Phyllomedusa 6(1):11-21, **2007**

ISSN 1519-1397

Ecology of *Alopoglossus angulatus* and *A. atriventris* (Squamata, Gymnophthalmidae) in western Amazonia

Laurie J. Vitt[1], Teresa Cristina S. Ávila-Pires[2], Maria Cristina Espósito[2], Shawn S. Sartorius[1,4], and Peter A. Zani[3]

[1] Sam Noble Oklahoma Museum of Natural History and Department of Zoology, University of Oklahoma, Norman, Oklahoma 73072, USA.

[2] Coordenação de Zoologia, Museu Paraense Emílio Goeldi/ MCT, Caixa Postal 399, 66017-970, Belém, Pará, Brazil.

[3] Department of Biology, Lafayette College, Easton, PA 18042, USA.

[4] Present Address: U.S. Fish and Wildlife Service, Ecological Services, Billings Sub-Office, 2900 4th Ave. N., Billings, MT 59101 USA.

Abstract

Ecology of *Alopoglossus angulatus* and *A. atriventris* (Squamata, Gymnophthalmidae) in western Amazonia. We studied the ecology of *Alopoglossus angulatus* and *A. atriventris* in western Amazonia. Both species are found in leaf litter of lowland tropical forest, but *A. angulatus* tends to be found near water whereas *A. atriventris* is found in terra firme forest. Both tend to be active in shade on sunny and cloudy days. Body size of adults differs (*A. angulatus* larger), but species differences in size-adjusted morphology are minor. Sexual dimorphism exists in relative head length (males larger) only in *A. atriventris*. Diets are similar, with roaches, spiders, grasshoppers/crickets, and springtails dominating the diet. Overall, these lizards are similar ecologically even though they occur together at many sites. Leaf litter and shaded forest appear to be requisites for survival at the local level.

Keywords: Squamata, Gymnophthalmidae, *Alopoglossus*, microteiid, lizard ecology, Amazônia.

Introduction

Lizards in the family Gymnophthalmidae are among the poorest known ecologically in the New World even though more than 160 species are distributed widely through much of South and Central America (Zug *et al*. 2001, Pough *et al*. 2004). Most are small, and most live in leaf litter (e.g., Duellman 1978, 1987, Ávila-Pires 1995, Vitt and de la Torre 1996, Vitt *et al*. 1998a), but some live along the land-water interface (e.g., Vitt *et al*. 1998b). Nevertheless, some species are widespread in cerrados (seasonally wet savannas) and caatingas (semi-arid regions) where they often occur at high density (Moraes 1993, Vitt 1995, Rodrigues

Received 27 October 2006.
Accepted 11 April 2007.
Distributed June 2007.

1996, Colli *et al*. 2002). Reduced limbs and body elongation have evolved several times independently, and some species are semi-aquatic (Beebe 1945, Hoogmoed 1973, Ávila-Pires 1995, Vitt and Ávila-Pires 1998, Pianka and Vitt 2003). Their evolutionary relationships are just beginning to be understood (Pellegrino *et al*. 2001, Doan 2003, Castoe *et al*. 2004, Doan and Castoe 2004, Rodrigues *et al*. 2005).

We describe in detail the ecology of two rainforest species of *Alopoglossus* studied in western Amazonia. *Alopoglossus angulatus* is widespread in most of Amazonia, while *A. atriventris* occurs only in the western part. Both are found in leaf litter and neither has been well studied. Brief summaries of some of the data presented here (e.g., mean SVL, general diet summary) have been used in other analyses (Vitt *et al*. 2003a, Vitt and Pianka 2005), but thorough data presentation and analyses have not appeared previously. We describe habitat, microhabitat, and the thermal environments used by these lizards, their size, morphology, and sexual dimorphism, and their diets. These data should prove useful for continuing phylogenetic analyses of ecological data and should provide a background for these species in assessing habitats for conservation.

Materials and Methods

We collected data on a total of 59 *A. angulatus* and 22 *A. atriventris* at five localities in the western Amazon rainforest: (1) northeastern Ecuador in Sucumbíos Province (0°0’, 76°10’ W) near the Rio Cuyabeno (hereafter “Cuyabeno”) during February – April 1994 (rainy season); (2) approximately 5 km N of Porto Walter, Acre (hereafter “Rio Juruá”), (8°15’ S, 72°46’ W) in undisturbed terra firme rainforest of the Juruá River Basin during February–April 1996 (rainy season); (3) the Rio Ituxi in the southwestern portion of Amazonas (hereafter “Rio Ituxi”) (8°20’ S, 65°43’ W) in moderately disturbed rain forest during January–April 1997 (rainy season); (4) approximately 40 km E of Guajará-Mirim, Rondônia, Brazil (hereafter “Rondônia”) (10°19’ S, 64°34’ W) in tropical lowland forest during January–March 1999 (rainy season); and (5) south of the Amazon River and nearly due south of Manaus, Amazonas (hereafter “Rio Solimões”) (3°20’ S, 59°04’ W) in moderately disturbed rainforest during December–January, 1998-1999 (rainy season) (Figure 1).We combined data from all sites to provide this general account of the ecology of these lizards.

