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SMALL IN A BIG WORLD: ECOLOGY OF LEAF-LITTER GECKOS IN NEW WORLD TROPICAL FORESTS

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Abstract: We studied the ecology of four species of closely related leaf litter geckos, *Coleodactylus amazonicus*, *C. septentrionalis*, *Lepidoblepharis xanthostigma*, and *Pseudogonatodes guianensis* in tropical rainforests of Brazil and Nicaragua. All are found in leaf litter of undisturbed tropical forest where mean hourly surface temperatures vary from 23.5–29.1 C. Surface temperatures, where individual *C. amazonicus* were found, averaged 27.4 C and air averaged 29.9 C. *Coleodactylus amazonicus* was the smallest species and *L. xanthostigma* was the largest. The latter was the most different morphologically as well. Tail loss rates varied from 45.5–81.8% among species. All four species ate very small prey items, largely springtails, homopterans, termites, small insect larvae, and spiders. Nevertheless, considerable differences existed among species. Some variation existed among populations of *C. amazonicus*. Prey size was correlated with lizard SVL within and among species. All four species are typically the smallest species in their respective lizard assemblages. Small body size may have consequences for predation. Partially due to small body size, these lizards are vulnerable to extirpation resulting from effects of tree removal on thermal attributes of their leaf litter environment.

Key words: Squamata; Gekkonidae; *Coleodactylus*; *Lepidoblepharus*; *Pseudogonatodes*; Lizard ecology; Rainforest.

New World tropical forests are well known for their biotic diversity (Wilson, 1988) and the complexity of potential species interactions (Erwin, 1983). Aside from their remarkably diverse vegetation (Valencia et al., 1994), these forests contain a striking diversity of animal species, including most major vertebrate groups (Azevedo-Ramos and Gallati, 2001; Dixon and Soini, 1975; Janzen, 1993; Oren, 2001; Vogt et al., 2001). Both Caribbean lowland forest and Amazonian lowland rainforests share a mat of leaf litter covering the ground within mature forest, a microhabitat type that contains not only numerous invertebrate species, but many small frogs and lizards (Allmon, 1991; Caldwell and Vitt, 1999; Duellman, 1987, 1990; Duellman and Mendelson, 1995; Hoogmoed, 1973; Lieberman, 1986; Scott, 1976; Vitt and Caldwell, 1994). Among the smallest vertebrates in these tropical forests are gekkonid lizards in the clade that includes the genera *Coleodactylus*, *Pseudogonatodes*, and *Lepidoblepharis*, all of which live exclusively in leaf litter. Moreover, these are typically the smallest lizard species in their respective assemblages (e.g., Duellman, 1978, 1987; Lieberman, 1986; Vitt and Zani, 1996*a*, 1998*a,b*; Vitt et al., 1999). Because they are smaller than many invertebrates, these geckos could be competitors with or prey of many invertebrates (see Vitt, 2000). Also, because many frog and lizard species eat nearly anything small enough to fit in their mouths, these tiny geckos are at risk of predation by other predacious terrestrial vertebrates and birds.

We examine in detail the ecology of four species representing all three genera. One species, *Coleodactylus amazonicus*, was studied at six localities in the northern, central, and western Amazon, so we provide some insight into geographic variation in the ecology of this species, recognizing that some of these populations may be distinct taxa (M. T. Rodrigues, personal communication). We describe microhabitat use, morphology, tail loss rates, activity,

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thermal ecology, and diets. We comment on some of the many consequences of small body size in extremely complex and diverse tropical lowland forests. Finally, we suggest that these lizards are at high risk of local extirpation because their ecological traits make them vulnerable to consequences of changes in land use.

MATERIALS AND METHODS

Coleodactylus amazonicus was studied at the following localities: Rondônia, Brazil (3° 22′ S latitude, 51° 51′ W longitude) in 1985 during the peak of the dry season (hereafter Rondônia 85); transitional forest in southern Roraima, Brazil (2° 0′ N latitude, 62° 50′ W longitude) in 1993 during the wet season (hereafter, Roraima); the Curuá-Una region of central Pará, Brazil (3° 31′ S latitude, 59° 54′ W longitude) in 1995 during the wet season; the Rio Ituxi in western Amazonas, Brazil (8° 20′ S latitude, 65° 43′ W longitude) in 1997 during the wet season; the Rio Formoso in Rondônia (10° 19′ S latitude, 64° 33′ W longitude) in early 1999 during wet season (hereafter Rondônia 99), and; southeast of Manaus in Amazonas, Brazil (3° 20′ S latitude, 59° 4′ W longitude) in late 1999 during the wet season (hereafter, Solimões). *Coleodactylus septentrionalis* was studied concurrently with *C. amazonicus* in transitional forest in southern Roraima, Brazil in 1993 during the wet season. *Lepidoblepharis xanthostigma* was studied in Caribbean lowland forest in Rio San Juan Province, Nicaragua (11° 3′ N latitude, 85° 40′ W longitude) in dry season of 1993. *Pseudogonatodes guianensis* was studied near the Rio Jurua in Acre, Brazil (8° 15′ S latitude, 72° 46′ W longitude) during wet season of 1996. We emphasize that two species occurred together in only one locality (Roraima). Thus our comparisons among species and populations are not intended to imply that these species and/or populations interact in any way.

Because these geckos were studied concurrently with sympatric species of tropical forest lizards, we recorded habitat type and microhabitat data for every individual of all species. Consequently, numerous habitats not containing these geckos were searched. We present only those data pertinent to these particular species. To collect data on activity and microhabitat use, we conducted haphazard searches in the forest from early morning until near dark. This method has proven effective in lowland forest habitats (e.g., Vitt et al., 2000). For each lizard observed, we recorded the habitat type and microhabitat in which the lizard was first observed. Because of the small body size of these lizards, we did not take body temperatures (T_b). For some lizards, we recorded substrate temperatures (T_{ss}) at the exact spot where the lizard was found along with air temperatures (T_a) to 0.2 C with Miller-Weber rapid-register thermometers. For two populations of *C. amazonicus* and a population of *P. guianensis*, we sampled temperatures in leaf litter microhabitats where these lizards were found using electronic temperature devices. We include those data to characterize thermal conditions in microhabitats used by the lizards. Temperatures were recorded at five-minute intervals 24 h per day using HOBO or TidBit electronic temperature recording devices supplied by OnSet Computer Company at two localities (Rio Ituxi and Rio Jurua). These devices have been shown to produce temperature profiles similar to copper models for lizards of relatively small body size (Vitt and Sartorius, 1999; Shine and Kearny, 2001) and thus can be considered accurate estimators of operative temperatures (Hertz et al., 1993). A total of 26 days were sampled at the Rio Ituxi and 30 days at the Rio Jurua. At the Curuá-Una site, we used an Omega OM-550 data logger with type-T thermocouples to record leaf litter temperatures at 30-minute intervals (see Vitt et al., 1997*a* for details). A total of 24 days were sampled at this site. We restrict the presentation of microhabitat temperature data to those hours during which the geckos were observed active. For perspective, we also plot temperature data taken in a forest treefall at one of the sites (Curuá-Una). For this paper, we combined temperature data for all days at each site and calculated hourly means.

All captured lizards were returned to our field laboratories within 2 h of capture, killed by immersion in Chlorotone following approved protocols (Anonymous, 1987), and measured for the following morphological variables with vernier or electronic calipers: snout–vent length (SVL), tail base (original, unregenerated portion), length of regenerated tail portion, if any, head width, length, and height, body width and height, and hindleg length. Measurements were to 0.1 mm. Total mass was taken with Pesola spring scales (0.1 g) or Acculab field balances (0.01 g), depending upon locality. Lizards were then fixed in 10% formalin and later transferred to 70% ethanol for permanent storage. Prior to transfer to alcohol, lizards were dissected, stomachs removed and either immediately analyzed or placed in 70% ethanol for later analysis, and reproductive organs were examined.

