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## Contributions of C<sub>3</sub> and C<sub>4</sub> plants to higher trophic levels in an Amazonian savanna

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**Abstract** We studied the energy flow from C<sub>3</sub> and C<sub>4</sub> plants to higher trophic levels in a central Amazonian savanna by comparing the carbon stable-isotope ratios of potential food plants to the isotope ratios of species of different consumer groups. All C<sub>4</sub> plants encountered in our study area were grasses and all C<sub>3</sub> plants were bushes, shrubs or vines. Differences in  $\delta^{13}\text{C}$  ratios among bushes ( $\bar{x} = -30.8$ , SD = 1.2), vines ( $\bar{x} = -30.7$ , SD = 0.46) and trees ( $\bar{x} = -29.7$ , SD = 1.5) were small. However the mean  $\delta^{13}\text{C}$  ratio of dicotyledonous plants ( $\bar{x} = -30.4$ , SD = 1.3) was much more negative than that of the most common grasses ( $\bar{x} = -13.4$ , SD = 0.27). The insect primary consumers had  $\delta^{13}\text{C}$  ratios which ranged from a mean of  $-29.5$  (SD = 0.47) for the grasshopper *Tropidacris collaris* to a mean of  $-14.7$  (SD = 0.56) for a termite (*Nasutitermes* sp.), a range similar to that of the vegetation. However, the common insectivorous and omnivorous vertebrates had intermediate values for  $\delta^{13}\text{C}$ , indicating that carbon from different autotrophic sources mixes rapidly as it moves up the food chain. Despite this mixing, the frogs and lizards generally had higher values of  $\delta^{13}\text{C}$  ( $\bar{x} = -21.7$ , SD = 1.6;  $\bar{x} = -21.9$ , SD = 1.8, respectively) than the birds ( $\bar{x} = -24.8$ , SD = 1.8) and the only species of mammal resident in the savanna ( $\bar{x} = -25.4$ ), indicating that they are generally more dependent on, or more able to utilise, food chains based on C<sub>4</sub> grasses.

**Key words** Amazonia · Stable isotope · Savanna · Trophic level · Carbon

### Introduction

Tropical savannas consist of two vegetation classes, grasses and sedges, and dicotyledonous shrubs and trees, which have distinct functional roles in the ecosystem (Boutton et al. 1983). The frequency of fire alters the proportions of grassy and woody vegetation in well-drained areas, trees and shrubs increasing in areas protected from fire (e.g. San José and Fariñas 1983; Sanaiotti and Magnusson 1995; Whelan 1995). Similar changes may be induced by changes in grazing regimes (Hobbs 1996).

C<sub>4</sub> grasses, which typically dominate in tropical savannas, have distinctly less negative carbon stable-isotope ratios than most other components of the vegetation (Lajtha and Marshall 1994), and soil carbon isotope ratios have been used for historical reconstructions (e.g. Desjardins et al. 1996; Martinelli et al. 1996). Carbon isotope ratios can also be used to trace energy flow through ecosystems, and there are many studies of stable-isotope ratios in aquatic systems (Lajtha and Michener 1994). The plant communities that have the highest biomass or cover often do not contribute the greatest proportion of primary production to higher trophic levels (e.g. Forsberg et al. 1993; Schlacher and Woolbridge 1996). Community studies in terrestrial systems are rare. Fry et al. (1978) investigated the relative dependence of 25 species of termites on C<sub>3</sub> and C<sub>4</sub> grasses in a Texas grassland. Boutton et al. (1983) and Lepage et al. (1993) investigated termite food habits in African savannas and documented different reliance on herbaceous and woody plants at sites which differed in the types of woody plants available. However, no studies have investigated the contributions of C<sub>3</sub> and C<sub>4</sub> plants to a diverse array of primary and secondary consumers in a tropical savanna.