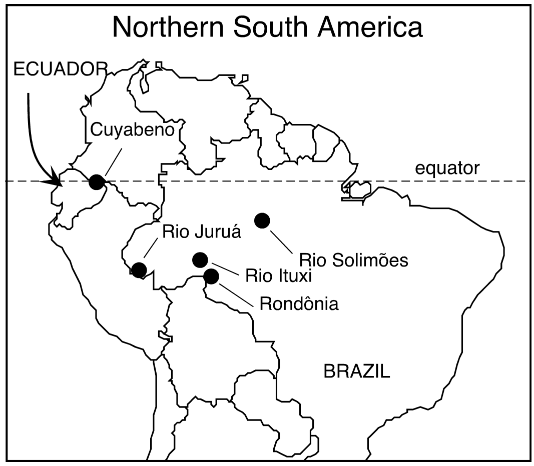

Figure 1 - Map showing localities in which *Alopoglossus* were studied.

For most lizards observed or captured, we recorded habitat type, microhabitat, whether it was sunny or cloudy, exposure of lizards, and time of day. We condensed our original seven microhabitat categories to five: ground, inside folded palm frond, leaf litter, tree trunk, and water. Likewise we condensed our original 18 habitat categories (all localities combined) to five broad categories: stream (linear structure with banks), swamp (includes pond edge), undisturbed terra firme forest, disturbed terra firme forest, and low primary forest (holds water during and after rains—includes wet palm forest). Exposure categories were: shade, filtered sun, and, full sun (full exposure to sky regardless of whether it was sunny or cloudy).

We were only able to measure cloacal temperatures (T_b) for two individual *A. atriventris*. However, we measured substrate (microhabitat) and air temperatures at the exact spot where many lizards were captured. Because of the small size of these lizards (thus low thermal inertia) and the observation that most were in shade or filtered sun (avoiding heat gain), these likely approximate T_b. We assigned time of day each lizard was observed to hourly categories for analysis and compared species activity periods with a Wilcoxon Signed Rank test.

Following capture, lizards were taken to our field laboratories, euthanized following standard procedures (Anonymous 1987), and the following morphological measurements were taken: snout-vent length (SVL), length of tail base (original portion), and regenerated tail (if any) to 1.0 mm; total body mass to 0.01 g with Acculab digital field balances; head width (widest point), head length (tip of snout to anterior edge of tympanum), head height (greatest height), body width, body height, foreleg length (body posterior to limb to tip of longest toe), and hindleg length (body anterior to limb to tip of longest toe) to 0.01 mm with digital calipers. Lizards were then fixed in 10% formalin and stored in 10% formalin until they could be moved to 70% ethanol (usually 3 days to 1 month, depending on locality). To quantify sexual dimorphism (if any), we first compared size (SVL) of lizards 40 mm SVL and larger (all sexually mature) with a Mann-Whitney U test. We included lizards ≥ 40 mm to be absolutely certain that no juveniles were included in the analysis. To test for species and sexual differences in size-adjusted morphology, we first $\log_{10}$-transformed all morphological variables. We then performed a MANCOVA with log-SVL as the covariate and species and sex as class variables to determine whether an overall model effect existed. We then used a stepwise discriminate analysis on regression residuals keeping only variables contributing significantly to the model ($P < 0.05$). Pseudoprobabilities generated by stepwise regression were used to indicate variables that contributed most to the relationship.

Later, stomachs were removed and reproductive organs were examined. Stomach contents were spread on a Petri dish, prey items carefully separated, identified to family level when possible, and measured for length and width. We later grouped prey into 20 broad categories, similar to those used by others (e.g., Pianka and Vitt 2003). We considered ants as a category separate from other hymenopterans because their collective morphotype differs from most others. Because individual prey items were compressed into a bolus approximating the shape of a prolate spheroid, we used the following formula to estimate individual prey volumes:

$$V = \frac{4}{3}\pi\left(\frac{length}{2}\right)\left(\frac{width}{2}\right)^2$$

Alternative methods exist for determining prey sizes and not all methods produce comparable results (Magnusson *et al*. 2003). We encourage investigators to carefully weigh the benefits of alternative methods when designing diet studies within the context of equipment and time constraints. We used the program BugRun, a 4th Dimension®-based analysis to produce dietary summaries, calculate mean prey size (length, width, and volume) for each lizard, estimate total prey volume, and calculate niche breadth using the inverse of Simpson's (1949) diversity measure (Pianka 1973, 1986):

$$\beta = \frac{1}{\sum_{i=1}^{n} p_i^2}$$

where *p* is the proportional utilization of each prey type *i* and Niche breadth values (β) vary from 1 (exclusive use of a single prey type) to *n* (equal use of all prey). We $\log_{10}$- transformed all quantitative data to normalize distributions for further analyses.

Linear regression on log_{10}-transformed variables determined whether prey size and number of prey eaten varied with lizard body size. ANCOVAs with log_{10} SVL as the covariate and sex as the class variable were used to determine whether prey size or number of prey eaten differed between species or sexes. Plots of log_{10} -stomach volume versus log_{10}-SVL determined the relationship between stomach volume and lizard size. Relative fullness of lizards was estimated by totaling volume of all prey for each stomach and regressing these values on SVL. Percentage of lizards with prey in the stomachs was calculated by dividing number of lizards containing prey by the total sample size and multiplying by 100 (Huey *et al*. 2001).