In addition to simply comparing SVL among species and populations, we used a Principal Components Analysis (PCA) to examine potential differences in bauplan. Because all morphological variables are correlated with lizard size, we first performed regression on log-transformed variables against log transformed SVL for all species pooled. We then calculated the residuals from those regressions to adjust for species/population differences in lizard size, and used the residuals in the PCA. For lizards with broken or regenerated tails, we substituted estimated tail lengths (see below). We compared factor scores from the PCA among species/populations with ANOVAs.

We calculated tail loss rates for each species by dividing the number of lizards with missing or regenerated tails by the total number of lizards in sample. We use these only as indicators of potential risk of predation. We have no data on condition of tails for lizards that were predated (see Schoener, 1979; Schoener and Schoener, 1980). For lizards with complete tails (no indication that they had ever been broken), we regressed tail length on SVL and, if significant linear relationships existed, we used the equation for the tail to SVL relationship to estimate original tail lengths of lizards with missing or regenerated tails. Using these estimates of original tail length, we were then able to calculate relative position at which tail break had occurred and relative length of regenerated tail as compared to the original.

To examine diets, we opened stomachs of sampled lizards, carefully separated prey items, identified them to family or the next highest possible taxonomic category, counted them, and measured each item for length and width to 0.01 mm, using electronic calipers or an ocular micrometer in a dissecting microscope. Prey items in lizard stomachs are compressed with limbs and wings pressed against the body approximating the shape of a prolate spheroid. Hence, we estimated volumes for individual prey items with the formula:

$$V = 4/3\pi(\text{prey length}/2)(\text{prey width}/2)^2$$

We then grouped prey items into the following broad categories for further analysis: ants, beetles, centipedes, earthworms, embiopterans, flies, hemipterans, homopterans, insect larvae, isopods, lepidopterans, lizard shed skin, grasshoppers & crickets, millipedes, mites, non-ant hymenopterans, opiliones, pseudoscorpions, psocopterans, roaches, snails, spiders, springtails, termites, thysanopterans, ticks, vertebrates, and walking sticks. Ants were considered different from other hymenopterans because of the distinct wingless morphology of workers, their surface activity, and their high relative abundance. Diet data were analyzed with BugRun 1.7, a program based in 4$^{\text{th}}$ Dimension®. Prey measurements and lizard SVL were $\log_{10}$ transformed for analyses. The program produces dietary tables summarizing the diet, calculates niche breadths, and produces additional data sets for other analyses. Complete diets were summarized for each species or population and proportional utilizations of prey types were calculated for numerical and volumetric data by dividing values for each prey type by column totals and multiplying by 100 to convert to percentages. Prey niche breadths were calculated as the inverse of Simpson's (1949) measure (see Pianka, 1973, 1986).

$$B = 1 \Big/ \sum_{i=1}^{n} p_i^2$$

Niche breadth values vary from 1 to *n* with low values indicating reliance on one or a few prey types and high numbers indicating relatively even use of numerous prey types. Another data set produced by BugRun 1.7 includes means of prey width, length, and volume for each individual lizard. These data were $\log_{10}$ transformed to normalize the distributions, merged with the lizard morphology data set, and regressed with $\log_{10}$ SVL to determine if lizard body size influences the size of prey items eaten. We used linear regression to test the association between

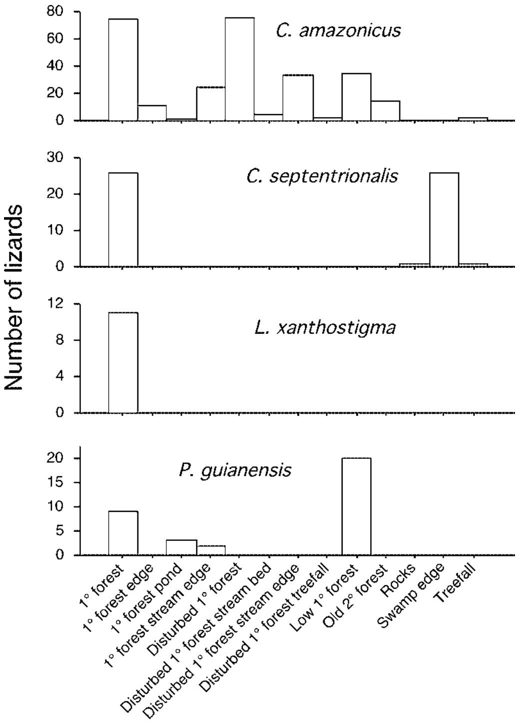


FIG. 1.—Habitat occurrence for four species of Neotropical leaf litter geckos.

mean prey size and mean lizard SVL among species/populations. Because prey size within species/populations was correlated with lizard SVL, we also performed an ANCOVA to test the hypothesis that prey size and lizard size are not associated in the same manner among species/populations.

BugRun 1.7 also produces a consumer-resource matrix with lizard species as rows and resources as columns. We calculated overlaps in prey use among the gecko species and populations and compared those overlaps with overlaps generated by two different randomization methods (see Winemiller and Pianka, 1990) making no assumptions about potential differences among species or populations in resource availability. Overlaps were calculated with the following formula:

$$\oslash_{jk} = \frac{\sum_{i=1}^{n} g_{ij} \sum_{i=1}^{n} g_{ik}}{\sqrt{\sum_{i=1}^{n} g_{ij}^{2} \sum_{i=1}^{n} g_{ik}^{2}}}$$

where symbols are the same as above with j and k representing lizard species (Pianka, 1973, 1986).

Briefly, the analysis computes proportional utilizations (p_i), then computes electivities (e_i) normalized to vary from 0–1, and finally calculates the geometric means (g_i) of p_i and e_i to minimize biases associated with p_i and e_i data. The g_i were then used to calculate dietary overlaps among species. A new set of overlaps was calculated in the same way by first randomizing the addresses in the matrix of resource data for each lizard species such that the number of resources and niche breadths remained the same. Another set of overlaps was calculated the same way but resource addresses with values of zero were not shuffled. Each of these was calculated 1000 times. If 95% of the overlaps resulting from the randomization procedure were greater than observed overlaps, we concluded that species differ significantly in diets. If less than 95% of the overlaps produced by the randomization procedure were greater than observed overlaps, we conclude that the lizards randomly select from a set of prey items eaten by all leaf litter geckos.

The Macintosh versions of Statview 4.5 was used for statistical analyses. Voucher specimens have been deposited in the following museums: Museu de Zoologia da Universidad de São Paulo (MZUSP) in São Paulo, Brazil, the Museu Paraense Emílio Goeldi (MPEG) in Belém, Brazil, the National Museum of Nicaragua in Managua, Nicaragua, and the Sam Noble Oklahoma Museum of Natural History (OMNH) in the United States.

RESULTS

Habitat and Microhabitat Use and Thermal Ecology

Nearly all individuals of the four species were found in leaf litter. Among 277 *C. amazonicus*, 274 were in leaf litter, one was on open ground, one was on a fallen branch, and one was under a piece of wood. Among 53 *C. septentrionalis*, 52 were in leaf litter and one was on open ground surrounded by leaf litter. All 11 *L. xanthostigma* were in leaf litter and 33 of 34 *P. guianensis* were in leaf litter. The other one was on open ground surrounded by leaf litter. Most individuals of the four

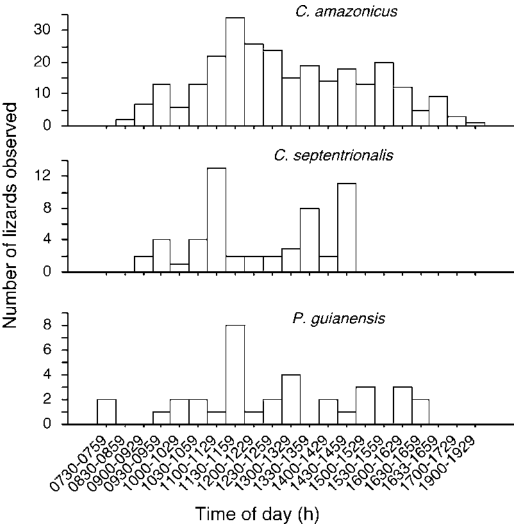


FIG. 2.—Activity cycle for three common species of Neotropical leaf litter geckos. All populations of *C. amazonicus* are combined.

