SIZE AND CARBON ACQUISITION IN LIZARDS FROM AMAZONIAN SAVANNA: EVIDENCE FROM ISOTOPE ANALYSIS

William E. Magnusson,[1] Albertina P. Lima,[1] Allessandra S. Faria,[1] Reynaldo L. Victoria,[2] and Luiz A. Martinelli[2]

[1]*Coordenação de Pesquisas em Ecologia,
Instituto Nacional de Pesquisa da Amazônia, CP 478, 69011-970 Manaus Am, Brazil*
[2]*Centro de Energia Nuclear na Agricultura, Av. Centenário 303, 13416-000 Piracicaba SP, Brazil*

Abstract. We studied the effects of lizard size, and availability of C_3 and C_4 plants, on stable carbon-isotope ($\delta^{13}C$) ratios of lizards in an Amazonian savanna. Availability of C_3 and C_4 plants was estimated from 500-point quadrats in each of 38 plots of 3.75 ha. Ratios of $\delta^{13}C$ in muscle tissue were used to estimate the contributions of C_3- and C_4-based food chains to the diets of four species of lizards: *Cnemidophorus lemniscatus, Kentropyx striata, Ameiva ameiva,* and *Anolis auratus.* The relative contributions of C_3 and C_4 plants to the diets of the lizards were affected by the extent of shrub cover in *C. lemniscatus, A. auratus,* and possibly in *K. striata.* However, there was a strong effect of lizard size among and within lizard species. These results are at variance with a previous evaluation of diet overlap among size classes of these species that was based on overlap in prey taxonomic categories. This indicates that species and/or size classes of predators on arthropods may obtain their energy from food chains based on different autotrophic sources, despite high overlap in the taxonomic categories of prey.

Key words: Amazonia; carbon acquisition in lizards; diet overlap, lizards; food chain; lizard size; overlap; savanna; stable isotope.

Introduction

Body-size differences among adults of morphologically similar species are often attributed to interspecific competition (Hutchinson 1959, Schoener 1965, Wilson 1975, Dickman 1988, Fleming 1991, Fox and Kirkland 1992). Those studies were based on birds and mammals, groups in which adult sizes are reached in a small fraction of the life span, and in which adults usually provide most or all of the food for juveniles. However, for groups such as arachnids, fish, reptiles, and amphibians, individuals may pass the greater part of their lives at subadult sizes, and juveniles are usually trophically independent of adults. For these groups, relationships among species may depend more on interactions among individuals of different sizes than on competition between adults of different species (Christian 1982, Polis 1984, Werner and Gilliam 1984, Lima and Magnusson 1998).

Ontogenetic changes in diet are often mediated by gross changes in morphology at metamorphosis. For example, tadpoles are herbivores or detritivores, but frogs are carnivores (Wassersug 1974). Given that most of the invertebrates eaten by frogs probably do not depend on autotrophs from tadpole habitats, tadpoles and frogs can be considered to be trophically independent. Different size classes of the same species may belong to different food chains because they occupy different habitats (Werner and Gilliam 1984). However,

different size classes of the same species may eat the same general class of prey, occupy the same habitat, and still show ontogenetic variation in the type of prey eaten (Lima and Moreira 1993, Lima 1998).

For generalist predators on arthropods, the size of the item that can be swallowed may determine the type of arthropod eaten because different taxonomic categories of arthropods have different ranges of sizes (e.g., Schoener and Janzen 1968, Dominguez and Salvador 1990). Differences in diet among species of lizards are often attributed almost exclusively to differences in the sizes of the lizards (e.g., Toft 1985, Dominguez and Salvador 1990). However, the masses of lizards living in Amazonian savannas may vary by two orders of magnitude within species in one assemblage (Magnusson and Silva 1993). In that assemblage, differences between species of lizards in the taxonomic categories of prey consumed were found to be greater than differences due to lizard size (Magnusson and da Silva 1993).

A major assumption of Magnusson and da Silva (1993), and other studies that have investigated inter- and intraspecific niche overlap in species and size classes that feed from the same trophic level and occupy similar habitats (e.g., Winemiller and Pianka 1990, Caldwell and Vitt 1999), was that similarity in taxonomic prey categories reflects overlap in food chains, and hence dependence on similar autotrophic sources. To test this assumption, it is necessary to have a method of tracing energy or nutrients along food chains that is independent of the taxonomic identity of prey.

Carbon-isotope ratios in consumers can be used to trace carbon flow through ecosystems (Lajtha and Michener 1994), and Magnusson et al. (1999) showed significant differences among higher taxonomic groups of secondary consumers in the proportion of dietary carbon obtained from C_3 and C_4 plants in a savanna area. Bushes and trees are C_3 plants and most grasses and sedges in tropical savannas are C_4 plants. Some species of arthropods obtain most of their food from either C_3 or C_4 plants, but different species of the same genus may differ in the proportions of C_3 and C_4 plants in the diet, and some species use plants with either photosynthetic pathway (e.g., Fry et al. 1978, Magnusson et al. 1999). Therefore there is no reason to expect a relationship between the taxonomic levels (usually order or family) used in most studies of diet overlap and the primary carbon sources of the arthropods.

