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At the Water's Edge: Ecology of Semiaquatic Teiids in Brazilian Amazon

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ABSTRACT.—**We describe activity patterns, diet, reproduction, sexual dimorphism, and thermal ecology of the semiaquatic teiids *Crocodilurus amazonicus* and *Dracaena guianensis*, from two localities in the Brazilian Amazon. Most *C. amazonicus* were first sighted in water or on open ground, were active during the hottest hours of the day, and usually had low body temperatures associated with substrate temperatures. *Dracaena guianensis* were found mainly perching on shrubs and used higher perches located closer to the center of lakes compared to *C. amazonicus*. Both species appear to rely primarily on crypsis to escape detection by predators but will dive into water as a final means of escape. *Crocodilurus amazonicus* has a broad diet which includes terrestrial and aquatic prey, particularly spiders and hemipterans, whereas *D. guianensis* feeds primarily on aquatic snails. No association between body dimensions and prey dimensions was evident. Sexual size dimorphism was not significant in either species, contrary to results reported for other teiids elsewhere, but males of *C. amazonicus* had relatively longer bodies and tails than females. Clutch size of both species was small relative to their body size and relative to other Amazon teiids, apparently influenced by their semiaquatic habits and by locomotor constraints. We found reproductive females during March (wet season) and July (dry season), suggesting an extended reproductive season.**

Ranging from northern United States to Chile and Argentina, teiids are a prominent group in the New World herpetofauna. The family contains nine extant genera and approximately 118 species (Zug et al., 2001; Reeder et al., 2002) that inhabit a wide variety of environments, from Amazon rain forests to North American deserts. A great deal of knowledge exists on the ecology of terrestrial teiids, especially on *Aspidoscelis* (McGovern et al., 1984; Anderson, 1988; Taylor et al., 1992), *Cnemidophorus* (Vitt et al., 1997; Mesquita and Colli, 2003a,b), *Kentropyx* (Vitt and Carvalho, 1992; Vitt et al., 1995; Vitt et al., 2001), *Ameiva* (Vitt, 1982; Colli, 1991; Vitt and Colli, 1994), and *Tupinambis* (Colli et al., 1998; Herrera and Robinson, 2000; Kiefer and Sazima, 2002). However, almost nothing is known about the two semiaquatic genera, *Crocodilurus* and *Dracaena*, even though both are included in Appendix II of CITES as a result of hunting for the skin market (Convention on International Trade in Endangered Species of Wild Flora and Fauna, 1979).

Crocodilurus is monotypic, and *Crocodilurus amazonicus* is a large, semiaquatic lizard distributed throughout the Amazon and Orinoco basins (Ávila-Pires, 1995). Bertoni (1926) reported a specimen presumably from northern Paraguay (Paraná basin) but provided no exact description of the locality. Adults attain a snout–vent length (SVL) of 218 mm and have a characteristic laterally compressed tail, with a prominent, double dorsal crest (Ávila-Pires, 1995). *Crocodilurus amazonicus* is known from rivers, lakes, and inundated forests (Pires and Prance 1985), and in Brazilian Amazon it is commonly known as "jacarerana," a Tupi-indian word that means "similar to a caiman." One account on the diet of a single adult reported 10 young *Bufo marinus*, a large odonate, and one hemipteran (Márcio Martins in Ávila-Pires, 1995).

Dracaena contains two species: *Dracaena guianensis* from the Amazon basin, and *Dracaena paraguayensis* from the Paraguay basin (Vanzolini and Valencia, 1965; Ávila-Pires, 1995). Body size is large, *D. paraguayensis* reaches 450 mm SVL (Vanzolini and Valencia, 1965) and *D. guianensis* reaches at least 412 mm SVL (Duellman, 1978). *Dracaena paraguayensis* is restricted to the Pantanal, a seasonal floodplain of the Paraguay River Basin, feeds primarily on aquatic snails, usually seeks refuge in holes in dry ground or

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in termite nests, and has a complex courtship consisting of puffing behavior (Amaral, 1950; Strüssmann, 1997). *Dracaena guianensis* is known from seasonally flooded lowlands, swamps, and margins of rivers and streams (Vanzolini and Valencia, 1965; Ávila-Pires, 1995). In Brazilian Amazon, it is known as "jacuruxi," a Tupi-indian word formed by "jacuru" (snake), and also "uxi" (the tree *Endopleura uxi*), probably an allusion to the resemblance between the enlarged tubercles on the dorsum of *D. guianensis* and the small, elliptical fruits of *E. uxi*. *Dracaena guianensis* spends most of its time in low trees (Vanzolini, 1961) and also rests in the water; in both cases it is cryptic (Ávila-Pires, 1995). When disturbed, they dive into water (Vanzolini, 1961; Dixon and Soini, 1986). The diet consists mainly of gastropods, which are taken underwater, but can also include arboreal invertebrates, eggs, and other animal prey during the dry season (Ávila-Pires, 1995). The only reproductive data on this species is an account by Goeldi (1902) of two eggs found in a termite nest at the margins of a river.