TABLE 1.—Percent of leaf litter geckos active on sunny versus cloudy days and relative exposure of lizards to filtered sun, shade, or sun.

	Cloud cover		Lizard exposure		
Species	Cloudy	Sunny	Filtered sun	Shade	Sun
C. amazonicus	56.4	43.6	28.7	68.0	3.3
C. septentrionalis	35.8	64.2	53.7	44.4	1.9
P. guianensis	64.7	35.3	20.6	79.4	0.0

species were found in one of several primary forest habitats, but *C. amazonicus* was found in a wider variety of forest patches (Fig. 1), sometimes using lightly disturbed primary forest as long as leaf litter and shade were present. *Coleodactylus septentrionalis* was found for the most part in terra firme forest (1° forest) and at the edge of swamps in forest. *Lepidoblepharis xanthostigma* was found only in terra firme forest. *Pseudogonatodes guianensis* was found in both undisturbed terra firme forest and undisturbed low primary forest.

These geckos were found active only during the day. Among the three species for which we had adequate data, *C. amazonicus* and *P. guianensis* were active throughout the day with greater numbers of *C. amazonicus* observed about mid-day (Fig. 2). *Coleodactylus septentrionalis* were active throughout the day, but activity appeared to peak just before mid-day and again late in afternoon. Lizards were about equally likely to be active on cloudy as on sunny days but appeared to avoid direct exposure to sunlight (Table 1). T_{ss} and T_a taken at the point where 50 individual *C. amazonicus* were captured averaged 27.4 ± 0.21 C and 29.9 ± 0.18 C, respectively. We make the assumption that T_{ss} approximates lizard T_b because the lizards are very small and thus have little thermal inertia, and because lizards were rarely exposed to sun which might allow them to gain heat.

Mean hourly temperatures in leaf litter varied from 24.0 ± 0.02 to 26.0 ± 0.03 C at the Rio Ituxi, 23.5 ± 0.03 to 25.3 ± 0.03 C at the Rio Jurua, and 23.6 ± 0.09 to 29.1 ± 1.11 C at the Curuá-Una site (Fig. 3). Because the number of temperatures used to calculate hourly means was large (partially as a result of many samples and partially a result of combining days), SE were extremely small. Plots of all temperatures recorded (not shown) reveal that temperatures below 27 C were available in leaf litter throughout the day. In sharp contrast, hourly means of leaf litter in a forest treefall at the Curuá-Una site exceeded 27 C for six hours (1000–1600 h; Fig. 3).

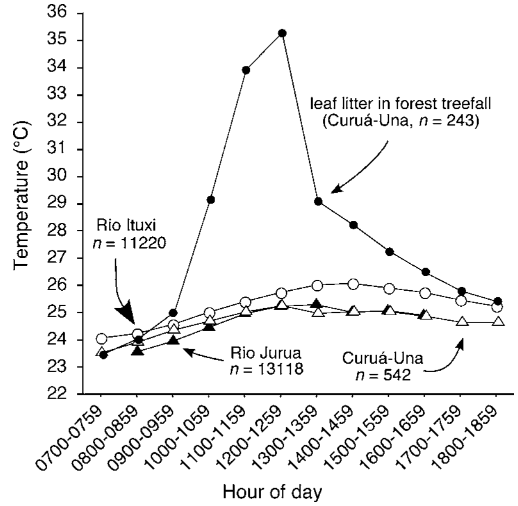


FIG. 3.—Hourly mean temperatures in three rainforest leaf litter microhabitats occupied by leaf litter geckos. Temperatures in a forest treefall are also shown for perspective. Most SEs are less than the size of points shown but considerable variation does exist.

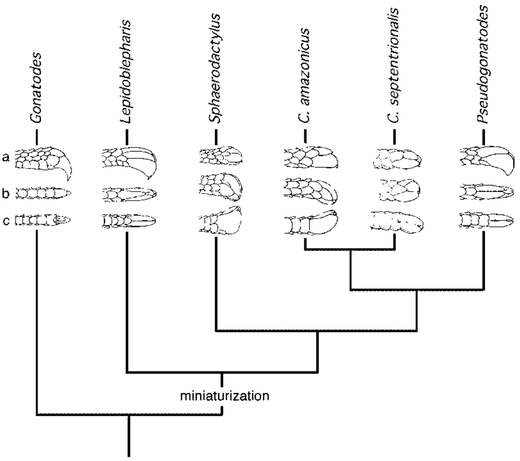


FIG. 4.—Evolutionary relationships among Neotropical leaf litter geckos showing differences in foot structure (toe drawings from Kluge, 1995 except for those of *C. septentrionalis*, which were taken from Avila-Pires, 1995). a = lateral view, b = dorsal view, c = ventral view of toes.

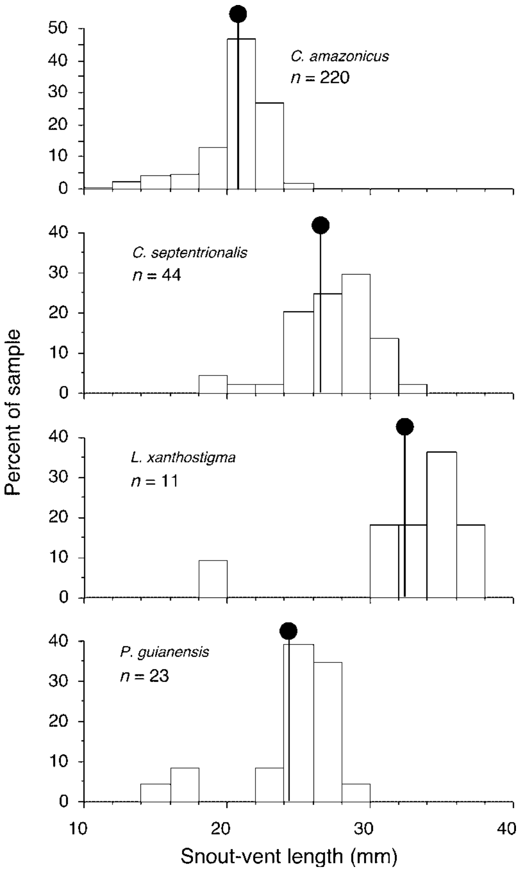


FIG. 5.—Body size distributions for Neotropical leaf litter geckos. Lines with closed circles indicate sample means.

Lizard Size and Morphology

Superficially, these small, closely related geckos look alike but can be distinguished at the generic level by distinct differences in toe morphology (Fig. 4; Kluge, 1995). Among the species we studied, *C. amazonicus* was the smallest whereas *L. xanthostigma* was the largest (Fig. 5). Hatchlings of *C. amazonicus* were as small as 11.6 mm SVL and those of *P. guianensis* were as small as 14.4 mm SVL. We did not collect hatchlings of the other species. Morphology varied considerably among species as well (Table 2).