Most statistical analyses were performed with JMP 6.0 or StatView (both marketed by SAS Inst.). Voucher specimens were deposited in the herpetology collection of the Museu Paraense E. Goeldi (MPEG) in Belém (Brazil), the Museo de Zoología de la Pontificia Universidad Católica (QCAZ) in Quito (Ecuador) and the Sam Noble Oklahoma Museum of Natural History (OMNH) in Norman (USA).

Results

General ecology

Both species of *Alopoglossus* are small, dark colored, and difficult to see until they move when in leaf litter (Figure 2). Most *A. angulatus* were found in habitats associated with water whereas most *A. atriventris* were found in terra firme forest (Figure 3). Nevertheless, differences in habitat use were not significant, although marginal (Wilcoxon signed-rank test, Z = -1.83, P = 0.068). A vast majority of individuals of both species were first found in leaf litter (Figure 4) and no difference in microhabitat occurrence was detected (Wilcoxon signed-rank test, Z = -1.34, P = 0.180). No *A. angulatus* were observed above leaf litter. Only two *A. atriventris* were observed above leaf litter. Both were on the base of tree trunks in the forest, less than 1 m off ground (both at 0.6 m). Trunk diameters were 16 and 40 cm. Thirty-three of 58 (56.9%) *A. angulatus* and 14 of 22 (63.6%) *A. atriventris* were found on cloudy days, the remainder on sunny days. Of those, 41 (70.7%) *A. angulatus* and 13 (59.1%) *A. atriventris* were in shade, 22 (27.5%) *A. angulatus* and 15 (25.9%) *A. atriventris* were in filtered sun, and 2 (3.5%) *A. angulatus* and 2 (3.4%) *A. atriventris* were in full sun exposure. The two *A. angulatus* in full sun exposure were active on sunny days but the two *A. atriventris* in full sun exposure were active on cloudy days. T_b of two *A. atriventris* for which we had data averaged 26.1°C (24.9, 27.2°C). T_{ss} and T_a for 10 *A. angulatus* averaged 25.1 ± 0.3°C (22.9–26.6°C) and 25.9 ± 0.4°C (22.8–28.2°C), respectively and for 10 *A. atriventris*, 25.7 ± 0.4°C (23.5–28.0°C) and 26.6 ± 0.4°C (23.8–29.2°C), respectively. The small differences in T_{ss} and T_a between species were not significant (ANOVAs, $F_{1,18}$ = 0.79, P = 0.79 and $F_{1,18}$ = 1.24, P = 0.28).

Individuals of both species were observed active throughout the day with peak activity occurring in mid-day for *A. angulatus* and late morning for *A. atriventris* (Figure 5). Differences in activity periods were significant (Wilcoxon Signed Rank test, Z = –2.37, P = 0.018).

Morphology and sexual dimorphism

Among adults (SVL = 40 mm), *Alopoglossus angulatus* reach larger overall size (SVL) than *A. atriventris* (Figure 6) and species differences for both sexes are significant (males, Mann-Whitney U test, Z = –2.49, P = 0.012; females, Mann-Whitney U test, Z = –2.76, P = 0.006). No detectable sexual size dimorphism exists in adults of *A. angulatus* (Mann-Whitney U test, Z = –1.31, P = 0.189) or *A. atriventris* (Mann-Whitney U test, Z = –0.75, P = 0.455). Adult *A. angulatus* averaged 55.4 ± 1.6 mm SVL and

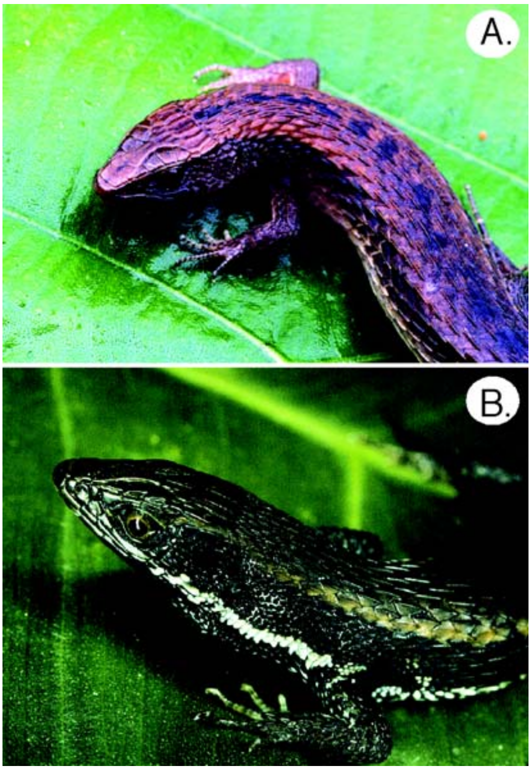

Figure 2 - (A) Female *Alopoglossus angulatus* from the Rio Formoso, Rôndonia, Brazil collected in 1998 (OMNH 37337). (B) Male *Alopoglossus atriventris* from Cuyabeno, Ecuador collected in 1994 (OMNH 36439).