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In this paper, we document the carbon isotope ratios for most of the common plants in a Neotropical savanna and calculate the probable percentage contribution of grassy and woody vegetation to energy acquisition in common species of vertebrates and some of the most conspicuous species of herbivorous ants, termites and grasshoppers. We hypothesised that primary consumers would show various degrees of specialisation on C<sub>3</sub> and C<sub>4</sub> plants, as shown in previous studies, and wished to determine whether vertebrate secondary consumers feed from pathways originating principally from grasses, dicotyledons or mixtures. We used percent cover as a surrogate variable for availability of different plant types to determine whether differences in isotope ratios were likely due to differences in availability. A measure of the amount of primary production or biomass available to animals from each source might have been preferable but the measurement of primary production or mean biomass of hundreds of species of plants in an environment subject to strong seasonality and frequent fires was far beyond our limited resources and unlikely to add any precision to the measure of availability to a wide range of consumers with different microhabitats and behavioural patterns. If the vertebrates are capable of feeding from various pathways, changes in the relative proportions of grasses and dicots due to altered fire regimes are likely to have less effect than if they depend trophically on only one of the major savanna plant life forms.

We attempted to determine the isotope ratios of most of the available plants, as little information is available on the diets of herbivores in this savanna. The animal species were selected to include a wide range of principally savanna species from a variety of guilds. In this paper, we ask whether isotope ratios differ among species of plants and species of animals within and between higher taxonomic groupings from a single savanna. How ratios vary within species between savannas will be considered in a future study.

## Materials and methods

The study was conducted in the savanna on the peninsula which juts into the Tapajós River in front of the village of Alter do Chão (2°30' S 54°58' W), Pará, Brazil. The vegetation in the area has been described in detail by Miranda (1993), Sanaïotti and Magnusson (1995), and Sanaïotti (1996). This savanna has many species of trees and bushes which form islands in a grassland dominated by *Paspalum carinatum*. Detailed studies of most of the vertebrates included in this study have been carried out in the same savanna during the past 15 years (Strüssmann et al. 1984; Magnusson et al. 1985, 1986; Magnusson 1993; Magnusson and da Silva 1993; Bayliss 1995; Francisco et al. 1995; Sanaïotti and Magnusson 1995; Galatti 1996).

Leaves were collected from individuals of the most common plant species for isotope analyses, within an area of about 4 ha of relatively uniform savanna vegetation. We attempted to obtain isotope ratios for most of the common plants as little information was available on the diets of the animals and no information was available on the range of isotope values within plant life forms in Amazonian savannas. For most statistical analyses, species was the unit of replication. Therefore, we collected only one sample of most species of plants to maximise statistical power for a given number

of isotope analyses. To provide an indication of within-species variation in plants, we collected two to four replicates for 20% of the species. One to seven adult individuals of 19 animal species were collected within the same area. Most analyses were based on individuals, except for ants and termites which were analysed as composite samples of individuals from each nest. The animal species were selected to include a wide range of taxonomic groups from a variety of guilds. The vertebrates were also species shown in our previous studies to use principally or exclusively savanna vegetation. Species that forage in savannas and in adjacent woodlands were not included, except among the ants and termites. We collected these at sites >50 m from closed-canopy woodland, and we believe that the individuals we used were from colonies that primarily had access only to savanna vegetation. All samples were collected during the wet season (January–May) in 1996 or 1997.

Plants were air dried indoors and animals were frozen for transport to Manaus, where they were dried to constant mass in an oven at 50°C, ground finely, and despatched to the CENA/USP laboratories in Piracicaba. There, they were sealed in evacuated glass ampoules (break-seal tubing) containing cupric oxide and burned in an oven at 600°C for 12 h. The resulting CO<sub>2</sub> was purified in a vacuum line and injected in a Micromass 602E mass spectrometer (Finnegan Mat, Bremen, Germany) fitted with double inlet and collector systems. Standards consisted of the Pee Dee Belemnite (PDB) formation from South Carolina, USA. The results are expressed in δ<sup>13</sup>C relative to the PDB standard in the conventional δ per mil notation as follows:

$$\delta^{13}\text{C} = \left[ \left( \frac{^{13}\text{C}/^{12}\text{C}}{s} \right) - \left( \frac{^{13}\text{C}/^{12}\text{C}}{\text{std}} \right) - 1 \right] \times 1000$$

where <sup>13</sup>C/<sup>12</sup>C are the isotopic ratios of sample (s) and PDB standard (std). The overall (sample preparation plus analysis) analytical precision is ±0.2‰.