PCA on eight size-adjusted morphological variables produced four factors accounting for 65.0% of the variation in bauplan. Factor I described a gradient weighted by relative mass and relative head size accounting for 23.1% of morphological variation (Fig. 6; Table 3). Factor II described a gradient weighted by relative body width and relative tail length (negative loading) accounting for 19.1% of morphological variation. Factor III described a gradient based on relative hindleg length accounting for 13.1% of morphological variation. Factor IV described a gradient based on relative body height accounting for 10.7% of morphological variation. ANOVAs on factor scores revealed significant differences among species for all three factors (P values for factors I, II, and III were <0.0001, <0.0001, and 0.0002, respectively). No significant difference was detected among species for Factor IV ($P = 0.0796$) and it will not be further considered. For factor I, significant pairwise differences were detected between *C. septentrionalis* and both *P. guianensis* and *C. amazonicus* and between *P. guianensis* and *L. xanthostigma* (Games-Howell post-hoc test, P values $<$ 0.05). For factor II, all pairwise comparisons were significant (Games-Howell post-hoc test, $P < 0.05$). For factor III, *C. septentrionalis* was significantly different from both *C. amazonicus* and *L. xanthostigma* (Games-Howell post-hoc test, $P < 0.05$).

Tail Loss

Tail lengths (original complete tails) were significantly correlated with lizard SVL in all

TABLE 2.—Summary statistics for morphological variables on four species of leaf litter geckos. Values shown are means ± SE, sample size appears after comma and minimum–maximum values are in parentheses under each entry.

Variable	*C. amazonicus*	*C. septentrionalis*	*L. xanthostigma*	*P. guianensis*
Snout–vent length (mm)	20.7 ± 0.2, 220 (11.6–24.6)	27.2 ± 0.5, 44 (18.4–32.0)	32.5 ± 1.5, 11 (19.0–37.0)	24.4 ± 0.8, 23 (14.4–28.5)
Mass (g)	0.21 ± 0.01, 219 (0.04–0.4)	0.45 ± 0.02, 44 (0.15–0.7)	0.71 ± 0.10, 11 (0.10–1.4)	0.29 ± 0.02, 23 (0.08–0.5)
Head width (mm)	3.33 ± 0.02, 207 (2.5–4.1)	4.14 ± 0.05, 44 (3.1–4.5)	4.89 ± 0.11, 10 (4.2–5.4)	3.64 ± 0.07, 23 (2.7–4.0)
Head length (mm)	4.58 ± 0.04, 206 (3.4–7.1)	5.75 ± 0.08, 44 (4.1–6.6)	7.44 ± 0.14, 10 (6.8–8.4)	5.14 ± 0.14, 23 (3.4–6.2)
Head height (mm)	2.22 ± 0.02, 206 (1.5–3.4)	2.62 ± 0.04, 44 (1.9–3.2)	3.29 ± 0.08, 10 (3.0–3.8)	2.44 ± 0.08, 23 (1.2–3.0)
Body width (mm)	3.92 ± 0.04, 207 (2.1–5.2)	5.19 ± 0.13, 44 (3.0–6.9)	5.61 ± 0.12, 10 (4.9–6.1)	4.30 ± 0.16, 23 (2.6–5.6)
Body height (mm)	2.77 ± 0.03, 207 (1.6–3.8)	3.62 ± 0.10, 44 (2.3–5.0)	4.41 ± 0.13, 10 (3.6–5.0)	3.27 ± 0.12, 23 (2.2–4.4)
Hindleg length (mm)	7.25 ± 0.05, 207 (4.6–8.9)	8.63 ± 0.13, 44 (5.9–10.2)	11.44 ± 0.34, 10 (9.3–12.6)	8.19 ± 0.19, 23 (5.7–9.7)
Foreleg length (mm)	5.27 ± 0.06, 133 (3.6–6.9)	6.80 ± 0.14, 44 (4.2–8.8)	8.25 ± 0.23, 10 (6.6–9.1)	5.64 ± 0.19, 23 (3.3–7.1)

species (P values < 0.0139; Table 4). An ANCOVA on tail length with SVL as the covariate revealed no significant difference among populations of *C. amazonicus* ($F_{1,5} = 1.8$, $P = 0.1292$, after removing the non-significant interaction term). Consequently, we combined all data for *C. amazonicus* for further comparisons. An ANCOVA comparing tail length among species with SVL as the covariate revealed a significant effect ($F_{1,2} = 44.3$, $P < 0.001$ after removing the non-significant interaction term). All species pairs were significantly different (all P values < 0.0013, Fisher's protected least significant difference test [PLSD]). Tail loss rates varied from 45.5–81.8% among species and original tails accounted for 43.7–51.3% of total length among species (Table 5). When tails were lost, on average, more than half of the tail was missing or had been missing prior to regeneration. The greatest portion of the tail lost was in *C. amazonicus*, in which an average of only 24.5% of the original tail remained. The lowest portion of the tail lost was in *C. septentrionalis*, which averaged 49.5% of the original tail remaining. Nevertheless, considerable variation exists in position of tail breaks as shown in Fig. 7. Length of regenerated tails (including

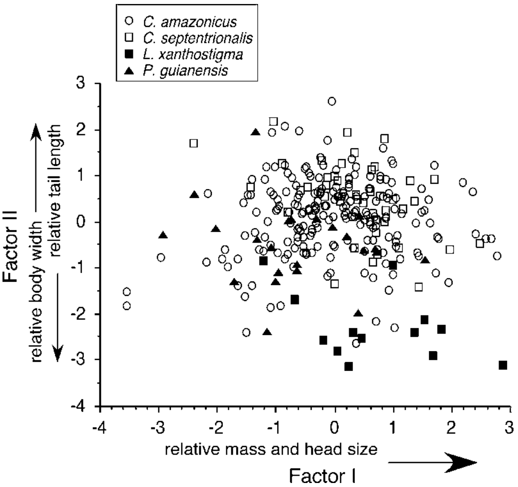


FIG. 6.—Plot of first two factors from a Principal Components Analysis on size-adjusted morphological variables of four Neotropical leaf litter geckos. *Lepidoblepharus xanthostigma* was most different from the other species. See Table 2 for factor scores.

TABLE 3.—Factor scores from a Principal Components Analysis on seven size-adjusted morphological variables for four species of leaf litter geckos.

Variable	Factor 1	Factor 2	Factor 3
Relative mass	0.685	0.448	<0.001
Relative head width	0.621	0.078	0.226
Relative head length	0.621	−0.368	−0.407
Relative head height	0.521	−0.132	−0.014
Relative body width	−0.021	0.771	0.053
Relative body height	−0.001	0.122	−0.002
Relative hindleg length	−0.015	−0.089	0.864
Relative tail length	0.180	−0.641	0.370
Eigenvalue	1.851	1.526	1.049
Percent of variation	23.1	19.1	13.1

TABLE 4.—Statistics on the relationship between tail length and SVL and regression equations for four species of leaf litter geckos. In the equations, estimated tail length = y and SVL = x. These equations were used to estimate original tail lengths for geckos with recently broken or regenerated tails (see text).

Variable	*C. amazonicus*	*C. septentrionalis*	*L. xanthostigma*	*P. guianensis*
R^2	0.544	0.201	0.958	0.780
F test	$F_{1,107} = 130.1$	$F_{1,22} = 6.8$	$F_{1,3} = 70.2$	$F_{1,7} = 29.3$
P value	<0.0001	0.0162	0.0139	0.0010
Equation	$y = 0.760(x) + 1.636$	$y = 0.382(x) + 10.881$	$y = 1.371(x) - 8.134$	$y = 0.665(x) + 4.242$

the original; tail base) averaged considerably less than original tails (64.9–78.8%).