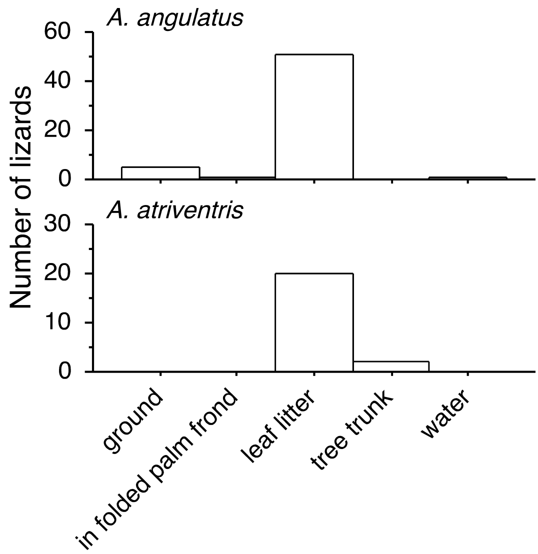

Figure 3 - Habitat use by *Alopoglossus angulatus* and *A. atriventris* in western Amazonia.

weighed 4.09 ± 0.29 g and adult *A. atriventris* averaged 44.9 ± 2.9 mm SVL and weighed 2.02 ± 0.42 g. Our MANCOVA on morphological variables revealed a significant model effect (Wilks' Lambda = 0.008, F = 54.5, P < 0.001). We then applied the stepwise discriminate analysis on regression residuals to test for species differences in size-adjusted morphological variables. Only one variable, relative head length was retained (P < 0.05). Even though species differed in relative head length, 32.5% (28 of 86) of individuals were misclassified (wrong species) based on relative head length. We conclude that species differences in overall morphology likely have little ecological significance. We then re-ran the MANCOVA on each species separately, calculated residuals restricted to regressions within each species, and applied the stepwise discriminate analysis manually removing nonsignificant morphological variables to examine sexual differences in morphology. For *A. angulatus*, the model effect of the MANCOVA was significant (Wilks' Lambda = 0.008, F = 68.1, P < 0.001). After stepwise reduction of variables, relative mass and relative tail length remained significant (F values < 0.043). Nevertheless, 34.7% (18 of 49) of lizards were misclassified (wrong sex). For *A. atriventris*, the model effect of the MANCOVA was also significant (Wilks' Lambda = 0.005, F = 66.6, P < 0.001). After stepwise reduction of variables, only relative head length remained significant (F < 0.001). Seven of 37 (18.9%) were misclassified. We conclude that even though sexual differences exist in both species,

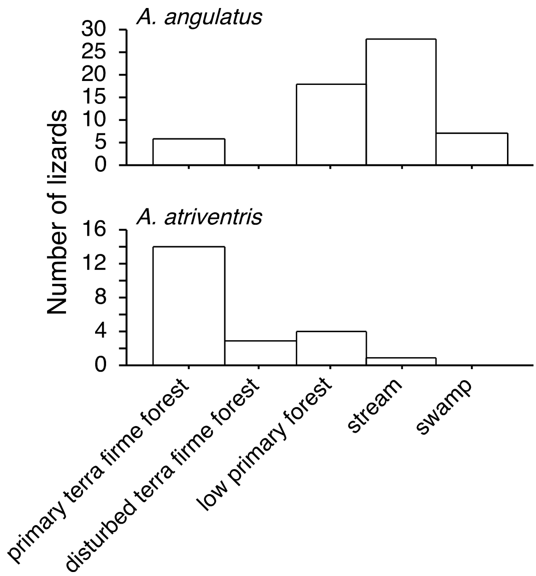

Figure 4 - Microhabitat use by *Alopoglossus angulatus* and *A. atriventris* in western Amazonia.

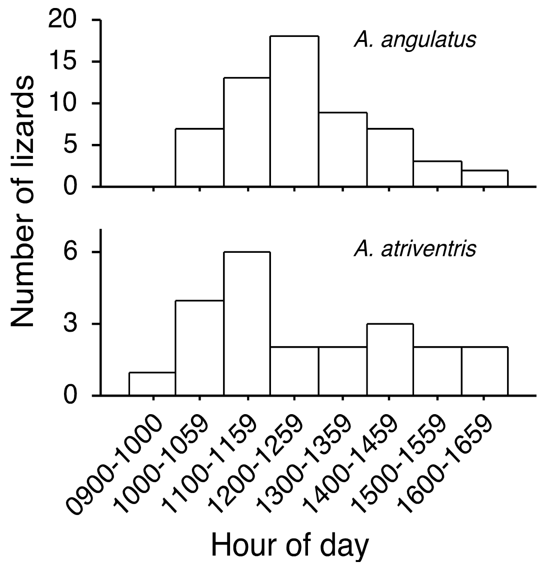

Figure 5 - Number of *Alopoglossus angulatus* and *A. atriventris* observed during each hour of the day.

they are not reliable for sexing individuals and sexual dimorphism is not impressive in *A. angulatus*. However, sexual dimorphism in relative head length occurs in *A. atriventris*.