We studied the ecology of *C. amazonicus* and *D. guianensis* at two localities in the Brazilian Amazon and herein describe aspects of activity, diet, reproduction, sexual dimorphism, and thermal ecology.

MATERIALS AND METHODS

We collected lizards in Humaitá (07°31′S, 63°01′W), Amazonas state, in southwestern Amazonia, and Amapá (01°00′N, 51°24′W), Amapá state, in northeastern Amazonia (*D. guianensis* only in Amapá). The population of *C. amazonicus* from Humaitá occurred in a small tributary (Puruzinho Igarapé) on the left bank of the Madeira River. In Amapá, lizards were sampled in a system of lakes and inundated savannas (Pires and Prance, 1985).

We collected lizards by hand or using a shotgun, on a small boat or a canoe, during the hottest hours of the day (1100–1600 h). At the time of capture, we took body, substrate, and air temperatures to the nearest 0.2°C, with Miller and Weber® cloacal thermometers. We also recorded microhabitat, activity when individuals were first sighted and time and date of capture. We used the following microhabitat categories: burrow, shrub, fallen branches, log, ground, and water. We scored lizard activity as stationary, crawling, running, or swimming. In the lab, we killed live individuals with an injection of Tiopental®, measured, and fixed them with 10% formalin. We deposited all specimens in the Coleção Herpetológica da Universidade de Brasília (CHUNB). To determine the contribution of environmental temperatures to lizard cloacal temperatures, we used a stepwise multiple regression (Tabachnick and Fidell, 1996).

Diet.—We identified prey items in broad taxonomic categories (usually order) under a stereoscopic microscope. Length and width (± 0.01 mm) of intact prey were recorded with Mitutoyo® electronic calipers, and prey volume (V; mm^3) estimated as an ellipsoid:

$$V = \frac{4}{3}\pi\left(\frac{w}{2}\right)^2\left(\frac{l}{2}\right),$$

where w is prey width and l is prey length. We calculated the numeric and volumetric percentages of each prey category for individual lizards and for pooled stomachs. From numeric and volumetric percentages of prey, we computed niche breadths (B) for each lizard and also for pooled stomachs, using the inverse of Simpson's diversity index (Simpson, 1949):

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

where p is the numeric or volumetric proportion of prey category i, and n is the number of categories. In addition, we calculated the percentage of occurrence of each prey category (number of stomachs containing prey category i, divided by the total number of stomachs). Prey items that were too fragmented to allow a reliable estimation of their volumes were excluded.

To determine the relative contribution of each prey category, we calculated an importance index for individuals and pooled stomachs using the following equation:

$$I = \frac{F\% + N\% + V\%}{3},$$

where $F\%$ is the percentage of occurrence, $N\%$ is the numeric percentage, and $V\%$ is the volumetric percentage. To investigate the relationship between prey and head dimensions, we used a canonical correlation analysis with two sets of variables: maximum prey length and width versus lizard head width, height, and length.

Sexual Dimorphism.—We recorded the following morphometric variables for each individual: snout–vent length (SVL); body width (at its broadest point) and height (at its highest point); head width (at its broadest point), height (at its highest point), and length (from the tip of the snout to the commissure of the mouth); and tail length (from the cloaca to the tip of the tail). We took all measurements with Mitutoyo® electronic calipers to the nearest 0.01 mm. To maximize sample size, we estimated tail length of lizards with broken or regenerated tails using a regression analysis relating tail length to SVL on

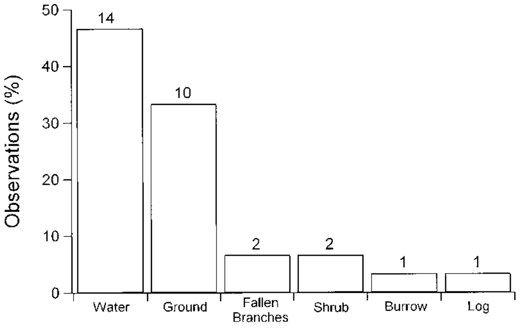

FIG. 1. Frequency distribution of active *Crocodilurus amazonicus* across microhabitat categories. Numbers on top of bars indicate sample sizes.

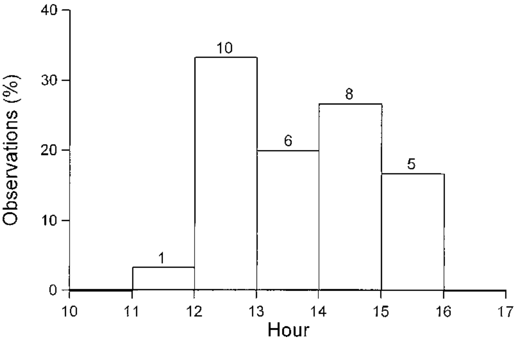

FIG. 2. Frequency distribution of *Crocodilurus amazonicus* according to time of capture. Numbers on top of bars indicate sample sizes.

data from lizards with intact tails. Because results from a preliminary analysis of sexual dimorphism on tail length were not significant, we pooled all data to estimate tail lengths. We log-transformed (base 10) all morphometric variables prior to analyses to meet the requirements of normality (Zar, 1998).