Diets

The number of prey types recorded for each population/species of geckos was significantly correlated with sample size (R^2 = 0.774, $F_{1,7} = 24.3$, $P = 0.0017$; Fig. 8). However, prey diversity based on volumetric data was not correlated with sample size ($F_{1,7} < 0.1$, P = 0.9767). Even though additional prey types were added as sample size increased with species, prey types comprising most of the diet volumetrically did not change. Although some dietary variation existed among populations of *C. amazonicus* (Fig. 9), springtails, termites, homopterans, and insect larvae dominated their diets at all sites. *Coleodactylus septentrionalis* ate mostly termites and grasshoppers and crickets. *Lepidoblepharis xanthostigma* had a diet volumetrically dominated by vertebrates. Spiders and springtails accounted for most of the remainder of their diet. However, close examination of diet data for that species revealed that a single lizard had eaten a relatively large frog accounting for all of the vertebrate material. In addition, sample size for this species was low (N = 9). Consequently, any conclusions are tentative at best. Nevertheless, other leaf litter geckos did not eat vertebrates (sample sizes/species varied from 22–196). *Pseudogonatodes guianensis* ate mostly insect larvae and small grasshoppers and crickets.

The null model analysis (Winemiller and Pianka's "pseudocommunity" analysis) of dietary data provided some insight into prey use among populations and species. Overlaps in volumetric data varied from 0.651 between Rio Ituxi and Rondônia 99 *C. amazonicus* to 0.022 between *X. septentrionalis* and *L. xanthostigma* (Table 6). At the first nearest neighbor rank, empirically measured dietary overlaps were not significantly greater than those generated by either simulation (Fig. 10). However, at ranks 2–7 type I overlaps were significantly lower than measured overlaps. Variability in dietary overlaps (as measured by SD) was higher for measured overlaps at ranks 2–7 as well (Fig. 10). Populations of *C. amazonicus* were similar in diets across several ranks (Fig. 11); the first, second, and in some cases, third nearest neighbors in dietary niche space were other populations of *C. amazonicus*. Ranked dietary overlaps in diets of *C. septentrionalis* and *P. guianensis* dropped at rank 2 indicating low overlaps with

TABLE 5.—Statistics on tail break frequencies, relative tail lengths, and relative position at which tail autotomy occurred for four species of leaf litter geckos. T_b = tail base, T_r = regenerated portion of tail, and $tail_{est}$ = estimated original tail length. Numbers in parentheses are min–max for relative tail length and position and number broken/total number for % regenerated tails.

Variable	*C. amazonicus*	*C. septentrionalis*	*L. xanthostigma*	*P. guianensis*
% regenerated tails	50.7 (112/221)	45.5 (20/44)	81.8 (9/11)	60.9 (14/23)
Lizards with complete tails				
Tail/SVL (%)	84.1 ± 0.7 (109)	77.8 ± 1.2 (24)	106.0 ± 5.8 (4)	85.9 ± 2.6 (9)
Tail/(SVL + Tail) (%)	45.6 ± 0.2 (109)	43.7 ± 0.4 (24)	51.3 ± 1.4 (4)	46.1 ± 0.8 (9)
Lizards with lost or regenerated tails				
$T_b/tail_{est}$ (%)	24.5 ± 2.4 (112)	49.5 ± 5.6 (19)	36.1 ± 9.3 (10)	44.6 ± 6.1 (14)
$(T_b + T_r)/tail_{est}$ (%)	70.0 ± 2.2 (112)	69.0 ± 5.6 (19)	64.9 ± 7.6 (10)	78.8 ± 3.8 (14)

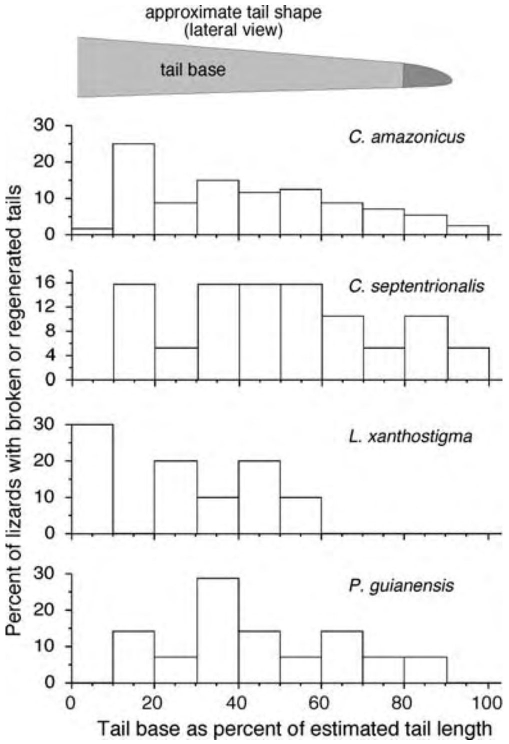


FIG. 7.—Relative positions of tail breaks for four Neotropical leaf litter geckos. To aid interpretation, a drawing above the graph shows a tail that was broken near the tip with a small regenerated portion. Its tail base (the original portion) represents 80% of the original tail length.

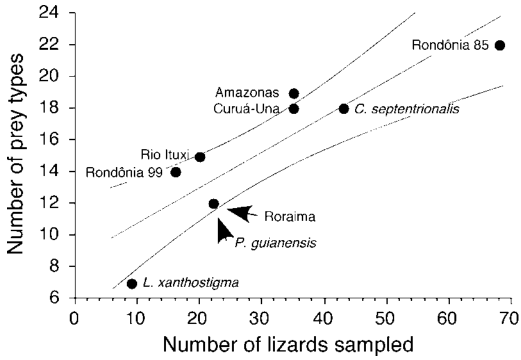


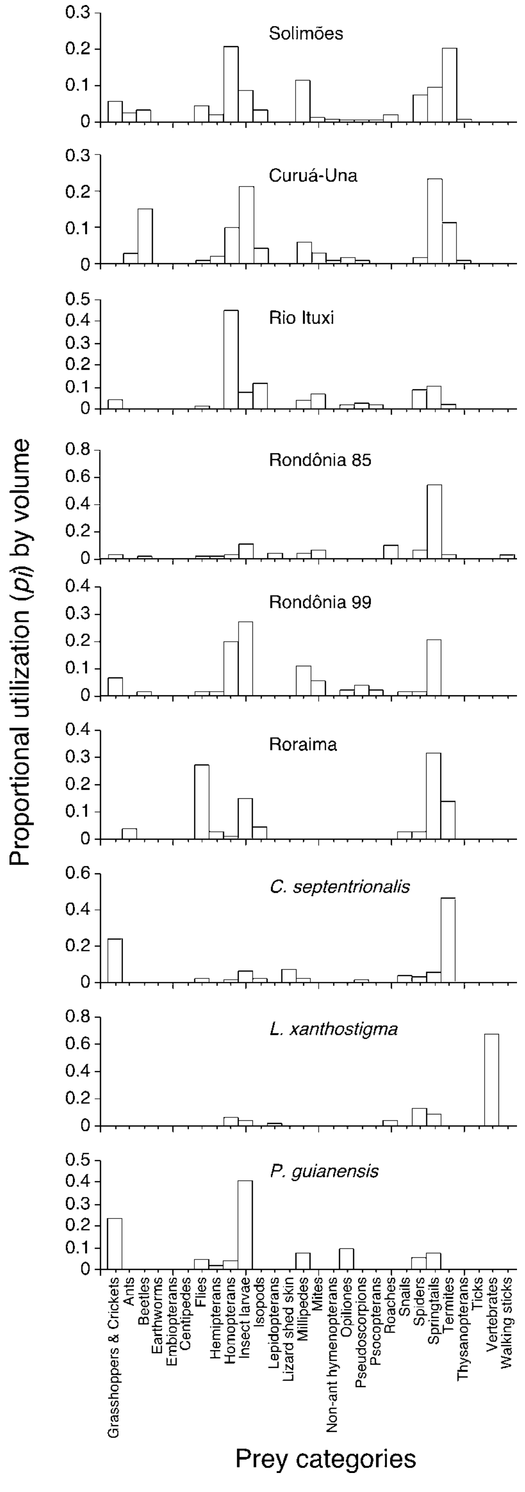
FIG. 8.—Relationship between number of prey types for all species and populations of Neotropical leaf litter geckos and the number of lizards sampled. Each point represents a species or population.

most other species and populations. The diet of *L. xanthostigma* remains different from all others at all but the last rank, most likely a result of the frog eaten by a single individual.