In this study, we use carbon isotope ratios to test the hypothesis raised by Magnusson and da Silva (1993) that differences in dietary overlap among similar size classes between species are greater than differences among size classes within species, for the assemblage of lizards inhabiting the savannas near Alter do Chão, central Amazônia. This is also a test of the assumption that overlap in taxonomic categories reflects overlap in resource use by syntopic predators on arthropods.

MATERIALS AND METHODS

The study was carried out between July 1997 and May 1998 in the region of Santarém (2°31′ S, 55°00′ W; <100 m altitude), Brazil. Data were collected in 38 plots distributed throughout the savannas in the region (Fig. 1). The cover of monocotyledons (grasses and sedges), shrubs, and trees in each plot was sampled along four parallel lines of 250 m, spaced 50 m from each other. The cover of vegetation <2 m high was estimated by the point quadrat method (Bullock 1996), using a 2 mm diameter metal rod. One quadrat was placed at each 2 m along each line, giving 500 points per plot. The presence of cover of monocotyledons and/or shrubs was recorded for each point. The presence or absence of the canopy of a tree above each point was also recorded. The cover of monocots and cover of shrubs were not highly correlated (Pearson $r = 0.16$) because 34–78% of quadrats had no ground cover.

The relative cover of plants <2 m high can be estimated with precision from the proportions of points overlain by each plant category because the error is of the order of the diameter of the metal rod. However, the estimate of tree cover is much more subjective because the general outline of the canopy has to be estimated, and this is an exercise in fractal geometry (Mandelbrot 1967). Therefore, the data on the proportion of the points under tree canopies give only a relative index of tree cover and should not be compared directly with the cover of the lower strata, which was measured on an absolute scale.
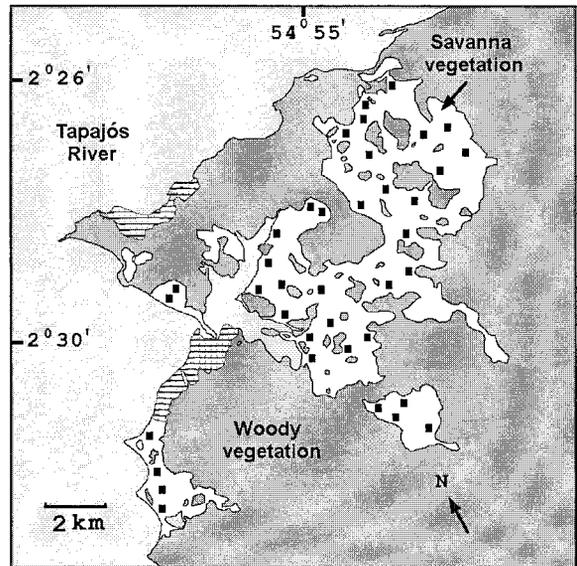

FIG. 1. Map of the study area showing areas with woody vegetation in the form of heaths and forests (dark gray), water bodies (light gray), savannas (white), and heavily disturbed areas such as pasture and urban areas (horizontal lines). Sample plots are shown as black squares.

The carbon-isotope ratios of species of plants were based on determinations for 42 species from the same savanna area (Magnusson et al. 1999: Table 2). The three common species of grasses had a mean δ¹³C ratio of −13.4 (SD = 0.27), and the grass species with the lowest δ¹³C ratio had a δ¹³C ratio of −13.7. These grasses accounted for >90% of the cover of C_4 plants in all of the quadrats sampled. The 39 species of shrubs and trees had a mean δ¹³C ratio of −30.4 (SD = 1.3), and the highest δ¹³C ratio was −27.9. There was no significant difference between trees and bushes, but the grasses had significantly more positive δ¹³C ratios than the dicotyledons (separate variances t test: $t_{13.7} = 66$, $P < 0.001$).

We attempted to collect an individual of each species of lizard in each plot using a compressed-air rifle. However, some species were not collected in some plots because they were not encountered, or because the individuals escaped. Animals were collected under IBAMA (Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renovaveis) permit 000747-/90-41 SUPES AM (Superintendencia do IBAMA no Estado do Amazonas). Sample sizes were as follows: *Ameiva ameiva*, 9; *Cnemidophorus lemniscatus*, 36; *Kentropyx striata*, 26; *Anolis auratus*, 31.

Samples of muscle tissue from each lizard were frozen within 3 h of collection and maintained in a freezer (approximately −10°C) for periods varying from a few days to two months. They were then dried to constant mass in an oven at 50°C, ground finely, and dispatched to the Centro de Energia Nuclear na Agricultura/Universidade de São Paulo laboratories at Piracicaba. There,

TABLE 1. Data for each of the quadrats sampled for lizards and vegetation cover in an Amazonian savanna, Brazil.