Only muscle tissue was used for most vertebrates, except for some small *Anolis* lizards, which were ground whole, as were the invertebrates. The only species of mammal which occurs exclusively in the savanna, *Bolomys lasiurus* suffered a population crash before the study (W.E. Magnusson, unpublished data). We supplemented the sample for the only individual captured with samples from three animals that had been stored individually in 10% formalin for 10 years. Formalin storage has little effect on isotope ratios, provided that specimens are stored individually (C.A. Lima, unpublished data). Animals were collected under IBAMA permit number 073/94-DIFAS.

Cover of plant life forms (trees, bushes and vines, and grasses) was estimated independently of species composition because many species occur in both the shrub layer (height < 2 m) and the tree layer (height ≥ 2 m). Percentage cover of plant life forms was estimated by point quadrats (Bullock 1996) along four parallel 250-m transects, spaced 50 m apart, in the centre of the study area. A thin (<3-mm diameter) vertical rod was placed at 1 m intervals along each transect and the life form of the tallest species of plant contacting the rod was recorded for vegetation ≤2 m high. Generally only one species was contacted at each point and it was not feasible to tease apart the tangled vegetation to determine which species was contacting the rod at lower levels at the few points with more than one species. Presence or absence of tree cover was recorded for each point, independent of the number of species whose canopies overlapped the point. Therefore, presence of shrubs and grasses was mutually exclusive, but trees could occur with grasses or shrubs.

Species cover was estimated along the same transects at 2-m intervals using the same methodology, but the total cover of each species was calculated, independent of whether it was in the shrub or tree layer, and each species was counted when the canopies of more than one tree overlapped the sampling point.

The relative contribution of woody plants (dicotyledonous trees, shrubs and vines) to a species' diet was calculated from the formula  $P_W = (\delta^{13}\text{C}_{\text{SA}} - \delta^{13}\text{C}_G) / (\delta^{13}\text{C}_W - \delta^{13}\text{C}_G)$ , where δ<sup>13</sup>C<sub>SA</sub> is the presumed isotope ratio of the mixture of plants eaten by that species of animal, δ<sup>13</sup>C<sub>W</sub> is the mean ratio for woody plants, and δ<sup>13</sup>C<sub>G</sub> is the mean isotope ratio for grasses. The δ<sup>13</sup>C<sub>SA</sub> for primarily carnivorous species, and species that cultivate fungi, was reduced by 2‰ below ratios measured from body parts to account

for a presumed decrease of about 1‰ for each trophic level (Boutton et al. 1983; Tieszen et al. 1983; Hobson et al. 1996). Species with mixed herbivorous/insectivorous diets were decreased by 1.5‰ (Forsberg et al. 1993). Herbivorous species were decreased by 1‰.

Statistical analyses were carried out in the SYSTAT program (Wilkinson 1990). When counts of cases per cell are not equal, SYSTAT uses the Tukey-Kramer adjustment by a harmonic mean for Tukey multiple-comparison tests (Wilkinson 1990). Nested analysis of variance with species as the nested factor was used to test for differences among life forms and higher taxonomic groups. These analyses included only species for which replication was available. As species may not be strictly independent (Harvey and Pagel 1991), significant results for life forms indicate patterns that may or may not be independent of phylogeny. As there are insufficient data to estimate genetic distances among the species, we did not attempt to remove the effects of phylogeny.

## Results

C<sub>4</sub> grasses covered 67% of the area but 16% of the grass occurred as an understory with trees. (Table 1). Bushes and trees together covered 20% of the area, and ~13% had no live vegetative cover. The species of plants we sampled for δ<sup>13</sup>C represented 95% of the total cover in the ground plus tree layer in the sample transects, and no species for which we did not sample δ<sup>13</sup>C covered more than 1.5% of the area (Table 2).

All grasses at our site were C<sub>4</sub> species with δ<sup>13</sup>C > -14‰. All the dicotyledons had δ<sup>13</sup>C ratios ≤ -28‰ (Table 2). Within the dicots, there were significant differences among species (nested ANOVA:  $F_{3,11} = 6.9$ ,  $P = 0.01$ ) and a non-significant tendency to vary among growth forms (ANOVA:  $F_{2,37} = 2.6$ ,  $P = 0.08$ ). Differences among growth forms were slight (≤ 1‰) and of no practical value to differentiate diets without detailed knowledge of the specific composition of the diet of each animal.