To partition the total morphometric variation between size and shape variation, we defined body size as an isometric size variable (Rohlf and Bookstein, 1987) following the procedure described by Somers (1986). We calculated an isometric eigenvector, defined a priori with values equal to $p^{-0.5}$, where p is the number of variables (Jolicoeur, 1963). Next, we obtained scores from this eigenvector, hereafter called body size, by postmultiplying the $n \times p$ matrix of log-transformed data (where n is the number of observations) by the $p \times 1$ isometric eigenvector. To remove the effects of body size from the log-transformed variables, we used residuals of a regression analysis between body size and each original variable. Hereafter, we refer to the resulting size-adjusted variables as shape variables. To test the null hypothesis of no difference between sexes, we conducted separate analyses on body size (ANOVA) and the shape variables (MANOVA).

Reproduction.—We sexed lizards by dissection and direct examination of gonads. Females were considered reproductive if vitellogenic follicles or oviductal eggs were present. We regarded the simultaneous presence of enlarged vitellogenic follicles and either oviductal eggs or corpora lutea as evidence for the sequential production of more than one clutch of eggs during the year. Males were considered reproductive if enlarged testes and convoluted epididymides were present. We estimated size at maturity for females based on the smallest individual containing vitellogenic follicles or oviductal eggs and, for males, based on the smallest individual bearing enlarged testes and convoluted epididymides.

We carried out statistical analyses using SYSTAT 11.0 for Windows, with a significance level of 5% to reject null hypotheses. Throughout the text, means appear ± 1 SD.

RESULTS

About 80% ($N = 24$) of *C. amazonicus* were first sighted in water or open ground at river (Humaitá) or lake (Amapá) margins (Fig. 1). We found active lizards from 1100–1600 h, but most were active during the hottest hours of the day, from 1200–1500 h (Fig. 2). Approximately 17% of individuals were exposed to direct sunlight, 43% were in mixed sun/shade, and 40% were in the shade. Body temperatures were usually low but higher than environmental temperatures (Table 1). A stepwise multiple regression analysis indicated that body temperature was more strongly associated with substrate temperature ($r = 0.294$; $F_{3,26} = 13.062$; $P < 0.001$). These results indicate that *C. amazonicus* uses primarily margins of lakes and streams during the hottest hours of the day (Fig. 2).

Dracaena guianensis were found mainly perching on shrubs, using higher perches than *C. amazonicus* and closer to the center of the lakes. Body temperatures of *D. guianensis* were higher than environmental temperatures (Table 1).

TABLE 1. Body and environment temperatures (°C) of *Crocodilurus amazonicus* and *Dracaena guianensis*. Values indicate mean ± SD. Range in parentheses.

	C. amazonicus ($N = 30$)	*D. guianensis* ($N = 1$)
Cloacal	31.23 ± 1.89 (27.4–35.0)	32.20
Substrate	30.43 ± 2.43 (25.60–38.20)	29.00
Air at 5 cm from the substrate	28.29 ± 1.45 (26.40–32.80)	29.00
Air at 1.5 m	27.62 ± 1.47 (26.00–32.40)	29.00

Diet.—Approximately 10.5% ($N = 6$) of the stomachs of *C. amazonicus* we analyzed were empty. We identified 23 prey categories, with hemipterans and spiders being the most frequent numerically and volumetrically (Table 2). The mean diversity index obtained from numeric percentages of prey was 1.72 ± 0.85. When using volumetric percentages of prey, the mean diversity index was 1.20 ± 0.32. Results based on data from pooled stomachs were similar (Table 2). Numerically, the diet consisted mainly of hemipterans, gastropods, and spiders, whereas hemipterans were more important volumetrically and one individual ate a snake, which was the single biggest prey item volumetrically. Numeric and volumetric diversity indices were 6.84 and 5.86, respectively. The importance indices of prey categories calculated from individual and pooled stomachs were similar (Table 2), spiders and hemipterans being the most important prey. All stomachs of *D. guianensis* we analyzed contained only gastropods. Each lizard ate approximately 2 ± 1.41 gastropods, representing 14,072 ± 13,175.92 mm^3 of stomach contents.

Correlations between prey and head measurements of *C. amazonicus* were low, ranging from less than 0.0001 between head length and maximum prey width and 0.079 between head length and maximum prey length. No association between body dimensions and prey dimensions was evident: the first canonical variable was 0.229 and the hypothesis that all canonical correlations were zero was not rejected ($P = 0.935$).