Points with vegetation cover			δ^{13} C ratio of lizards				Lizard snout–vent length (cm)			
Trees	Shrubs	Mono-cots	A. auratus	A. ameiva	C. lemnis-catus	K. striata	A. auratus	A. ameiva	C. lem-niscatus	K. striata
135	82	160	−17.4	−21.81	−17.89	−21.15	4	12.0	5.0	6.5
84	45	224	−16.94	···	−20.32	−18.89	4.2	···	6.1	4.8
158	43	200	−15.6	···	−17.80	−16.69	4.3	···	4.7	4.5
65	33	203	−16.29	···	−18.55	−16.57	4.3	···	5.8	5.5
146	37	234	−16.04	−19.47	···	−15.34	4.0	4.7	···	4.0
109	31	128	···	···	−19.22	−20.13	···	···	5.4	5.3
89	77	141	−18.29	−19.95	−21.09	−20.28	4.5	4.5	5.3	5.0
128	58	186	−19.93	···	−19.10	−21.46	5.2	···	5.3	6.1
61	64	164	−18.49	···	−17.41	···	3.8	···	4.0	···
129	30	205	−17.96	−20.72	−17.77	···	3.4	11.0	5.0	···
195	109	159	−18.84	···	−20.54	−24.43	4.1	···	5.8	9.8
38	23	213	−15.21	···	−16.43	···	4.1	···	5.5	···
114	60	210	−16.00	−19.62	−19.09	−20.03	3.5	6.5	5.2	6.7
66	58	144	−16.96	···	−17.75	−19.49	4.8	···	4.8	6.4
80	67	149	−16.59	−20.97	−17.23	−18.21	3.6	5.7	5.0	5.6
57	45	203	−18.32	···	−15.96	···	3.7	···	5.4	···
125	58	272	−18.98	···	−18.87	−21.55	3.8	···	4.7	7.4
76	23	111	−15.99	···	−15.98	···	4.6	···	4.3	···
82	17	98	−14.05	···	−15.41	−17.33	4.4	···	4.4	5.0
145	72	152	···	−18.76	−21.31	−23.85	···	4.1	6.0	9.5
116	65	241	−17.09	···	−16.39	−18.01	3.1	···	4.5	4.7
110	80	295	···	···	−23.07	−19.59	···	···	6.1	4.3
108	76	283	−17.40	−21.22	−18.38	−18.25	4.1	5.0	4.4	5.7
135	56	177	−15.86	···	−18.87	−17.27	4.8	···	4.4	4.7
94	51	117	−19.35	···	−17.89	−19.49	4.0	···	5.2	6.8
108	54	187	−16.98	···	−21.23	−20.36	4.0	···	7.0	7.5
99	49	135	−18.69	···	···	···	3.7	···	···	···
64	21	215	−13.60	−19.07	−17.52	···	4.4	5.8	4.4	···
83	57	270	−18.92	···	−15.56	−21.17	4.0	···	5.0	9.2
108	49	260	···	···	−18.05	−23.01	···	···	5.8	9.7
125	73	156	−19.53	···	−18.79	−21.31	4.8	···	3.8	9.2
106	72	270	···	···	···	−20.15	···	···	···	9.1
98	47	241	···	···	−18.34	···	···	···	5.6	···
121	50	182	−15.99	···	−18.08	−22.67	4.2	···	6.0	9.3
92	61	206	−16.22	···	−18.72	···	5.1	···	6.3	···
94	62	213	···	···	−17.41	···	···	···	4.3	···
86	53	228	−16.05	···	−17.84	···	4.4	···	6.2	···
146	49	200	−16.84	···	−19.83	···	5.0	···	6.0	···
86	69	228	···	···	−18.89	···	···	···	6.5	···

Notes: The index of vegetation cover is the number of the 500 points covered by each vegetation life form. The δ^{13}C ratios and snout–vent lengths are for one lizard of each species sampled in each quadrat.

they were sealed in evacuated glass ampoules (break-seal tubing) with cupric oxide and burned in an oven at 600°C for 12 h. The resulting CO_2 was purified in a vacuum line and injected in a Micromass 602 E mass spectrometer (Finnegan Mat, Bremer, Germany) fitted with double inlet and collector systems. Secondary standards consisted of charcoal from corn ears and *Eucalyptus* wood with known relationships to the primary standard, which is the Peedee Belemnite (PDB) formation from South Carolina, USA. The results are expressed in δ^{13}C relative to the PDB standard in conventional δ per thousand notation as the following:

$$\delta^{13}C = [(^{13}C/^{12}C)_{sam} - (^{13}C/^{12}C)_{std} - 1] \times 1000$$

where $^{13}C/^{12}C$ are the isotopic ratios of sample (sam) and PDB standard (std). The overall (sample preparation plus analysis) analytical precision is ±0.2‰.