The average δ<sup>13</sup>C value for C<sub>4</sub> grasses was -13.4‰ (SD = 0.27), and the average value for dicots was -30.4‰ (SD = 1.3) [ $\bar{x} = -30.8‰$  (SD = 1.2), -30.7‰ (SD = 0.46) and -29.7‰ (SD = 1.5) for bushes, vines and trees respectively]. Species of small shrubs such as *Chamaecrista ramosa* and *Galactia jussiaena*, which occur in relatively open areas mixed with the grasses, were as negative as most other dicots (-30.6‰ and -28.8‰ respectively).

Some animal species (*Syntermes molestus*, *Ammodramus humeralis*, *Elaenia cristata*, *Anolis auratus*, *Kentropyx striata*, *Bufo granulosus*) varied greatly in δ<sup>13</sup>C among individuals or colonies (Table 3). The leaf-cutter ants, which harvest leaves to grow fungi as food,

apparently collect mainly C<sub>3</sub> plants in this savanna and the grasshopper species *Tropidacris collaris* ate almost exclusively C<sub>3</sub> species (Fig. 1). As grasses account for about 76% cover, this indicates a strong selection for dicots by the grasshopper and the ants. One species of termite, *Nasutitermes* sp., apparently eats almost exclusively C<sub>4</sub> grasses (Fig. 1). The other termite species, *S. molestus* varied widely between colonies (Table 3) and more intensive sampling will be necessary to determine the principal source of carbon for this species.

Most of the vertebrate groups apparently had mixed sources of carbon (Fig. 1). However, there were significant differences among classes (nested ANOVA:  $F_{3,36} = 9.1$ ,  $P = 0.001$ ), and a non-significant tendency for species to vary within classes ( $F_{9,36} = 1.9$ ,  $P = 0.08$ ). Tukey multiple-comparison tests with the Tukey-Kramer adjustment for unequal sample sizes indicated significant differences between lizards and birds ( $P = 0.001$ ), and between frogs and birds ( $P = 0.012$ ) but no significant difference between frogs and lizards ( $P = 0.98$ ).

Most species of birds obtained more than 50% of their carbon from dicots (Fig. 1). The only species of mammal which forages exclusively in the savanna at this site, *B. lasiurus*, obtained most of its carbon from dicot pathways in proportions similar to those for most birds. The lizards and frogs had obtained less than 50% of their carbon from dicots (Fig. 1).

## Discussion

Trees had similar mean δ<sup>13</sup>C (-29.7‰, SD = 1.5) to vines (-30.7‰, SD = 0.46), and bushes (-30.8‰, SD = 1.2). This was unexpected, as the trees generally are exposed to more irradiance than the shrubs, which are often shaded by the trees (cf. Sternberg et al. 1989; Martinelli et al. 1999). The overall mean for dicots was -30.4‰ (SD = 1.3) and the mean for grasses was -13.4‰ (SD = 0.27). The large difference between the C<sub>3</sub> and C<sub>4</sub> plants makes analysis of carbon isotopes a useful tool to indicate the relative use of C<sub>3</sub> and C<sub>4</sub> food chains by animals in this savanna.

All animal species studied frequently occur in Amazonian savannas, and many are grassland specialists. Although the grasshopper *T. collaris* completes its entire life cycle within the savanna and eats a variety of plants (unpublished observations), about 90% of its dietary carbon is derived from C<sub>3</sub> plants which, in this area, are mainly dicotyledonous trees and shrubs. Both species of leaf-cutter ants also obtain the major part of their diet (~70%) from C<sub>3</sub> plants. One species of termite, *Nasutitermes* sp. and one of the colonies of *S. molestus* had obtained most of their carbon from C<sub>4</sub> grasses. As termites are major prey items for many of the lizards and frogs (Strüssmann et al. 1984; Magnusson and da Silva 1993; Bayliss 1995; Galatti 1996), they may be important agents for the transfer of grass primary production to higher trophic levels in this system.