Sexual Dimorphism.—Male *C. amazonicus* ranged from 80–248 mm SVL and females ranged from 83–250 mm SVL (Table 3). No significant difference in body size existed between sexes (ANOVA $F_{1,59} = 0.001$; $P = 0.973$); however, males and females differed in shape variables (i.e., size-adjusted residuals; Wilk's Lambda = 0.484, $P < 0.0001$). The stepwise discriminant analysis selected SVL, tail length, body height, head width, and head length as the most powerful discriminators between the sexes, the first two variables contributing the most to the model (Table 4). We repeated the analysis without SVL, but the order variables were selected did not change, indicating that no important variables were left out of the model because of any correlation with SVL. The analysis indicated that males had relatively longer bodies and tails than females (Table 3).

Males of *D. guianensis* ranged from 300–355 mm SVL, whereas females ranged from 236–278 mm SVL. Males appeared to be bigger than females (Table 3), but low sample sizes precluded statistical analyses.

Reproduction.—The smallest reproductive male and female of *C. amazonicus* measured 185 and 205 mm SVL, respectively (Fig. 3). Clutch size averaged 5.5 ± 0.71 (range: 5–6, $N = 2$) based on egg counts, and 4.0 ± 2.82 (range: 2–6, $N = 2$) based on vitellogenic follicles. Clutch size based on combined eggs and follicles averaged 4.75 ± 1.89 (range: 2–6, $N = 4$) and was not significantly correlated with female SVL ($r = 0.323$; $P = 0.596$). Mean egg length was 34.72 ± 1.72 mm, mean egg width was 18.52 ± 1.30 mm, and mean egg volume was 6267.58 ± 986.98 mm^3. Egg volume and female SVL were not correlated ($r = –0.28$, $P = 0.41$). We found reproductive females during March (wet season) and July (dry season).

The smallest reproductive male and female of *D. guianensis* measured 300 and 320 mm SVL, respectively. The single reproductive female, captured in July (dry season), had six enlarged vitellogenic follicles and six corpora lutea, suggesting that *D. guianensis* can produce more than one clutch during the breeding season.

DISCUSSION

Crocodilurus amazonicus and *D. guianensis* were found mostly at the margins, or in streams and lakes in seasonally flooded forests and savannas, as previously described elsewhere (Ávila-Pires, 1995). Among teiids, only these species exhibit semiaquatic habits (Vanzolini and Valencia, 1965; Ávila-Pires, 1995). Other teiids, such as *Kentropyx striata* and *Tupinambis teguixin*, are occasionally found in seasonally flooded areas, but they use branches away from the water (Vitt and Carvalho, 1992; Ávila-Pires, 1995).

Both *C. amazonicus* and *D. guianensis* are more active during midday. Even though body temperatures for both species were higher than environmental temperatures, they were relatively lower than other teiids that inhabit forested areas, such as *Ameiva festiva* (35.6 ± 0.5°C; Vitt and Zani, 1996a), *A. ameiva* (38.8 ± 0.42°C; Vitt and Colli, 1994), *Kentropyx calcarata* (35.7 ± 0.8°C; Vitt, 1991), *K. pelviceps* (31.9 ± 0.8°C; Vitt et al., 1995), *K. altamazonica* (35.9 ± 0.4°C; Vitt et al., 2001), and *T. teguixin* (35.0 ± 0.7°C; Vitt and Carvalho, 1995). Considering that sunlight was available in all habitats used by lizards, it seems that lower body temperatures result from their close association with water. This relationship was also reported for *Neusticurus ecpleopus*, which also shows low body temperatures (27.0 ± 0.02°C, Vitt et al., 1998), and seems to be a feature of semiaquatic lizards (Wikramanayake and Green, 1989; Wikramanayake and Dryden, 1993; Traeholt, 1997; Pianka and Vitt, 2003).

We found a strong and significant relationship between body and substrate temperature for *C. amazonicus*, and most individuals were stationary

TABLE 2. Diet composition of *Crocodilurus amazonicus* (N = 57). [a] Number of stomachs containing prey item, [b] IIS-importance index based on individual stomachs, and [c] IPS-importance index based on pooled stomachs.