The relative contribution of woody plants (dicotyledonous trees, shrubs, and vines) to a species diet was calculated from the formula $Pw = (\delta^{13}C_{SA} - \delta^{13}C_{G})/(\delta^{13}C_{W} - \delta^{13}C_{G})$, where Pw was the proportion of carbon from woody plants, $\delta^{13}C_{SA}$ was the presumed isotope ratio of the mixture of plants eaten by that animal, $\delta^{13}C_{W}$ was the mean isotope ratio for woody plants, and $\delta^{13}C_{G}$ was the mean isotope ratio for grasses. The $\delta^{13}C_{SA}$ for the lizards was reduced by 2‰ below ratios from muscle tissue ($\delta^{13}C_{M}$) to account for a presumed decrease of ~1‰ for each trophic level (Boutton et al. 1983, Tieszen et al. 1983). Analyses of all plants and animals were conducted in the same laboratory. Therefore the relationship between secondary and primary standards does not affect the estimates of the proportion of carbon from C_3 and C_4 sources.

Results are presented in terms of Pw as the aim of the study was to determine the relative contributions of woody plants and grasses to carbon acquisition by the lizards. However, there is a simple algebraic relationship between Pw and δ^{13}C, and use of Pw does not
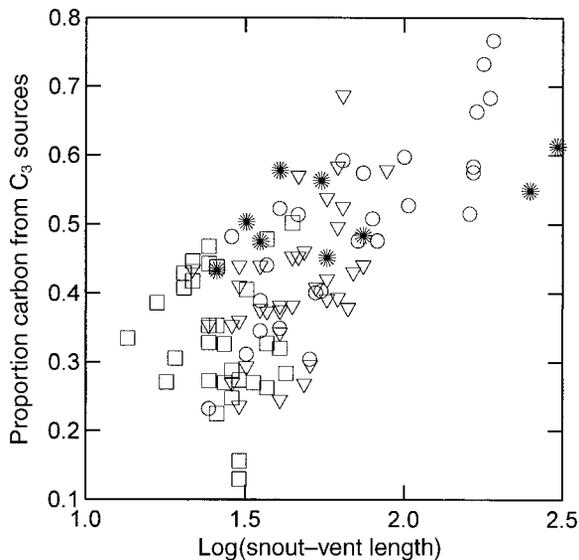
FIG. 2. Relationship between the estimated proportion of carbon derived from food chains originating from C_3 plants in body tissue of lizards, and the size (snout–vent length measured in centimeters) of lizard for all species combined. Asterisks represent *Ameiva ameiva,* squares *Anolis auratus,* triangles *Kentropyx striata,* and circles *Cnemidophorus lemniscatus.*

affect the relative variability. The probability values for tests of the null hypotheses associated with independent variables vary by <0.001 whether Pw, $\delta^{13}C_M$, or $\delta^{13}C_{SA}$ are used as independent variables.

Covariance, multiple regression and *t* test analyses were done in the SYSTAT 5.1 program (Wilkinson 1990). Tolerances (Tol.) <0.1 were used as indicators of potential problems with multicolinearity (Kirby 1993). Interactions in the covariance analyses were tested by including a multiplicative term that included the categorical and continuous variables.

RESULTS

Carbon-isotope ratios varied among and within species (Table 1). However, for all lizards sampled, independent of species, there was a general tendency for the proportion of dietary carbon derived from dicotyledons to increase with lizard size (Fig. 2). It was not possible to test the difference between the effects of species and size statistically because analysis of covariance indicated a significant size by species interaction ($F_{3,94} = 5.56$, $P = 0.001$). However, for any size of lizard, the range of isotope ratios, and hence proportion of carbon from C_3 and C_4 plants, was similar among species (Fig. 2). Therefore, the general magnitude of the effect of size was much larger than the general magnitude of the effect of species. Because of the species by size interaction, species were analyzed separately.

For *Cnemidophorus lemniscatus,* multiple regression analysis indicated that the proportion of carbon (Pw)

derived from C_3 food chains was significantly affected by lizard size (SI, $P = 0.001$, Tol. = 0.95) and the proportion of the plot covered by shrubs (SH, $P = 0.036$, Tol. = 0.73), but not by the proportion of the plot covered by trees (TR, $P = 0.079$, Tol. = 0.75) or grasses and sedges (GS, $P = 0.871$, Tol. = 0.87; Pw $= -0.8 + 0.41TR + 0.82SH - 0.02GS + 0.06SI$, $R^2 = 0.53$, $F_{4,31} = 8.7$, $P < 0.001$). The partial regressions indicated positive effects of lizard size and the proportion of the plot covered by shrubs (Fig. 3).