**Table 1** Percentage cover of grasses, bushes and areas with no live vegetative cover in the study area, based on 1000 point samples along four 250-m transects

Cover	Under trees	Not under trees	Total
Grass	16	51	67
Bushes	9.7	10.7	20.4
No vegetation	< 0.1	12.6	12.6

**Table 2** Mean  $\delta^{13}\text{C}$  (‰) values, their standard deviation, the number of individuals in the sample, and percentage cover in a 1-km transect through the area, for savanna plants at Alter do Chão.

Life forms (*t* tree, *s* shrub, *v* vine, *g* grass) are the most common for the species at Alter do Chão

Species	Mean $\delta^{13}\text{C}$	SD	<i>n</i>	Life form	Cover (%)
<i>Aegiphila lhotzkyana</i>	–	–	–	s	1
<i>Alibertia edulis</i>	–32.2	–	1	s	0
<i>Anacardium occidentale</i>	–30.5	–	1	t	1
<i>Bowdichia virgilioides</i>	–29.2	–	1	t	2
<i>Byrsonima coccolobifolia</i>	–27.9	–	1	t	1
<i>Byrsonima crassifolia</i>	–28.5	–	1	t	4.4
<i>Casearia javitensis</i>	–30.2	–	1	s	0.8
<i>Casearia sylvestris</i>	–31.6	–	1	s	0.02
<i>Centrosema venosa</i>	–	–	–	v	0.8
<i>Chamaecrista ramosa</i>	–30.6	–	1	s	0
<i>Chamaecrista flexuosa</i>	–	–	–	s	1.4
<i>Chomelia parviflora</i>	–30.2	2.8	2	s	1.2
<i>Cissampelos ovalifolia</i>	–	–	–	s	0.2
<i>Copaifera martii</i>	–30.6	0.6	3	s	0
<i>Cupania diphyla</i>	–31.0	–	1	s	0
<i>Declieuxia fruticosa</i>	–31.2	–	1	s	1.2
<i>Dioclea bicolor</i>	–31.0	–	1	v	0.2
<i>Dolioscarpus brevipedicellatus</i>	–30.6	–	1	v	0
<i>Erythroxylum campestris</i>	–	–	–	s	0.4
<i>Erythroxylum suberosum</i>	–28.6	1.6	4	s	0.2
<i>Eugenia biflora</i>	–31.8	–	1	s	4.6
<i>Galactia jussiaena</i>	–28.8	–	1	s	1.6
<i>Himatanthus sucuba</i>	–29.4	1.3	3	t	0.6
<i>Hirtella racemosa</i>	–32.2	–	1	s	0.2
<i>Lafoensia pacari</i>	–28.6	–	1	t	3.0
<i>Manihot caerulea</i>	–31.0	0.4	2	s	0.6
<i>Miconia albicans</i>	–30.1	–	1	s	0.4
<i>Miconia fallax</i>	–31.0	–	1	s	0
<i>Myrcia fallax</i>	–33.4	–	1	s	0.4
<i>Myrcia multiflora</i>	–30.1	–	1	s	0
<i>Myrcia sylvatica</i>	–31.4	–	1	s	2.0
<i>Neea ovalifolia</i>	–31.5	–	1	s	0.4
<i>Odontadenia lutea</i>	–30.2	0.5	3	v	0.2
<i>Paspalum carinatum</i>	–13.7	–	1	g	60.4
<i>Polycarpea corymbosa</i>	–	–	–	s	0.2
<i>Polygala variabilis</i>	–	–	–	s	0.2
<i>Pouteria ramiflora</i>	–31.8	–	1	t	4.2
<i>Psychotria barbiflora</i>	–31.4	–	1	s	0.2
<i>Qualea grandiflora</i>	–28.7	–	1	t	5.0
<i>Salvertia convallariodora</i>	–29.2	–	1	t	6.8
<i>Sclerobium paniculatum</i>	–31.3	–	1	t	0
<i>Sebastiania corniculata</i>	–28.3	–	1	s	0
<i>Simarouba amara</i>	–28.4	–	1	t	0
<i>Smilax santaremensis</i>	–31.4	0.4	3	t	0.2
<i>Tabebuia ochracea</i>	–31.1	–	1	t	0.4
<i>Tabernaemontana coriacea</i>	–31.7	0.6	3	t	0.2
<i>Tapirira guianensis</i>	–31.9	–	1	t	0
<i>Tocoyena formosa</i>	–	–	–	s	0.6
<i>Trachypogon plumosus</i>	–13.3	–	1	g	3.0
<i>Vatairea macrocarpa</i>	–	–	–	t	0.8
<i>Xylopia aromatica</i>	–30.9	–	1	t	0.6
Unidentified Gramineae	–13.2	–	1	g	1.2
Unidentified Leguminosae	–	–	–	s	0.2