Prey size and the number of prey types used varied among gecko species and populations (Table 7). Lizard body size (SVL) accounted for 86.7% of the variation in mean prey size among species and populations ($F_{1,7} = 53.1$, $P = 0.0002$; mean prey volume = 0.226 [mean SVL] − 4.5; Fig. 12). Larger species and/or populations of leaf litter geckos ate larger prey on average. With all species and populations combined, a significant relationship between $\log_{10}$ of mean prey volume per individual lizard and $\log_{10}$ SVL exists ($R^2 = 0.286$, $F_{1,266} = 108.2$, $P < 0.0001$; Fig. 13). An ANCOVA on $\log_{10}$ of mean prey volume per individual lizard with $\log_{10}$ SVL as the covariate and locality/species as the class variable revealed no differences in slopes ($F_{1,8} = 0.9$, $P = 0.5136$) of the regression models for each species, so we removed the interaction term and reran the ANCOVA. The ANCOVA detected significant differences in mean prey size independent of differences in lizard SVL ($F_{1,8} = 9.7$, $P < 0.0001$). Eighteen of 36 pairwise comparisons were significant ($P < 0.05$, Fisher's PLSD). Only four of those were differences between populations of *C. amazonicus* (Rondônia 85 versus Rondônia 99, Rio Ituxi versus Rondônia 99, Rio Ituxi versus Curuá-Una, and Rondônia 85 versus Curuá-Una). Remaining differences were between species, and the magnitudes of the species differences were greater than those for populations of *C. amazonicus*. Thus, overall species differences in diets were greater than population differences within *C. amazonicus*. Moreover, *C. amazonicus* and *C. septentrionalis* from the same locality had very different diets.

DISCUSSION

Leaf litter geckos in this study are closely related phylogenetically (Kluge, 1995), and, among South American lizards, are rivaled in small body size by only a few sphaerodactyline geckos and a few gymnophthalmids (e.g., *Leposoma*; Vitt and Zani, 1996*a*, 1998*b*). They seem to be most common in relatively undisturbed lowland rainforest, but one species, *C. amazonicus*, can be found in a variety of habitats as long as leaf litter exists on the forest floor and the canopy is dense enough to keep



sunlight from heating up the forest floor. All are active throughout the day regardless of whether sun is available. Occasional nocturnal activity on moonlit nights has been observed in one species (*C. amazonicus*; Hoogmoed and Avila-Pires, 1989). Based on temperatures in the microhabitats where they are found, they appear to be active with body temperatures near 27 C. Leaf litter temperatures in shaded forest fall within the range of microhabitat temperatures recorded for captured geckos whereas leaf litter temperatures in a natural forest treefall were much higher, suggesting that treefalls are not suitable. We found only a few *C. amazonicus* and none of the other species in treefalls, suggesting that they avoid them. The observation that these lizards were found in leaf litter with slightly higher temperatures than hourly means suggests that the geckos are not randomly distributed on the leaf litter, but may select microsites with temperatures slightly higher than average. Most likely, opening the canopy would have negative impact on populations of these tiny geckos because the ground surface would heat up producing a thermally extreme microhabitat, even if leaf litter is present, as is the case for natural treefalls (see Vitt et al., 1998*a*).

The most striking aspect of the morphology of these leaf litter geckos is their small size. In Amazonian rainforest, *Coleodactylus*, *Lepidoblepharus* (e.g., *L. heyerorum*), and *Pseudogonatodes* are the smallest species within their respective lizard assemblages (see also Avila-Pires, 1995). For example, among eight Amazonian localities (not all included in our analyses), *Coleodactylus*, *Pseudogonatodes*, or *Lepidoblepharis* are the smallest species, and, with two exceptions, the next largest species are gymnophthalmids (*Prionodactylus argulus* at three sites, *P. eigenmanni* at one, *Leposoma parietale* at one, and *L. percarinatum* at one). At the Rio Xingu in Pará, *C. amazonicus* is the

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FIG. 9.—Summary of volumetric data on prey types eaten by Neotropical leaf litter geckos. Data are presented as proportional utilization coefficients (p_i) to facilitate comparisons among species and with other published data. Although some prey categories appear to have zero entries across species, trace amounts were present (see Appendix A).

TABLE 6.—Empirically generated dietary overlaps among populations of *C. amazonicus* and species of leaf litter geckos. g_i data were used to calculate overlaps (see Methods). Where locality only is indicated, the species is *Coleodactylus amazonicus*.

Species/population	Amazonas	Curua Una	Rio Ituxi	Rond. 85	Rond. 99	Roraima	*C. sep.*	*L. xanth.*	*P. guian.*
Amazonas	1.000								
Curuá-Una	0.645	1.000							
Rio Ituxi	0.641	0.383	1.000						
Rondônia 85	0.382	0.455	0.264	1.000					
Rondônia 99	0.627	0.584	0.651	0.498	1.000				
Roraima	0.461	0.400	0.194	0.427	0.332	1.000			
C. septentrionalis	0.552	0.256	0.140	0.133	0.208	0.303	1.000		
L. xanthostigma	0.118	0.061	0.117	0.156	0.082	0.050	0.022	1.000	
P. guianensis	0.422	0.379	0.254	0.253	0.644	0.297	0.339	0.066	1.000

smallest and *L. heyerorum* is the second smallest. In Amazonian Roraima, *C. amazonicus* is the smallest and *C. septentrionalis* is the second smallest. Only at the Rio San Juan in Nicaragua is there a smaller species. There, a gecko in the same clade, *Sphaerodactylus millipunctatus*, is smaller than *L. xanthostigma* (see Vitt and Zani, 1998*a*). We suggest that small body size has allowed these geckos to survive as leaf litter inhabitants in a variety of diverse lizard assemblages in tropical Central and South America. Small body size likely provides access to the highly complex structure of leaf litter on the forest floor, thus facilitating escape from some predators. In addition, small body size allows these lizards to take advantage of tiny prey items apparently abundant in leaf litter but not eaten by most larger lizards. These geckos eat some of the smallest invertebrates in the leaf litter (e.g., collembolans, tiny insect larvae, early instars of homopterans; see below). Even lizards in the sister taxon, *Gonatodes*, not only eat larger prey items than any of the leaf litter geckos, but prey that differ taxonomically (e.g., Vitt et al., 1997*b*, 2000).

Significant differences in bauplan are evident as well. All three genera have toe tips that lack the prominent exposed claws found in the sister taxon *Gonatodes* (Fig. 4). Rather, claws are reduced and hidden within a sheath of scales. The shape of the ungual sheath also differs among the three genera. In *Coleodactylus*, one scale makes nearly complete contact with the substrate. In *Lepidoblepharus* and *Pseudogonatodes*, the sheath is bilaterally

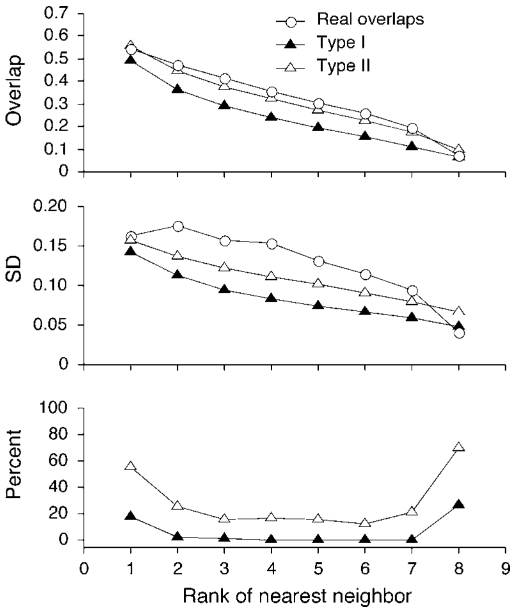

FIG. 10.—Pseudocommunity analysis on volumetric prey data (see Methods).