For *Kentropyx striata,* the proportion of carbon derived from C_3 food chains was significantly affected by lizard size ($P < 0.001$, Tol. = 0.86), but not by the proportion of the plot covered by trees ($P = 0.644$, Tol. = 0.81), grasses and sedges ($P = 0.279$, Tol. = 0.97), or shrubs ($P = 0.054$, Tol. = 0.72; Pw = 0.09 + 0.13TR + 0.91SH − 0.15GS + 0.05SI, $R^2 = 0.76$, $F_{4,21} = 16.3$, $P < 0.001$). However, the probability for the null hypothesis that there was no effect of shrub cover is low, and the general tendencies for both lizard size and shrub cover are positive (Fig. 4), as in *C. lemniscatus.*

For *Anolis auratus,* the proportion of carbon derived from C_3 food chains was significantly affected by the proportion of the plot covered by bushes ($P = 0.003$, Tol. = 0.77), but not by lizard size ($P = 0.622$, Tol. = 0.94), or the proportion of the plot covered by trees ($P = 0.839$, Tol. = 0.76), or grasses and sedges ($P = 0.807$, Tol. = 0.94; Pw = 0.28 − 0.05TR + 1.39SH − 0.04GS − 0.02SI, $R^2 = 0.34$, $F_{4,26} = 3.4$, $P = 0.025$). The proportion of dietary carbon derived from dicotyledons increased with the cover of bushes (Fig. 5).

For *Ameiva ameiva,* there was a significant relationship between the proportion of carbon derived from C_3 food chains and lizard size ($P = 0.32$, Tol. = 0.89), but not for tree cover ($P = 0.275$, Tol. = 0.89), shrub cover ($P = 0.060$, Tol. = 0.82), or grass cover (0.201, Tol. = 0.84; Pw = 0.28 − 0.33TR + 0.89SH + 0.25GS + 0.02SI, $R^2 = 0.79$, $F_{4,4} = 3.7$, $P = 0.117$). However, the sample size was much lower than for the other species, and the general tendency for an increase in Pw with cover of shrubs was similar to that for *C. lemniscatus* (Fig. 6).

DISCUSSION

The results presented here contribute to a growing body of literature showing the importance of population size structure to species' niches, and potential competitive and predatory interactions (e.g., Christian 1982, Polis 1984, Werner and Gilliam 1984, Lima and Magnusson 1998). We detected no significant effect of size on the proportion of dietary carbon derived from dicotyledons in *Anolis auratus. Anolis auratus* is a small species, and the range of size may be too low to detect size-related effects. The range of size was greater for *A. ameiva,* but no very small individuals were captured, and the total sample size was only nine individuals. However, these species with limited size ranges
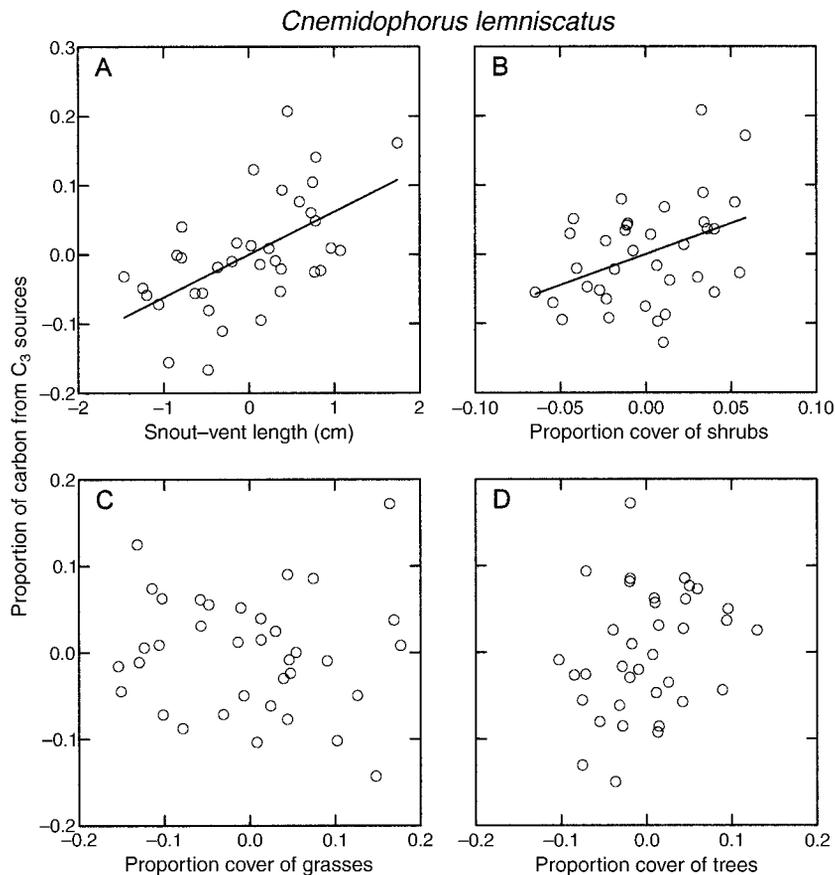
FIG. 3. Partial regressions derived from the multiple regression model testing (A) the effects of lizard size, (B) the proportion of the plot covered by shrubs, (C) the proportion of the plot covered by grasses and sedges, and (D) the proportion of the plot with tree cover on the estimated proportion of carbon derived from C_3 plants in body tissue of *Cnemidophorus lemniscatus.*

fell within the range expected based on the other species.