The lizards studied are typical of Amazonian savannas (Avila Pires 1995). However, *Cnemidophorus lemniscatus* occurs at higher densities in areas with bushes than in areas dominated by grass (Magnusson et al. 1986). Except for *K. striata*, all the lizards and frogs had obtained more than 50% of their dietary carbon from food chains originating in  $\text{C}_4$  grasses, indicating that grasslands are important for these groups. The teiid lizards (*Ameiva ameiva*, *K. striata*, *C. lemniscatus*) fre-

quently eat termites (Magnusson and da Silva 1993), as do the frogs *Bufo marinus* (Strüssmann et al. 1984; Bayliss 1995), and *B. granulatus* (Gallati 1996). Even *A. auratus*, which rarely, if ever, eats termites (Hogmoed 1973; Magnusson et al. 1985; Magnusson and da Silva 1993), obtained most of its carbon from food chains originating in  $\text{C}_4$  grasses. *K. striata* obtained about 50% of its diet from  $\text{C}_3$  food chains. Possible reasons for this difference is that *K. striata* eats fewer

**Table 3** Mean  $\delta^{13}\text{C}$  (‰) values, their standard deviations (SD) and ranges for each species of animal. Numbers in parentheses indicate species codes for Fig. 1

Species	Mean $\delta^{13}\text{C}$	SD	<i>n</i>	Range
Termites				
<i>Syntermes molestus</i> (1)	-21.6	5.5	2	-25.5, -17.7
<i>Nasutitermes</i> sp. (2)	-14.7	0.6	2	-15.1, -14.3
Leaf-cutter ants				
<i>Acromyrmex laticeps nigrosetosus</i> (3)	-26.7	0.1	3	-26.8, -26.6
<i>Atta laevigata</i> (4)	-26.4	0.3	3	-26.8, -26.2
Grasshopper				
<i>Tropidacris collaris</i> (5)	-29.5	0.5	3	-30.0, -29.0
Birds				
<i>Ammodramus humeralis</i> (6)	-22.3	5.6	3	-28.8, -18.6
<i>Columbina passerina</i> (7)	-25.7	1.1	3	-26.5, -24.9
<i>Elaenia cristata</i> (8)	-24.3	5.3	3	-28.3, -18.3
<i>Formicivora rufa</i> (9)	-26.8	1.5	7	-29.0, -24.9
<i>Myiarchus tyrannulus</i> (10)	-23.4	0.1	2	-23.5, -23.4
<i>Tangara cayana</i> (11)	-26.5	0.8	3	-27.0, -25.6
Mammal				
<i>Bolomys lasiurus</i> (12)	-25.4	0.9	4	-26.4, -24.5
Lizards				
<i>Ameiva ameiva</i> (13)	-21.0	1.2	5	-22.2, -19.1
<i>Anolis auratus</i> (14)	-23.0	3.4	6	-23.3, -19.2
<i>Cnemidophorus lemniscatus</i> (15)	-20.2	1.0	6	-21.7, -19.4
<i>Kentropyx striata</i> (16)	-26.1	4.1	4	-24.3, -23.2
Frogs				
<i>Bufo granulatus</i> (17)	-19.8	4.1	4	-25.4, -16.3
<i>Bufo marinus</i> (18)	-23.0	-	1	-
<i>Leptodactylus macrosternum</i> (19)	-22.9	3.0	3	-24.8, -19.5

termites than the other termites, and it forages among grasses much less than *A. auratus*. Also, the termites it eats are frequently alates (unpublished data), which are rich in lipids (Dimmitt and Ruibal 1980). Lipids may be 7–8‰ more negative than other biochemical fractions of the animal body (DeNiro and Epstein 1977), so more detailed studies should be done on the diet of *K. striata*.