Composition of the diet

The diet of both *Alopoglossus* species is dominated volumetrically by a combination of roaches, spiders, and grasshoppers/crickets (Table 1). These three categories account for 92.3% of the diet of *A. angulatus* and 94.3% of the diet of *A. atriventris* volmetrically. The primary difference between the two is that *A. angulatus* ate relatively more spiders and *A. atriventris* ate relatively more grasshoppers/ crickets volumetrically. Numerically, spiders, springtails (Collembola), and grasshoppers/ crickets dominate the diets of both species. These four prey categories account for 45.7% of the diet of *A. angulatus* and 53.6% of the diet of *A. atriventris* numerically. Niche breadths were similar for numerical (6.99 and 5.93 for *A. angulatus* and *A. atriventris*, respectively) and volumetric (2.55 and 2.47 for *A. angulatus* and *A. atriventris*, respectively) data.

One-hundred and seventy-seven prey items from 39 *A. angulatus* (79.6% of 49 sampled) averaged 3.55 ± 0.33 (0.2–43.47) mm in length, 1.38 ± 0.1 (0.12–7.7) mm in width, and 18.02 ± 4.13 (0.01–375.32) mm^3 in volume. Sixty-nine prey items from 19 A. *atriventris* (51.4% of 37 sampled) averaged 3.92 ± 0.41 (0. (79.6% of 49 sampled) 28–12.27) mm in length, 1.49 ± 0.19 (0.15–7.28) mm in width, and 22.2 ± 6.57 (0.01–326.89) mm^3 in volume. Significant relationships existed between log_{10}-transformed measures of prey size (individual means of prey length, width, and volume) and log_{10}-SVL (R^2 varied from 0.27–0.37 , P values varied from < 0.0001 to 0.001), log_{10}-number of prey (R^2 = 0.078, $F_{1,56}$ = 5.79, P = 0.0194), log_{10}-total prey volume (R^2 = 0.239, $F_{1,56}$ = 18.88, P = 0.0194). An ANCOVA on log_{10}- mean prey volume with log_{10}-SVL as the covariate revealed no significant interactions between species*sex,

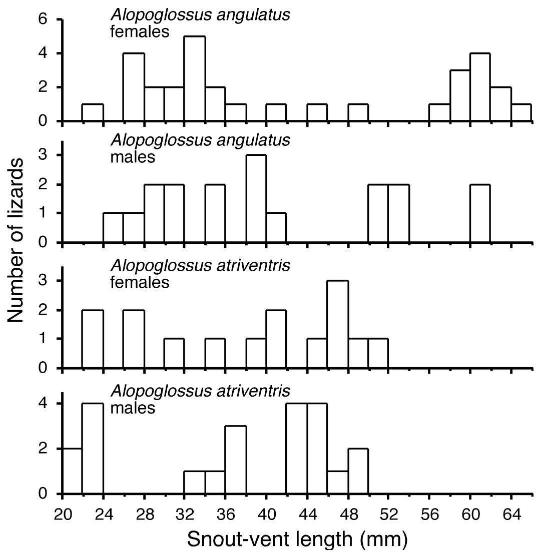

Figure 6 - Size distributions of male and female *Alopoglossus angulatus* and *A. atriventris* from western Amazonia.

sex*log_{10}-SVL, species* log_{10}-SVL, or species*sex* log_{10}-SVL (P values > 0.23) so these were removed from the ANCOVA. The resulting ANCOVA revealed no effect of species or sex on log_{10}- mean prey volume ($F_{1,54}$ = 0.83, P = 0.365 and $F_{1,54}$ = 2.51, P = 0.119). An ANCOVA on log_{10}- number of prey per stomach with log_{10}-SVL as the covariate revealed no significant interactions between species*sex, sex*log_{10}-SVL, species* log_{10}-SVL, or species*sex* log_{10}-SVL (P values > 0.21) so these were removed from the ANCOVA. The resulting ANCOVA revealed no effect of species or sex on log_{10}- number of prey ($F_{1,54}$ = 0.24, P = 0.625 and $F_{1,54}$ = 0.28, P = 0.601). An ANCOVA on log_{10}-total prey volume with log_{10}-SVL as the covariate revealed no significant interactions between species*sex, sex*log_{10}-SVL, species* log_{10}-SVL, or species*sex* log_{10}-SVL (P values > 0.13) so these were removed from the ANCOVA. The resulting ANCOVA revealed no effect of species or sex on log_{10}-total prey volume ($F_{1,54}$ = 1.35, P = 0.250 and $F_{1,54}$ = 1.98, P = 0.165).

Discussion

Both *A. angulatus* and *A. atriventris* occur in lowland tropical forest of the Amazon Basin (Ávila-Pires 1995). These small lizards are most often found in shaded or partially shaded leaf litter on the forest floor, but *A. angulatus* appears to have a slight tendency to be active near water whereas *A. atriventris* is usually active in leaf litter of terra-firme forest. Individuals of both species are active on sunny and cloudy days. Based largely on microhabitat temperature data (T_{ss} and T_a), these lizards occur in relatively cool (23–29°C) microhabitats. Both species were active throughout the day, but peak activity in *A. atriventris* was earlier (late morning) than in *A. angulatus*. This difference may reflect hourly differences in environmental temperatures in terra firme forest (warm earlier) than in microhabitats closer to water (warm later). The possibility also exists that considerable activity occurs underneath or within leaf litter, and if so, then some activity might not have been observed.