For the two species for which a wide range of sizes were collected, *Cnemidophorus lemniscatus* and *Kentropyx striata,* the pattern was similar to that seen in the whole assemblage, without regard to species. There was a strong effect of size on the proportion of dietary carbon derived from dicotyledons. This was not because those species dominated the combined-species analysis. More individuals of *Anolis auratus* were collected than *Kentropyx striata.* Also, *A. auratus* and *A. ameiva* represented the smallest and largest individuals, which would have had the largest leverage in the analysis. Regression of the proportion of dietary carbon derived from dicotyledons on log snout–vent length indicates that, on average, a lizard with a snout–vent length of 3 cm derived ∼26% of its diet from food chains based on C_3 plants, whereas 10-cm lizards derived ∼61% of their diet from food chains originating in C_3 plants. Differences among species were more subtle, and species identity affected the slope of the size-isotope ratio analysis rather than the mean value of $\delta^{13}C$.

The isotope analysis may underestimate the difference in food intake among size classes, because lizards may have low rates of energy (Pough 1983), and hence carbon turnover. A fraction of the carbon in adult lizards was ingested when they were smaller. However, we could not quantify that fraction as it depends on metabolic rate, growth rate, and the precise relationship between lizard size and rate of ingestion of carbon from different autotrophic sources, all of which are unknown for the lizards we studied.

The reason for the change in carbon sources with size is not clear. Larger lizards eat more C_3 fruits. However, the volume of fruits, including the indigestible seeds, was ≤14% in *K. striata* and ≤7% in the other species (Magnusson and da Silva 1993), and cannot account for an approximate doubling of carbon from C_3 sources between the smallest and largest size classes. Our extensive studies of lizards in the region (Magnusson et al. 1985, 1986, Magnusson 1987, 1993, Magnusson and Silva 1993) did not reveal any obvious habitat partitioning among size classes. *Anolis auratus* is often found on grass stems, but the other species use areas under bushes and around grasses. Locomotor
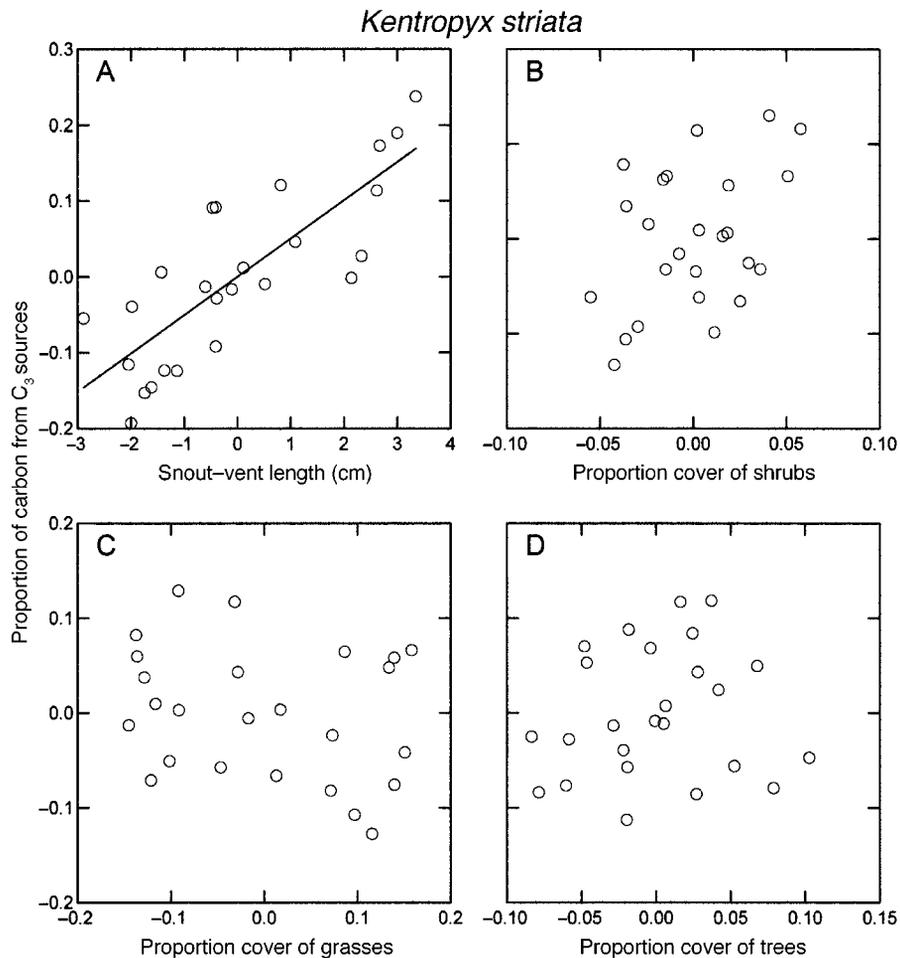
Kentropyx striata