	Occurrence		Stomach means				Pooled stomachs				Importance	
Prey items	F[a]	F%	*N*	%*N*	Vol. (mm^3)	%Vol.	*N*	%*N*	Vol. (mm^3)	%Vol.	IIS[b]	IPS[c]
Annelida	1	1.09	0.02 ± 0.13	0.44 ± 3.31	0.76 ± 5.73	0.03 ± 0.26	1	0.52	43.26	0.11	0.52	0.57
Araneae	14	15.22	1.00 ± 1.36	35.29 ± 39.74	90.52 ± 398.67	18.20 ± 36.81	46	23.88	4958.00	12.31	22.90	17.14
Blattaria	1	1.09	0.02 ± 0.13	0.44 ± 3.31	—	—	1	0.52	—	—	0.77	0.81
Decapoda												
Crabs	4	4.35	0.07 ± 0.26	2.02 ± 8.50	9.90 ± 74.71	0.45 ± 3.40	4	2.07	564.10	1.40	2.27	2.61
Shrimps	5	5.43	0.09 ± 0.29	2.20 ± 8.24	30.07 ± 192.13	2.37 ± 12.55	5	2.59	1714.00	4.25	3.33	4.09
Coleoptera	3	3.26	0.07 ± 0.32	1.90 ± 8.48	30.81 ± 185.53	2.84 ± 15.18	4	2.07	1756.00	4.36	2.65	3.23
Diptera	1	1.09	0.02 ± 0.13	0.88 ± 6.62	4.62 ± 34.89	1.10 ± 8.27	1	0.52	263.50	0.65	1.02	0.75
Hemiptera	16	17.39	0.42 ± 0.86	14.98 ± 30.03	110.85 ± 361.72	10.53 ± 29.38	25	12.95	5862.00	14.55	14.30	14.96
Homoptera	1	1.09	0.02 ± 0.13	0.12 ± 0.88	—	—	1	0.52	—	—	0.61	0.81
Hymenoptera												
Formicidae	5	5.43	0.09 ± 0.29	3.57 ± 12.16	1.01 ± 7.59	0.30 ± 2.23	5	2.59	57.33	0.14	3.10	2.72
Other	3	3.26	0.05 ± 0.23	2.92 ± 14.81	51.16 ± 386.26	1.75 ± 13.25	3	1.55	2916.00	7.24	2.64	4.02
Odonata	1	1.09	0.02 ± 0.13	1.75 ± 13.25	—	—	1	0.52	—	—	1.42	0.81
Orthoptera												
Grillidae	2	2.17	0.04 ± 0.19	2.19 ± 13.60	24.60 ± 132.00	2.29 ± 13.77	2	1.04	1402.00	3.48	2.22	2.23
Other	7	7.61	0.18 ± 0.54	5.76 ± 17.80	19.61 ± 76.16	6.05 ± 22.25	10	5.18	1118.00	2.77	6.47	5.19
Scorpiones	1	1.09	0.02 ± 0.13	0.44 ± 3.31	3.97 ± 29.95	1.75 ± 13.25	1	0.52	226.10	0.56	1.09	0.72
Insect larvae	7	7.61	0.19 ± 0.61	6.16 ± 20.21	34.36 ± 214.29	1.64 ± 9.74	11	5.70	1959.00	4.86	5.14	6.06
Lizard skin	1	1.09	0.02 ± 0.13	0.19 ± 1.47	—	—	1	0.52	—	—	0.64	0.81
Nonidentified	3	3.26	0.07 ± 0.32	3.74 ± 18.60	—	—	4	2.07	—	—	3.50	2.67
Gastropoda	2	2.17	0.82 ± 5.36	3.51 ± 18.56	—	—	47	24.35	—	—	2.84	13.26
Plant material	8	8.70	0.18 ± 0.47	6.32 ± 18.56	6.08 ± 45.92	1.75 ± 13.25	11	5.70	346.70	0.86	5.59	5.09
Spider sac	1	1.09	0.02 ± 0.13	0.88 ± 6.62	38.92 ± 293.87	1.52 ± 11.51	1	0.52	2219.00	5.51	1.16	2.37
Vertebrates												
Birds	1	1.09	0.02 ± 0.13	0.58 ± 4.42	—	—	1	0.52	—	—	0.84	0.81
Fishes	3	3.26	0.11 ± 0.49	1.96 ± 8.67	19.54 ± 140.34	1.81 ± 13.24	6	3.11	1114.00	2.76	2.34	3.04
Snakes	1	1.09	0.02 ± 0.13	1.75 ± 13.25	251.54 ± 1823.60	1.75 ± 13.25	1	0.52	13768.00	34.18	1.53	11.93

TABLE 3. Summary statistics (mean ± SD) of morphometric characters of all individuals of *Crocodilurus amazonicus* and *Dracaena guianensis*. All variables are in millimeters. Values in parenthesis represents adjusted values. See methods for the definition of body size.