Although *A. angulatus* and *A. atriventris* differ in SVL, they differ little in size-adjusted morphology. Heads of *A. atriventris* are relatively longer than those of *A. angulatus*, but this species difference may simply reflect effects of sexual dimorphism in head length of *A. atriventris* on the species comparison. Differences in morphology of male and female *A. atriventris* suggest males and females have responded differently to either natural selection or sexual selection. Larger heads in male lizards is common and cuts across many taxa globally. Increased head size of males is usually attributed to sexual selection in which males with relatively larger heads have a competitive advantage over males with relatively smaller heads in male–male interactions (e.g., Carothers 1984, Cooper and Vitt 1989, Anderson and Vitt 1990). Nevertheless, causes of sexual dimorphism are complex and can include both proximate (e.g., growth differences; resource use) and ultimate (sexual selection) causes

Table 1 - Diets of 39 *Alopoglossus angulatus* and 19 *A. atriventris* from western Amazonia. No. is number of prey of a given category, % No. is number of prey in a category divided by the total number of prey X 100, Vol. is volume of prey of a given category, % Vol. is volume of prey in a category divided by the total volume of prey X 100, and Freq. is the number of lizards that ate a particular prey type.

Prey category	Lizard species									
	Alopoglossus angulatus					*Alopoglossus atriventris*				
	No.	% No.	Vol.	% Vol.	Freq.	No.	% No.	Vol.	% Vol.	Freq.
Roaches	19	10.73	1708.67	53.58	16	7	10.14	887.52	57.95	6
Grasshoppers/ Crickets	8	4.52	237.55	7.45	7	9	13.04	316.25	20.65	7
Mantids and Phasmids	–	–	–	–	–	2	2.90	68.24	4.46	2
Homopterans	10	5.65	70.85	2.22	8	1	1.45	5.61	0.37	1
Beetles	4	2.26	12.76	0.40	4	1	1.45	1.12	0.07	1
Flies	12	6.78	3.31	0.10	7	2	2.90	0.16	0.01	2
Hemipterans	2	1.13	0.40	0.01	2	–	–	–	–	–
Hymenopte-rans (non-ant)	1	0.56	0.08	0	1	–	–	–	–	–
Ants	3	1.69	13.96	0.44	3	–	–	–	–	–
Lepidopterans	1	0.56	0.19	0.01	1	–	–	–	–	–
Springtails	24	13.56	5.00	0.16	12	14	20.29	0.71	0.05	4
Psocopterans	1	0.56	0.04	0	1	1	1.45	0.41	0.03	1
Larvae, eggs, pupae	5	2.82	42.50	1.33	4	3	4.35	8.39	0.55	2
Spiders	54	30.51	997.57	31.28	25	21	30.43	240.61	15.71	11
Mites	6	3.39	0.08	0	4	3	4.35	0.02	0	2
Pseudo-Scorpions	1	0.56	0.43	0.01	1	2	2.90	1.31	0.09	1
Opiliones	11	6.21	15.64	0.49	7	–	–	–	–	–
Isopods	5	2.82	26.86	0.84	4	1	1.45	0.10	0.01	1
Millipedes	–	–	–	–	–	1	1.45	0.49	0.03	1
Molluscs	9	5.08	19.44	0.61	6	1	1.45	0.64	0.04	1
Plant material	1	0.56	33.75	1.06	1	–	–	–	–	–
SUMS	177	100.00	3189.08	100.00	–	–	100.00	1531.58	100.00	–
Niche breadths		6.99		2.55		69	5.93		2.47	

(Schoener 1967, Watkins 1996, Schwarzkopf 2005) and are difficult to sort out based on short-term sampling studies.

Diets and niche breadths of these lizards are similar. Roaches, spiders, grasshoppers/crickets, and springtails are predominant prey types numerically and volumetrically. Although all of these are likely common in Amazon rainforest leaf litter, diets of syntopic leaf litter lizards and frogs differ considerably from diets of these two gymnophthalmids. For example, the tiny leaf-litter geckos *Coleodactylus amazonicus*, *C. septentrionalis*, *Lepidoblepharis xanthostigma*, and *Pseudogonatodes guianensis* feed primarily on springtails, homopterans, termites, insect larvae, and small spiders (Vitt *et al.* 2005). The most similar diets are found in some gymnophthalmids of the genus *Cercosaura* (formerly in *Prionodactylus*; Doan and Castoe 2005). For this discussion, we do not accept Doan's (2003) synonomy of *C. oshaughnessyi* and *C. argulus* (see Vitt *et al.* 2003b). Diets of *C. oshaughnessyi* and *C. eigenmanni* are dominated by grasshoppers/crickets, roaches, insect larvae, and spiders, a diet quite similar to that of the two species of *Alopoglossus*. We suggest that gymnophthalmids in general have diets that are somewhat more similar to each other than to lizards in more distant clades, likely reflecting dietary shifts away from other clades deep in their evolutionary history. These dietary shifts are likely associated with historic differences in morphology (including size) and behavior among clades. One of the historic dietary shifts identified by Vitt and Pianka (2005) was in the ancestor to gymnophthalmids and included data presented here. Reasons that varying numbers of species of gymnophthalmids can coexist in the same microhabitats (leaf litter) and feed on similar prey remain obscure, but the possibility exists that resources are rarely limiting in the structurally diverse mat of leaf litter on the floor of Neotropical forests.