FIG. 4. Partial regressions derived from the multiple regression model testing (A) the effects of lizard size, (B) the proportion of the plot covered by shrubs, (C) the proportion of the plot covered by grasses and sedges, and (D) the proportion of the plot with tree cover on the estimated proportion of carbon derived from C_3 plants in body tissue of *Kentropyx striata.*

ability is related to size in some arboreal lizards (Losos 1990). Larger lizards may be more efficient at foraging in leaf litter than smaller lizards, and for this reason may have higher rates of prey capture under bushes and trees. However, such subtle effects of microhabitat, if they exist, have not been studied in lizards that forage on the ground.

The large effect of lizard size and more subtle effect of species identity contrast with the results of Magnusson and da Silva (1993), who found a strong effect of species and a weak effect of size for the same assemblage of lizards. Those authors used taxonomic categories of invertebrates eaten to evaluate overlap in diets. Overlap in prey taxonomic categories is commonly used to evaluate niche overlap (e.g., Vitt and Carvalho 1995, Lima and Magnusson 1998, Caldwell and Vitt 1999, Vitt et al. 1999), and the potential for competition (e.g., Winemiller and Pianka 1990). Therefore, it is disturbing that the isotope study and direct observation of the diet led to different conclusions.

We believe that the different types of study inves-

tigate different aspects of resource use, and are therefore complementary. Studies of the taxonomic composition of diets are useful to indicate minimum differences among diets. If the predators eat different types of arthropods, they do not overlap in diet. However, this study has shown that species or size classes that overlap in the taxonomic categories of arthropods eaten are not necessarily taking prey from the same food chains. Stable isotope studies can reveal maximum potential overlap in use of primary carbon sources, but cannot reveal differences due to packaging of carbon from that source in different taxonomic categories of arthropods.

More refined taxonomic categories will not necessarily increase our ability to detect differences in food chains. Magnusson et al. (1999) reported that one colony of the termite *Syntermes molestus* had obtained most of its carbon from C_4 sources ($\delta^{13}C = -17.7$) and a nearby colony of the same species had obtained most of its carbon from C_3 sources ($\delta^{13}C = -25.5$). Closely related species of lizards tend to have taxonomically
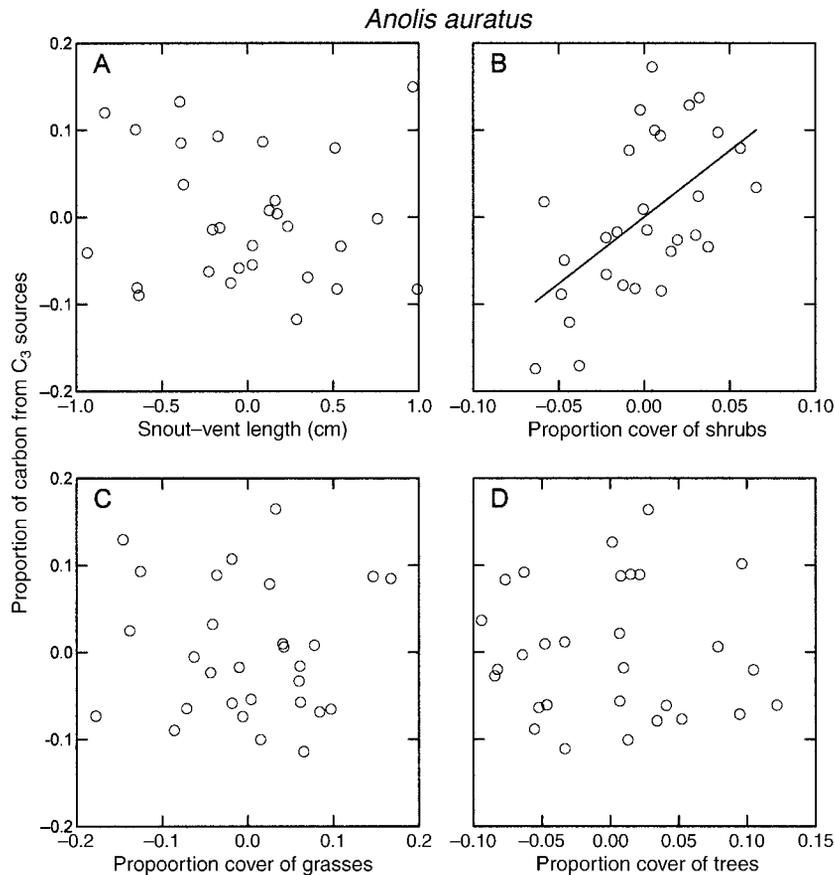
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similar diets, independent of habitat selection (Vitt et al. 1999). Therefore, very detailed behavioral studies are necessary to determine when taxonomic overlap in diet indicates that predators on arthropods belong to the same food chain.