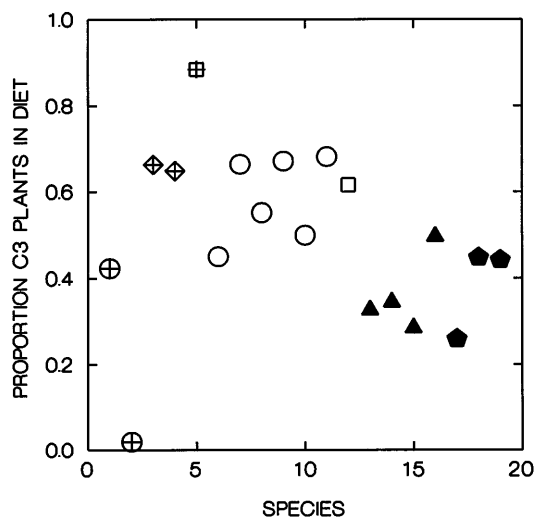
*B. granulatus* forages almost exclusively in the open savanna and often takes refuge in termite mounds

(Galatti 1996). Its dietary carbon was mainly (~74%) derived from grass-based food chains. *B. marinus* frequently crosses grasslands, but often feeds in patches of bushes and trees (Bayliss 1995). Only about half its diet is derived from grass-based food chains. *Leptodactylus macrosternum* is a sit-and-wait predator that eats a variety of arthropod prey, but few termites (Strüssmann et al. 1984). We have no data on habitat use in the savanna, and the individuals were captured on a beach beside the savanna. Nonetheless, about half its dietary carbon was derived from grass-based food chains.

Except for *A. humeralis*, a grassland species, all of the birds obtain most (50–80%) of their carbon from food chains originating in  $\text{C}_3$  autotrophs. Not enough is known of the diets of most species to determine whether this results directly from frugivory, or indirectly from feeding on insects which had fed on  $\text{C}_3$  species. However, *Formicivora rufa* is exclusively insectivorous, and about 70% of its dietary carbon is derived from chains originating in  $\text{C}_3$  plants.

Data for the only mammal, the omnivorous rodent *B. lasiurus*, were potentially confounded by the use of preserved specimens. However, the results for the preserved specimens (-24.5, -24.6, -25.9  $\delta^{13}\text{C}$ ) were similar to those for the freshly captured individual (-26.4  $\delta^{13}\text{C}$ ), indicating that preservation did not greatly affect the carbon isotope ratios. About 60% of its diet is derived from  $\text{C}_3$ -based food chains. Trapping data indicate a behavioural preference of this species for sites with both grasses and bushes (Magnusson et al. 1995).

Our limited data on herbivorous insects indicate that some species specialise on either dicots or grasses, as found by Fry et al. (1978) and Petelle et al. (1979) in isotope ratio studies in the U.S.A. Carbon from the  $\text{C}_4$



**Fig. 1** Estimated mean proportions of carbon from  $\text{C}_3$  plants in the diets of savanna animals. Numerical codes for species represented by the position along the *x*-axis are as in Table 3. Crossed circles, diamonds and square represent termites, leafcutter ant, and grasshopper species, respectively. Open circles and square, and closed triangles and pentagons indicate bird, mammal, lizard, and frog species, respectively

grasses and C<sub>3</sub> dicotyledons mixed rapidly as it moved up the food chain at Alter de Chão. However, there remained a distinct difference between the ectothermic and the endothermic vertebrates. Most endotherms obtained most of their carbon from C<sub>3</sub>-based food chains, whereas the ectotherms tended to rely on C<sub>4</sub>-grass-based food chains. This may have important implications for competition within and between groups, and for the conservation of savanna communities. Modification of the proportion of C<sub>4</sub> grasses in the system by grazing, human-caused fires or clearing of woody vegetation will differentially affect the food base of different groups of organisms. Future studies are needed to determine whether species can adapt to the differential availability of different autotrophic sources, or whether changes in carbon sources will change community structure.

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