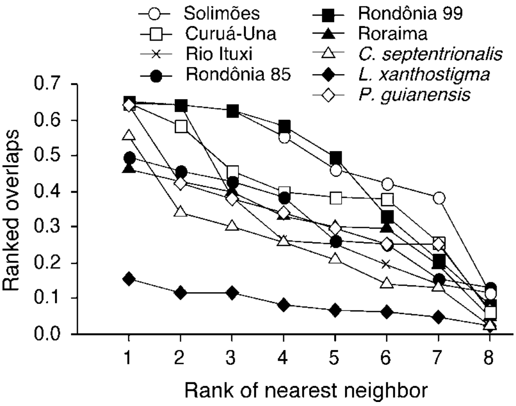

FIG. 11.—Plots by species of ranked overlaps versus the rank of each species' nearest neighbor in dietary niche space.

TABLE 7.—Summary statistics for prey sizes for from six populations of *Coleodactylus amazonicas* and three other leaf litter gecko species. Linear measurements are in mm and volumetric measurements are in mm^3. No. types is the number of prey categories (see Methods). Minimum and maximum values appear in parentheses.

	Coleodactylus amazonicus						Other leaf litter geckos		
Variable	Solimões	Curuá-Una	Rio Ituxi	Rondônia 85	Rondônia 99	Roraima	*C. septent.*	*L. xantho.*	*P. guianensis*
No. lizards	35	35	20	68	16	22	43	9	22
No. types	19	18	15	22	14	12	18	7	12
No. prey	467	370	161	604	258	240	318	23	164
Prey length	1.14 ± 0.04	1.22 ± 0.04	1.58 ± 0.07	1.23 ± 0.03	1.15 ± 0.06	1.33 ± 0.06	2.08 ± 0.1	2.52 ± 0.34	1.54 ± 0.09
	(0.27–6.23)	(0.21–6.15)	(0.17–5.08)	(0.20–7.18)	(0.27–6.44)	(0.45–9.49)	(0.31–10.89)	(1.35–8.91)	(0.20–8.30)
Prey width	0.36 ± 0.01	0.35 ± 0.01	0.47 ± 0.02	0.45 ± 0.02	0.35 ± 0.01	0.44 ± 0.02	0.81 ± 0.03	0.93 ± 0.12	0.43 ± 0.02
	(0.12–2.00)	(0.07–2.14)	(0.10–1.51)	(0.10–6.43)	(0.12–1.54)	(0.17–3.80)	(0.15–3.59)	(0.39–3.02)	(0.10–1.50)
Prey volume	0.23 ± 0.04	0.16 ± 0.03	0.33 ± 0.05	0.31 ± 0.07	0.13 ± 0.02	0.25 ± 0.05	2.23 ± 0.38	2.79 ± 1.82	0.28 ± 0.04
	(0.01–10.81)	(0.01–8.08)	(0.01–3.57)	(0.01–28.79)	(0.01–3.64)	(0.01–7.86)	(0.01–62.09)	(0.11–42.55)	(0.01–4.12)

symmetrical and laterally compressed such that no scale makes broad contact with the substrate. Although the function of these complicated ungular sheaths remains unclear, they may aid in moving across surfaces of leaves that do not provide firm support for the gecko's body. It is possible, for example, that claws would interfere with the gecko's ability to jump from leaf to leaf. *Lepidoblepharis xanthostigma* has a relatively larger head and relatively more streamlined torso than the other genera studied here. *Pseudogonatodes* has the smallest relative head size and is intermediate between *Lepidoblepharis* and *Coleodactylus* in relative body shape. Both species of *Coleodactylus* are the most robust in body shape. At this point, we can only speculate on reasons that underlie these differences. *Coleodactylus* frequently jump from leaf to leaf, and their short, robust body, coupled with their slightly expanded club-like toe tips may facilitate such behavior. We have observed *Lepidoblepharis* "swimming" on the surface film of water where they use lateral undulation to propel themselves forward. Their relatively elongate body may facilitate this type of locomotion. Evolutionarily, a reduction in relative head size has occurred in the more derived species and may facilitate capture of small prey.

We interpret the pseudocommunity analysis of leaf litter gecko diets as follows. First, similarity of measured overlaps at the nearest neighbor rank 1 results from the great degree of similarity in diets among populations of *C. amazonicus*. Common use of a few prey types accounted for most of this similarity. Moreover, this result supports our premise that similarities and differences observed reflect biological differences among the species,

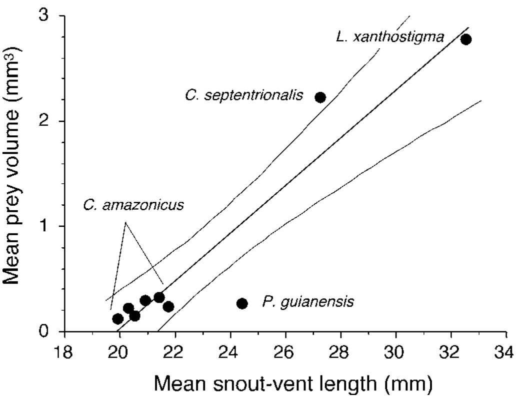

FIG. 12.—Plot of mean prey volumes (species and populations) for Neotropical leaf litter geckos against mean body size (SVL). Each point represents a mean for a species or population.

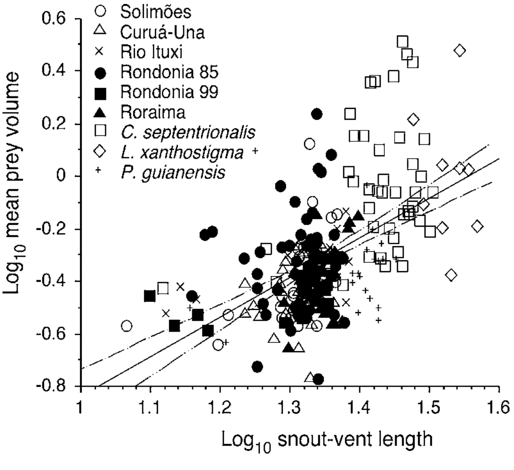

FIG. 13.—Mean prey volumes for individual lizards plotted against their SVL. Variables were log-transformed to approximate normal distributions.

rather than geographical variation in resource use, especially considering that the forests are structurally different and at least some variation in diets is likely associated with variation in seasons and localities in which we sampled.

At lower ranks, measured overlaps were more similar than expected by chance for the type I simulation indicating that even though diets differed among species, a few prey types dominated the diets of all species and populations, but rarer prey types were generally not shared. Although our understanding is limited by small sample size, *L. xanthostigma*, appeared to be a specialist compared with the others (Fig. 8). This may not be an accurate representation because of the disproportionate effect a single, relatively large frog in the diet of one lizard had on the diet summary for the species. Overall, we conclude that these tiny lizards feed on a variety of small prey but, with the exception of *P. guianensis*, seem to prefer collembolans, insect larvae, homopterans, and spiders. Surprisingly few ants were recorded in most leaf litter gecko stomachs even though these are common prey of some dendrobatid frogs in the same leaf litter (e.g., Caldwell and Vitt, 1999; Vitt and Caldwell, 1994). Most ants eaten by dendrobatid frogs, and presumably many ants that occur in leaf litter are myrmicine ants capable of producing noxious chemicals. These leaf litter geckos may detect and avoid ants and other noxious insects using their nasal chemosensory system (Cooper, 1995, 1997; Pianka and Vitt, 2003; Schwenk, 1995). The chemosensory system of scleroglossan lizards is much better developed than that in iguanian lizards, the latter of which are known to eat considerable numbers of ants (e.g., Pianka and Vitt, 2003; Vitt et al., 2003*a*). Some species even specialize on them (e.g., *Phrynosoma*; Pianka and Parker, 1975) indicating that ants are not necessarily bad prey items under the right circumstances.