The isotope analyses also revealed information on primary sources of carbon that may be relevant to management decisions. Grasses and sedges, and bushes and trees, are generally considered to constitute different functional groups in savannas (e.g., Boutton et al. 1983, Scholes and Archer 1997). Models of ecosystem function in savannas generally consider dichotomies between grasses and other plant life forms, or between the herb–shrub layer and the tree layer (e.g., Gignoux et al. 1996, Jeltsch et al. 1998). Management procedures, such as fire control, affect the ratio of grass to dicotyledons in savannas in general (Scholes and Archer 1997), and in the savanna we studied (Sanaiotti and Magnusson 1995). However, there is no published information on the plasticity of savanna lizards in relation to changes in availability of C_3- and C_4-based food chains.

There is evidence that at least two of the lizard species we studied are food limited. For samples from the

same plots, there was a significant positive relationship between arthropod availability and density of *Cnemidophorus lemniscatus* and *Kentropyx striata,* independent of vegetation structure (Faria 1999). The three species for which we had large sample sizes were capable of some adjustment to an increase in the proportion of arthropods from C_3 food chains. Shrub cover had significant, or near significant, positive effects on the proportion of dietary carbon derived from C_3 plants in those species. However, those effects were not as strong as those of lizard size in the two species with a wide range of sizes.

Species such as *Anolis auratus,* which obtain most of their carbon from grass-based food chains, may benefit from management regimes that promote greater grass cover. However, for *Cnemidophorus lemniscatus* and *Kentropyx striata,* the situation is more complicated. The different size groups appear to be functioning as different ecological species (sensu Polis 1984). An increase in availability of food for the smallest size classes through an increase in grass cover could result in a reduction in the availability of food for the larger size classes, which obtain most of their carbon from
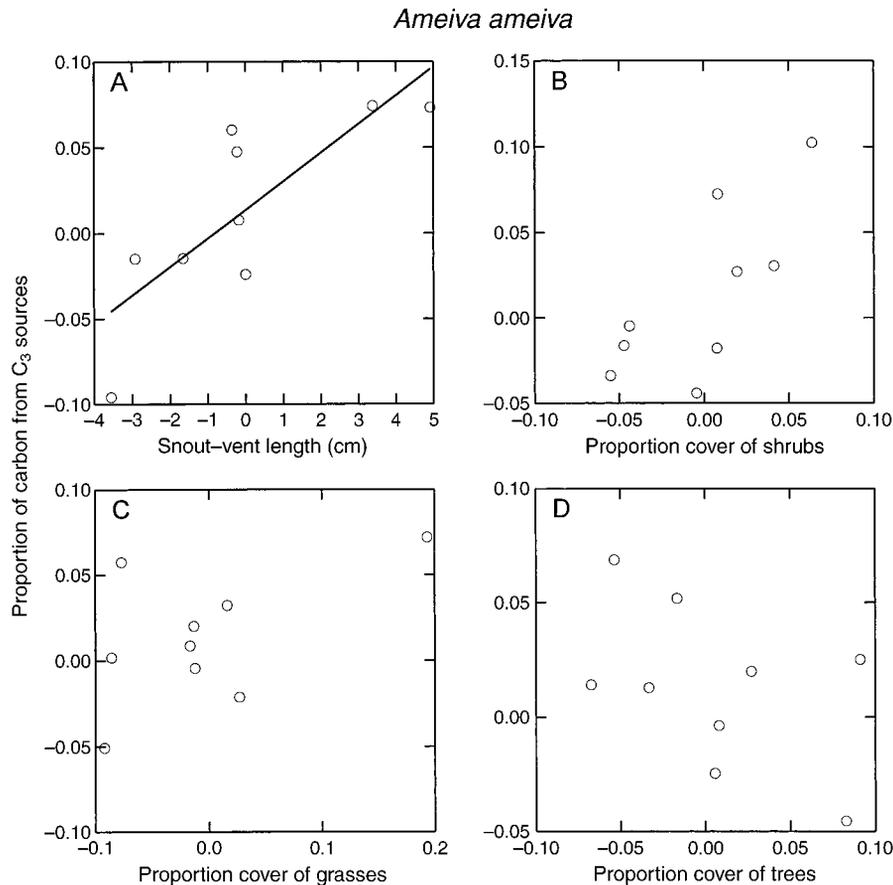
Ameiva ameiva

FIG. 6. Partial regressions derived from the multiple regression model testing (A) the effects of lizard size, (B) the proportion of the plot covered by shrubs, (C) the proportion of the plot covered by grasses and sedges, and (D) the proportion of the plot with tree cover on the estimated proportion of carbon derived from C_3 plants in body tissue of *Ameiva ameiva.*

C_3 sources. It is unlikely that a conventional analysis based on diet taxonomic categories could show this.

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