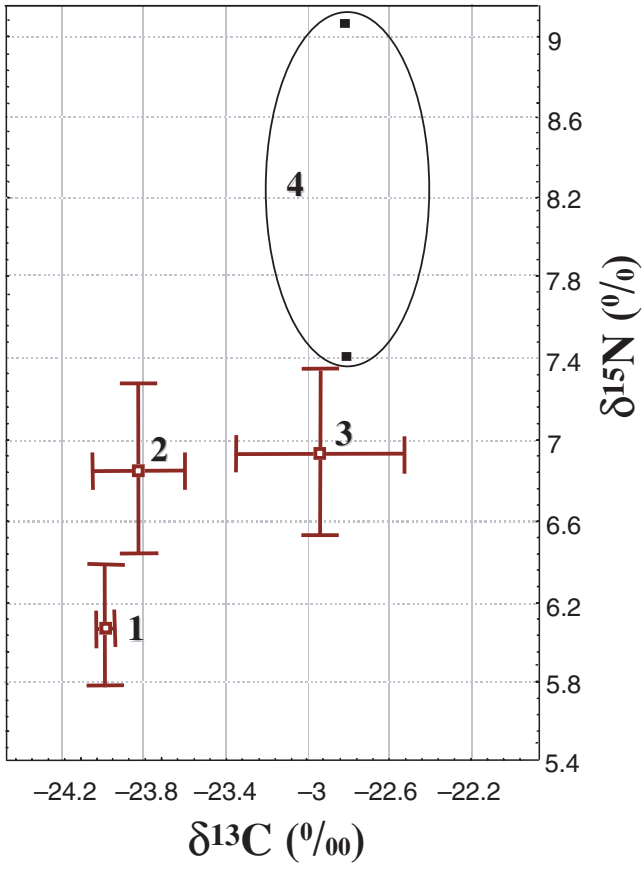

Figure 2. Mean and 95% confidence interval on $\delta^{13}C$ and $\delta^{15}N$ from the three main species sampled. $\delta^{13}C$ has been measured on bone collagen and $\delta^{15}N$ on hairs. 1: *Proechimys cuvieri* (n = 5); 2: *Oecomys rutilus* (n = 6); 3: *Rhipidomys nitela* (n = 6); 4: *Echimys chrysurus* (n = 2, $\delta^{13}C$ obtained from hair and transformed for collagen as these variables are significantly correlated, see text).

mushrooms) even if presence of fallen fruits and seeds, known to be eaten and dispersed by *Proechimys* (Forget 1996), is inconsistent with such a hypothesis. Thus, the canopy-effect hypothesis might not be adequate for interpreting our data collected on rodent consumers, because of our limited knowledge of the nature and variability of food resources. The canopy effect was measured on leaves and even if inter-specific variability of signal for neotropical leaves is well documented (Bonal *et al*. 2000, Buchmann *et al*. 1997, Guehl *et al*. 1998) little is known regarding the isotopic signal variation between fruits, seeds or bark at different heights (Guehl *et al*. 1998). Further investigations are necessary to characterize tropical rain-forest stratification isotopically.

Foraging behaviour and diet for the species studied are still poorly documented (Emmons & Feer 1997, Voss *et al*. 2001) though all of them are included in the arboreal or terrestrial granivore–frugivore guilds (Voss *et al*. 2001). In this general pattern some species complete their diet with particular items. For example, *Proechimys* is

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known to eat mycorrhizal fungi (Janos & Sahley 1995), and *Echimys* also eats leaves (Emmons & Feer 1997). Moreover, all of them (also including *Oecomys* and *Rhipidomys*) can also eat insects (Emmons & Feer 1997; stomach contents, data not shown).

All $\delta^{13}C$ measurements obtained here on the collagen for the different rodent species from Les Nouragues exhibit values ranging from −22.3‰ to −24.2‰. This reduced range might be due to different processes. First, according to the different photosynthetic signals, the main food resource of these rodents is represented by plants with a C_3 photosynthetic pattern. Bromeliaceae, with a CAM pattern ($\delta^{13}C$ between −10.6 and −13.8; Sternberg *et al*. 1984), do not represent a significant proportion of their food, although they are sometimes used as nest support (Emmons & Feer 1997). Second, as $\delta^{13}C$ (Ambrose & DeNiro 1986, Schoeninger & DeNiro 1984) and especially $\delta^{15}N$ (Minagawa & Wada 1984, Ponsard & Arditi 2000, Vander Zanden *et al*. 1999) vary with trophic level, the high isotopic values observed for *Rhipidomys* and *Echimys* (Figure 2) may also reflect a larger fraction of invertebrates in their diet, the same range as documented by Schoeninger *et al*. (1998) on insectivore vs. folivore prosimians. Concerning low nitrogen and carbon values for *Proechimys*, they might reveal a diet with consistent proportions of leguminous seeds known to be ^{15}N-depleted (Guehl *et al*. 1998) or mycorrhizal fungi with low $\delta^{13}C$ (Högberg *et al*. 1999).

The low variability among species and within species indicates a relative homogeneity in the diet and validates the use of bone collagen fraction, with its low biochemical turnover (Tieszen *et al*. 1983). The isotopic signals then generated by a long-period integration are relevant to the study as they dilute unusual food items into the principal diet (e.g. fallen fruits or seeds concentrated in a restricted period of the year; Forget 1996). Such an assumption validates this approach, with $\delta^{13}C$ representing both habitat use and food resource. Notwithstanding the difficulties in identifying food resources, isotope ratio values provide a reliable parameter for characterizing the ecological niche of these rodents by showing segregated signals. Combining this method with trapping data provides a promising tool to discriminate different taxa of syntopic rodents in a primary rain forest, and illustrate their specific strategies of spatial distribution and feeding.

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