Even though these lizards appear to eat a wide variety of small prey, it appears unlikely that differences in prey availability alone account for differences among species. In Roraima, *C. amazonicus* and *C. septentrionalis* occur together in leaf litter, yet their diets are very different (see also Ramos, 1979). *Coleodactylus septentrionalis* in Roraima fed mostly on termites whereas *C. amazonicus* in Roraima ate mostly springtails and small flies. Flies were rare in diets of other populations of *C. amazonicus* and thus the difference in diet of the Roraima *C. amazonicus* population may reflect the effects of interactions with *C. septentrionalis* at that site. These data add support to the notion that lizards, especially scleroglossans, are selective in their use of prey and do not simply take a random sample of what is available (see also Pianka, 1986; Vitt and Pianka, 2004).

The observation that larger individuals and species of leaf litter geckos eat larger prey is consistent with studies on other lizards, particularly scleroglossans (e.g., Vitt and Pianka, 2004). Primary exceptions to this postulate are lizard species that specialize on termites or ants such as iguanian lizards in the genera *Plica* and *Uracentron* (e.g., Vitt, 1991; Vitt and Zani, 1996*b*; Vitt et al., 1997*c*).

Prey items eaten by other species of lizards at all sites are considerably different from prey items eaten by these leaf litter geckos (e.g., Vitt and Zani, 1996*a*, 1998*a*,*b*). Indeed, prey items eaten by most other lizards are at least an order of magnitude larger than those eaten by these leaf litter geckos. In addition to potential predator escape advantages discussed above, small body size of these leaf litter geckos may have allowed them to take advantage of prey resources effectively unavailable to most other lizards. If small body size does account for their ability to use tiny prey, small body size in the clade could be a key innovation allowing exploitation of food resources not used by ancestral lineages. The kinds of prey eaten by these lizards may also be restricted to leaf litter microhabitats for the same reason as these lizards. Small body size (in geckos and invertebrates) may put them at risk of hypothermy and desiccation in more open habitats.

Considering the large number of tiny lizards (gekkonids and gymnophthalmids) and frogs (dendrobatids, microhylids, bufonids, and leptodactylids) that inhabit leaf litter in New World tropical forests, it is surprising how few detailed studies exist on their ecology (but see Caldwell and Vitt, 1999; Lieberman, 1986; Vitt and Caldwell, 1994). A recent book focusing on tiny vertebrates (Miller, 1996) identifies lizards as containing among the smallest sauropods that have ever lived. Among lizards, less than 5% of those included in a survey of lizards (Avery, 1996) were less than 30 mm

SVL. However, Avery's estimates are biased because he did not include Central America or any of tropical South America, both of which have many tiny gekkonids and gymnophthalmids. Most of Avery's discussion on the ecology of small size centers on *Anolis* and *Cnemidophorus*, both of which average more than an order of magnitude larger in mass than the geckos studied here. Moreover, most *Anolis* and *Cnemidophorus*, even when they hatch from eggs, are large enough to not be prey of most invertebrates (although tropical spiders, centipedes, and amblypygids can capture some fairly large lizards). Some of the most interesting aspects of the ecology of lizards the size of these geckos will be their potential interactions with invertebrates, both as prey and as competitors. High rates of tail loss that we have reported here suggest that predation attempts are common, and to date we have no information on predator success. However, the possibility exists that some tail loss in males results from social interactions (see Vitt et al., 1974), which would be detectable based on sexual differences in tail loss frequency. Tail loss rates for *C. amazonicus*, the species for which we have sufficient data, are slightly higher for females (52.6%, 51/97) than males (46.8%, 58/124), the opposite of predictions based on the hypothesis that male–male interactions result in tail loss.

Finally, it seems apparent, that like many other rainforest amphibians and reptiles that depend on relatively low temperatures, shade, and leaf litter, alteration of tropical rainforest will undoubtedly have dire consequences for these tiny lizards (e.g., Vitt and Zani, 1996*c*; Vitt et al., 1998*a,b*, 2002, 2003*b*). In addition to reducing inhabitable microhabitats, opening the forest provides access to large, highly active, heliothermic lizards that can prey on small vertebrates (Sartorius et al., 1999; Vitt et al., 1998*a*).

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APPENDIX A

Raw volumetric dietary data for leaf litter geckos. For *C. amazonicus* populations, SO = Solimões, CU = Curua-Una, RI = Rio Ituxi, RO85 = Rondônia 1985, RO98 = Rondônia 1999, and RR = Roraima.

	Coleodactylus amazonicus									
Prey category	SO	CU	RI	RO 85	RO 99	RR	*C. septentrionalis*	*L. xanthostigma*	*P. guianensis*	Totals
Grasshoppers & Crickets	5.89	0	1.89	3.29	2.09	0	165.55	0	10.42	189.13
Ants	2.31	1.55	0	0.46	0	1.92	0.08	0	0	6.32
Beetles	3	8.45	0.03	1.61	0.38	0.03	0	0	0	13.5
Centipedes	0	0	0	0.55	0	0	0.12	0	0	0.67
Earthworms	0	0.09	0	0	0	0	0.82	0	0	0.91
Embiopterans	0	0	0	0.01	0	0	0	0	0	0.01
Flies	4.29	0.23	0.51	1.92	0.3	15.95	9.73	0	1.77	34.7
Hemipterans	1.54	0.95	0	2.11	0.39	1.32	0.8	0	0.5	7.61
Homopterans	21.5	5.61	23.65	5.11	6.72	0.23	5.08	3.78	1.55	73.23
Insect larvae	8.75	12.06	3.67	18.48	9.34	8.69	39.74	2.42	18.49	121.64
Isopods	3.02	2.14	5.81	0	0	2.41	13.56	0	0	26.94
Lepidopterans	0	0	0	6.72	0	0	0	0.94	0	7.66
Lizard shed skin	0	0	0	0	0	0	44.67	0	0	44.67
Millipedes	11.95	3.25	1.73	5.81	3.69	0	14.16	0	3.27	43.86
Mites	0.95	1.52	3.25	10.02	1.75	0.08	1.3	0	0.02	18.89
Non-ant hymenopterans	0.49	0.24	0	0.76	0	0	0	0	0	1.49
Opiliones	0.61	0.77	0.58	0.08	0.64	0	2.99	0	4.1	9.77
Pseudoscorpions	0.53	0.2	1.26	0.87	1.2	0	5.74	0	0	9.8
Psocopterans	0.36	0.07	0.81	0	0.66	0	0	0	0	1.9
Roaches	1.82	0	0	16.18	0	0	0	1.88	0	19.88
Snails	0	0	0.12	0	0.39	1.22	21.58	0	0.03	23.34
Spiders	7.48	0.73	4.58	9.73	0.4	1.2	19.71	7.8	2.28	53.91
Springtails	9.66	13.31	5.01	99.37	6.88	18.66	36.74	4.69	3.25	197.57
Termites	21.47	6.24	0.66	4.42	0	8.14	326.19	0	0	367.12
Thysanopterans	0.47	0.32	0	0	0	0	0	0	0.06	0.85
Ticks	0	0	0	0.06	0	0	0	0	0	0.06
Vertebrates	0	0	0	0	0	0	0	42.55	0	42.55
Walking sticks	0	0	0	0.05	0	0	0	0	0	0.05
Totals	106.09	57.73	53.56	187.61	34.83	59.85	708.56	64.06	45.74	1318.03