	Crocodilurus amazonicus		*Dracaena guianensis*	
Character	Males (*N* = 30)	Females (*N* = 33)	Males (*N* = 4)	Females (*N* = 2)
Body size	294.640 ± 59.960	294.655 ± 57.985	503.167 ± 29.939	383.597 ± 127.892
Snout–vent length	187.500 ± 37.853	190.812 ± 36.001	328.750 ± 23.936	278.000 ± 59.397
	(0.003 ± 0.007)	(−0.005 ± 0.007)	(−0.002 ± 0.018)	(0.004 ± 0.000)
Tail length	401.289 ± 87.075	407.756 ± 83.820	588.750 ± 32.755	377.000 ± 216.375
	(0.001 ± 0.007)	(−0.003 ± 0.006)	(0.002 ± 0.036)	(−0.004 ± 0.008)
Body width	35.686 ± 7.833	36.155 ± 7.887	81.750 ± 10.436	64.895 ± 23.228
	(−0.001 ± 0.039)	(0.003 ± 0.032)	(−0.005 ± 0.045)	(0.010 ± 0.014)
Body height	24.969 ± 5.497	26.013 ± 5.808	55.000 ± 10.801	52.665 ± 15.365
	(0.007 ± 0.038)	(−0.002 ± 0.039)	(−0.018 ± 0.084)	(0.036 ± 0.042)
Head width	24.314 ± 5.974	22.522 ± 4.193	76.250 ± 8.539	49.715 ± 10.789
	(−0.010 ± 0.045)	(0.015 ± 0.053)	(0.016 ± 0.030)	(−0.032 ± 0.066)
Head height	19.563 ± 3.867	18.609 ± 3.133	50.500 ± 4.203	41.450 ± 8.839
	(−0.006 ± 0.034)	(0.013 ± 0.043)	(0.000 ± 0.023)	(−0.000 ± 0.006)
Head length	35.019 ± 6.325	34.983 ± 5.531	78.250 ± 6.131	62.205 ± 10.727
	(0.003 ± 0.053)	(0.002 ± 0.047)	(0.005 ± 0.017)	(−0.009 ± 0.025)
Forelimb length	57.161 ± 10.910	55.786 ± 10.325	95.250 ± 6.946	89.820 ± 12.784
	(−0.005 ± 0.027)	(0.006 ± 0.025)	(−0.005 ± 0.027)	(0.011 ± 0.014)
Hind-limb length	98.428 ± 19.254	94.813 ± 19.003	155.000 ± 15.790	135.040 ± 26.177
	(−0.010 ± 0.027)	(0.006 ± 0.031)	(−0.004 ± 0.031)	(0.007 ± 0.001)

when first sighted. Likewise, most *D. guianensis* were stationary at first sight. Even though teiids are regarded as active foragers that rely mainly on flight to evade predators (Anderson and Karasov, 1981; Magnusson et al., 1985), our results support previous observations suggesting that *C. amazonicus* and *D. guianensis* rely primarily on crypsis, ultimately diving into the water to escape (see also Dixon and Soini, 1986; Ávila-Pires, 1995). Because water is readily available where such species live, providing easily accessible and good hiding places from predators, this appears to be an effective antipredator tactic among semiaquatic lizards. Similar behavior has been reported for the tropidurid *Uranoscodon superciliosum* (Howland et al., 1990), gymnophytalmids in the genus *Neusticurus* (Vitt and Ávila-Pires, 1998; Vitt et al., 1998), and the varanid *Varanus salvator* (Auliya and Erdelen, 1999; Gaulke et al., 1999).

Diet.—*Crocodilurus amazonicus* has a broad diet, including terrestrial and aquatic animals, of which spiders and hemipterans were the most important. Conversely, *D. guianensis* apparently feeds primarily on aquatic snails. Several items in the diet of *C. amazonicus* were typical of semiaquatic lizards feeding in aquatic environments, such as water-bugs, shrimps, crabs, and fishes (Cover, 1986; Traeholt, 1994; Vitt and Ávila-Pires, 1998; Vitt et al., 1998). However, like most teiids (e.g., Vitt, 1991; Vitt and Carvalho, 1992; Vitt and Colli, 1994; Colli et al., 1998; Vitt et al., 2001) a considerable portion of the diet of *C. amazonicus* consisted of terrestrial prey, stressing the influence of phylogenetic history in lizard diets (Losos, 1996; Vitt et al., 2003). Even though we recorded only snails as prey in *D. guianensis*, during the dry season this species also feeds on arboreal invertebrates, eggs, and other animal prey (Ávila-Pires, 1995).

TABLE 4. Stepwise discriminant analysis of morphometric characters of *Crocodilurus amazonicus*, with error-rate estimates based on cross-validation.