Finally, it seems clear, as shown in studies of other small vertebrates of the Amazon rainforest, that the thick mat of leaf litter on the forest floor and the nearly continuous canopy are critical structural components of the habitat allowing these animals to persist. Leaf litter provides a structurally complex microhabitat filled with a diversity of small prey items, likely resulting in a superabundance of prey relative to lizard abundance (at least part of the time) and refuge from predators. The closed canopy creates a thermal environment allowing small lizard species that operate at relatively low temperatures to forage and move about with low risk of hyperthermy. Their small body size and thus low thermal inertia would place them at risk when clearings (natural or unnatural) allow sun access to the forest floor.

Acknowledgments

First, we thank all of the people who either helped coordinate our research in one or more areas or collaborated in data collection. They are: W. E. Magnusson, A. Lima, M. C. Araújo, J. P. Caldwell, V. Oliveira, M. Scheffer, and L. Coloma. Brazilian agencies contributing to logistics or research and collecting permits include SOS Amazônia and the Acre Union of Seringueiros in Rio Branco, the Instituto Nacional de Pesquisas da Amazonica (INPA), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, Portaria MCT no. 170, de 28/09/94), the Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA, permit no. 073/94-DIFAS), the Parque Estadual de Guajara-Mírim in Rondônia, and the Museu Paraense E. Goeldi in Belém. Brazilian research was conducted under a research convenio between the Sam Noble Oklahoma Museum of Natural History and the Museu Paraense E. Goeldi. We thank L. Coloma for coordinating our Amazonian research in Ecuador and the QCAZ in Quito for logistic support. The Estación Biológica de Cuyabeno in Ecuador was made available by the Universidad Católica and permits were issued by Ministry of Agriculture and Livestock of the Republic of Ecuador. All animals were treated in accordance with federal, state, and university regulations (Animal Care Assurance 73-R-100, approved 8 November 1994). We thank American and Varig Airlines for allowing excess baggage. This material is based partially upon work supported by the National Science Foundation under Grant Numbers DEB-9200779 and DEB-9505518 to LJV and J. P. Caldwell. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the author(s) and do not necessarily reflect the views of the National Science Foundation.

References

Anderson, R. A. and L. J. Vitt. 1990. Sexual selection versus alternative causes of sexual dimorphism in teiid lizards. *Oecologia (Berlin) 84*: 145–157.

Anonymous. 1987. *Guidelines for the use of live amphibians and reptiles in field research*. Publication of the American Society of Ichthyologists and Herpetologists, the Herpetologists' League, and the Society for the Study of Amphibians and Reptiles. 14 pp.

Ávila-Pires, T. C. S. 1995. Lizards of Brazilian Amazonia (Reptilia: Squamata). *Zoologische Verhandelingen 299*: 1–706.

Beebe, W. 1945. Field notes on the lizards of Kartabo, British Guiana, and Caripito, Venezuela. Part 3. Teiidae, Amphisbaenidae and Scincidae. Zoologica 30: 7–32.

Carothers, J. H. 1984. Sexual selection and sexual dimorphism in some herbivorous lizards. *American Naturalist 124*: 244–254.

Castoe, T. A., T. A. Doan and C. L. Parkinson. 2004. Data partitions and complex models in Bayesian Analysis: the phylogeny of gymnophthalmid lizards. *Systematic Biology 53*: 448–469.

Colli, G. R., R. P. Bastos and A. F. B. Araujo. 2002. The character and dynamics of the Cerrado herpetofauna. Pp 223–241 *in* P. S. Oliveira and R. J. Marquis (eds.), *The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna*. New York. Columbia University Press.

Cooper, W. E., JR. and L. J. Vitt. 1989. Sexual dimorphism of head and body size in the iguanid lizard *Sceloporus undulatus*: paradoxical results. *American Naturalist 133*: 729–735.

Doan, T. M. 2003. A new phylogenetic classification for the gymnophthalmid genera *Cercosaura*, *Pantadoctylus* and *Prionodactylus* (Reptilia: Squamata). *Zoological Journal of the Linnean Society 137*: 101–115.

Doan, T. A. and T. A. Castoe. 2005. Phylogenetic taxonomy of the Cercosaurini (Squamata: Gymnophthalmidae), with new genera for species of *Neusticurus* and *Proctoporus*. *Zoological Journal of the Linnean Society 143*: 405–416.

Duellman, W. E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. *Miscellaneous Publications of the Museum of Natural History of the University of Kansas 65*: 1–352.

Duellman, W. E. 1987. Lizards in an Amazonian rain forest community: resource utilization and abundance. *National Geographic Society Research 3*: 489–500.

Hoogmoed, M. S. 1973. Notes on the herpetofauna of Surinam. IV. The lizards and amphisbaenians of Surinam. *Biogeographica 4*: 1–419.

Huey, R. B., Pianka, E. R. and Vitt, L. J. 2001. How often do lizards 'run on empty'? *Ecology 82*: 1–7.