Step	Variable entered	*F*	*P*	Error-rate
1	Snout–vent length	21.24	< 0.0001	0.4918
2	Tail length	7.50	0.00821	0.1803
3	Body height	6.33	0.0147	0.1803
4	Head width	5.13	0.0274	0.1803
5	Head length	2.77	0.1019	0.1803

Sexual Dimorphism.—We found no significant sexual size dimorphism in *C. amazonicus* and *D. guianensis*, but male *C. amazonicus* had relatively longer bodies and tails than females. Sexual dimorphism can be attributed to three main causes. First, intersexual differences could be a mechanism to reduce competition for food resources between the sexes (e.g., Preest, 1994; Perry, 1996). Second, males with bigger heads should be favored in intrasexual competition for access to females (e.g., Trivers, 1976; Vitt and Cooper, 1985). Third, selection should benefit larger females by favoring increased offspring size or larger clutches (e.g., Carothers, 1984; Cooper and Vitt, 1989). We found no significant sexual dimorphism in body size nor a prey and head size correlation, contrary to results reported for other teiids elsewhere (see Anderson and Vitt, 1990; Vitt, 1991; Vitt and Carvalho, 1992; Vitt and Colli, 1994; Vitt et al., 1995, 2001; Mesquita and Colli, 2003b). However, such trends require additional sampling to enable confirmation; we had very low sample sizes for *D. guianensis*.

Reproduction.—Clutches of *C. amazonicus* and *D. guianensis* were small relative to their body size and relative to other Amazon teiids, such as *A. ameiva* (3.2 ± 0.01; Vitt and Colli, 1994), *K. calcarata* (4–10, Vitt, 1991), *K. pelviceps* (6.5 ± 0.3, Vitt et al., 1995), and *T. teguixin* (11–17, Herrera and Robinson, 2000). With the exception of *T. teguixin*, these species are smaller than *C. amazonicus* and *D. guianensis*; however, some of them have larger clutches. It is possible that clutch size of *C. amazonicus* and *D. guianensis* is influenced by their semiaquatic habits and by locomotor constraints, or the converse may be true (Vitt and Congdon, 1978; Shine, 1980; Vitt and Price, 1982; Sinervo et al., 1989). The positive association between clutch size and female body size is common in species that do not have a fixed clutch size (Tinkle et al., 1970; Dunham and Miles, 1985; Dunham et al., 1988). We found no such association, but because of the small number of gravid females we examined, additional data are necessary to confirm these findings. Reproductive female *C. amazonicus* and *D. guianensis* were collected in the dry season, but gravid female *C. amazonicus* were also collected during the wet season. These results are preliminary but suggest that both species have extended reproductive periods, similar to most teiids in the Amazon (Vitt, 1991; Vitt and Colli, 1994; Vitt et al., 1995).

Early reports suggested that *D. guianensis* was common in Amazonia (see Amaral, 1950), which contrast strongly with our field observations, suggesting the possibility of a population decline in recent years. We interviewed local people in Amapá, who indicated that the species was abundant prior to the "matança" (killing) for the skin market that took place during 1950–1960. In addition, large-scale cattle and water buffalo ranching is spreading in Amazon wetlands (várzea; Camarão et al., 1997). Because natural pastures, typical of low lying areas, are available only during low water periods, ranchers cut the floodplain (igapó) forest on high lying areas to increase pasture area (Junk and Piedade, 2000). In addition, large herds of water buffalos promote filling in of permanent lakes, because of their habit of wallowing (Junk and Piedade, 2000). These impacts promote the reduction of natural habitats and threaten persistence of *D. guianensis*.

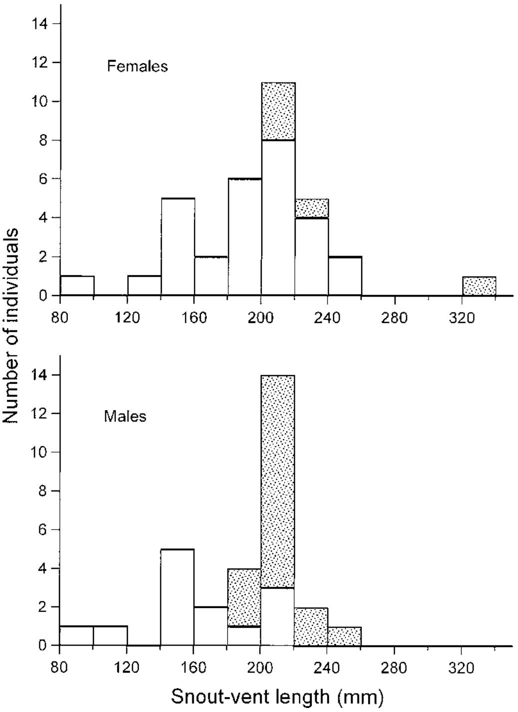

FIG. 3. Frequency distribution of male and female *Crocodilurus amazonicus* according to snout–vent length and reproductive condition. Open bars represent nonreproductive and stippled bars represent reproductive, individuals.

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LITERATURE CITED

AMARAL, A. D. 1950. Two new South American lizards. Copeia 1950:281–284.

ANDERSON, R. A. 1988. Sexual dimorphism and sexual selection in the lizard *Cnemidophorus tigris*. American Zoologist 28:52A.

ANDERSON, R. A., AND W. H. KARASOV. 1981. Contrasts in energy intake and expenditure in sit-and-wait and widely foraging lizards. Oecologia 49:67–72.