Magnusson, W. E., A. P. Lima, W. A. Silva, and M. C. Araújo. 2003. Use of geometric forms to estimate volume of invertebrates in ecological studies of dietary overlap. *Copeia 2003*: 13–19.

Moraes, R. C. 1993. Ecologia das especies de *Calyptommatus* (Sauria, Gymnophthalmidae) e partilha de recursos com outros dois microteiídeos. Unpublished M.Sc. Dissertation. Universidade de São Paulo, Brazil.

Pellegrino, K. C. M., M. T. Rodrigues, Y. Yonenaga-Yassuda, and J. W. Sites Jr. 2001. A molecular perspective on the evolution of South American microteiid lizards (Squamata, Gymnophthalmidae), and a new classification for the family. *Biological Journal of the Linnean Society 74*: 317–340.

Pianka, E. R. 1973. The structure of lizard communities. *Annual Review of Ecology and Systematics 4*: 53–74.

Pianka, E. R. 1986. *Ecology and natural history of desert lizards. Analyses of the ecological niche and community structure.* Princeton. Princeton University Press. 222 pp.

Pianka, E. R. and L. J. Vitt. 2003. *Lizards: windows to the evolution of diversity*. Berkeley. The University of California Press. 348 pp.

Pough, F. H., R. M. Andrews, J. E. Cadle, M. L. Crump, A. H. Savitzky, and K. D. Wells. 1998. *Herpetology*. Upper Sadler River. Prentice Hall. 577 pp.

Rodrigues, M. T. 1996. Lizards, snakes, and amphisbaenians from the quaternary sand dunes of the middle Rio São Francisco, Bahia, Brazil. *Journal of Herpetology 30*: 513–523.

Rodrigues, M. T., E. M. X. Freire, K. C. M. Pellegrino, and J. W. Sites Jr. 2005. Phylogenetic relationships of a new genus and species of microteiid lizard from the Atlantic Forest of north-eastern Brazil (Squamata, Gymnophthalmidae). *Zoological Journal of the Linnean Society 144*: 543–557.

Schoener, T. W. 1967. The ecological significance of sexual dimorphism in size in the lizard *Anolis conspersus*. *Science 155*: 474–476.

Schwarzkopf, L. 2005. Sexual dimorphism in body shape without sexual dimorphism in body size in water skinks (*Eulamprus quoyii*). *Herpetologica 61*: 116–123.

Simpson, E. H. 1949. Measurement of diversity. *Nature 163*: 688.

Vitt, L. J. 1995. The ecology of tropical lizards in the Caatinga of northeast Brazil. *Occasional Papers of the Oklahoma Museum of Natural History 1*: 1–29.

Vitt, L. J. and T. C. S. Ávila-Pires. 1998. Ecology of two sympatric species of *Neusticurus* (Sauria: Gymnophthalmidae) in the western Amazon of Brazil. *Copeia 1998*: 570–582.

Vitt, L. J. and E. R. Pianka. 2005. Deep history impacts present-day ecology and biodiversity. *Proceedings of the National Academy of Sciences 102*: 7877–7881.

Vitt, L. J. and S. de la Torre. 1996. *Guia para la Investigacion de las Lagartijas de Cuyabeno: A research guide to the lizards of Cuyabeno*. Quito. Museo de Zoologia (QCAZ), Centro de Biodiversidad y Ambiente, Pontificia Universidad Catolica del Ecuador, Monograph #1.

Vitt, L. J., E. R. Pianka, J. W. E. Cooper and K. Schwenk. 2003a. History and the global ecology of squamate reptiles. *American Naturalist 162*: 44–60.

Vitt, L. J., S. S. Sartorius, T. C. S. Ávila-Pires, and M. C. Espósito. 1998a. Use of time, space, and food by the gymnophthalmid lizard *Prionodactylus eigenmanni* from the western Amazon of Brazil. *Canadian Journal of Zoology 76*: 1681–1688.

Vitt, L. J., P. A. Zani, T. C. S. Ávila-Pires, and M. C. Espósito. 1998b. Geographical ecology of the gymnophthalmid lizard *Neusticurus ecpleopus* in the Amazon rain forest. *Canadian Journal of Zoology 76*: 1671–1680.

Vitt, L. J., T. C. S. Ávila-Pires, P. A. Zani, M. C. Espósito, and S. S. Sartorius. 2003b. Life at the Interface: Ecology of *Prionodactylus oshaughnessyi* in the western Amazon with comparisons to *P. argulus* and *P. eigenmanni*. *Canadian Journal of Zoology 81*: 302–312.

Vitt, L. J., S. S. Sartorius, T. C. S. Ávila-Pires, P. A. Zani, and M. C. Espósito. 2005. Small in a big world: ecology of leaf-litter geckos in New World tropical forests. *Herpetological Monographs 19*: 137–152.

Watkins, G. W. 1996. Proximate causes of sexual size dimorphism in the iguanian lizard *Microlophus occipitalis*. *Ecology 77*: 1473–1482.

Zug, G. R., L. J. Vitt and J. P. Caldwell. 2001. *Herpetology: an introductory biology of amphibians and reptiles.* San Diego. Academic Press. 630 pp.