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

Auliya, M. A., and W. Erdelen. 1999. A field study of the water monitor lizard (*Varanus salvator*) in West Kalimantan, Indonesia—new methods and old problems. Mertensiella 11:247–266.

Ávila-Pires, T. C. S. 1995. Lizards of Brazilian Amazonia (Reptilia: Squamata). Zoologische Verhandelingen, Leiden 1995:3–706.

Bertoni, A. W. 1926. El *Crocodilurus* o Yakarerâ en el Paraguay (Reptiles). Revista de la Sociedad Científica del Paraguay 2:187.

Camarão, A. P., J. R. F. Marques, C. L. G. Mendonça, J. A. R. Filho, and N. N. Carvalho. 1997. Composição botânica da forragem disponível e dieta de bubalinos do tipo baio em pastangens nativas de várzeas. *In* Anais da XXXIV Reunião da Sociedade Brasileira de Zootecnia, pp. 287–289. Juiz de Fora.

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

Colli, G. R. 1991. Reproductive ecology of *Ameiva ameiva* (Sauria: Teiidae) in the cerrado of central Brazil. Copeia 1991:1002–1012.

Colli, G. R., A. K. Péres Jr., and H. J. Cunha. 1998. A new species of *Tupinambis* (Squamata: Teiidae) from central Brazil, with analysis of morphological and genetic variation in the genus. Herpetologica 54:477–492.

Convention on International Trade in Endangered Species of Wild Flora and Fauna. 1979. The CITES Appendices I, II and III.

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

Cover Jr, J. F. 1986. *Basiliscus plumifrons* (Crested Green Brasilisk lizard). Food. Herpetological Review 17:19–19.

Dixon, J. R., and P. Soini. 1986. The reptiles of the upper Amazon basin, Iquitos region, Peru. Milwaukee Public Museum, Milwaukee, WI.

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

Dunham, A. E., and D. B. Miles. 1985. Patterns of covariation in life history traits of squamate reptiles: the effects of size and phylogeny reconsidered. American Naturalist 126:231–257.

Dunham, A. E., D. B. Miles, and D. N. Reznick. 1988. Life history patterns in squamate reptiles. *In* C. Gans and R. B. Huey (eds.), Biology of the Reptilia. Vol. 16. Ecology B. Defense and Life History, pp. 441–522. Alan R. Liss, Inc., New York.

Gaulke, M., W. Erdelen, and F. Abel. 1999. A radiotelemetric study of the water monitor lizard (*Varanus salvator*) in North Sumatra, Indonesia. Mertensiella 11:63–78.

Goeldi, E. A. 1902. Lagartos do Brazil. Boletim do Museu Paraense 3:499–560.

Herrera, E. A., and M. D. Robinson. 2000. Reproductive and fat body cycles of the Tegu Lizard, *Tupinambis teguixin*, in the Llanos of Venezuela. Journal of Herpetology 34:598–601.

Howland, J. M., L. J. Vitt, and P. T. Lopez. 1990. Life on the edge: the ecology and life history of the tropidurine iguanid lizard *Uranoscodon superciliosum*. Canadian Journal of Zoology 68:1366–1373.

Jolicoeur, P. 1963. The multivariate generalization of the allometry equation. Biometrics 19:497–499.

Junk, W. J., and M. T. F. Piedade. 2000. Concepts for the sustainable management of natural resources of the middle amazon floodplain: a summary. *In* German-Brazilian Workshop on Neotropical Ecosystems—Achievements and Prospects of Cooperative Research, pp. 697–702. Hamburg, Germany.

Kiefer, M. C., and I. Sazima. 2002. Diet of a juvenile tegu lizard *Tupinambis merianae* (teiidae) in southeastern Brazil. Amphibia-Reptilia 23:105–108.

Losos, J. B. 1996. Phylogenetic perspectives on community ecology. Ecology 77:1344–1354.

Magnusson, W. E., L. J. D. Paiva, R. M. D. Rocha, C. R. Franke, L. A. Kasper, and A. P. Lima. 1985. The correlates of foraging mode in a community of Brazilian lizards. Herpetologica 41:324–332.

McGovern, G. M., J. C. Mitchell, and C. B. Knisley. 1984. Field experiments on prey selection by the Whiptail Lizard *Cnemidophorus inornatus* in Arizona. Journal of Herpetology 18:347–349.

Mesquita, D. O., and G. R. Colli. 2003a. Geographical variation in the ecology of populations of some Brazilian species of *Cnemidophorus* (Squamata, Teiidae). Copeia 2003:285–298.

———. 2003b. The ecology of *Cnemidophorus ocellifer* (Squamata, Teiidae) in a Neotropical savanna. Journal of Herpetology 37:498–509.

Perry, G. 1996. The evolution of sexual dimorphism in the lizard *Anolis polylepis* (Iguania): evidence from intraspecific variation in foraging behavior and diet. Canadian Journal of Zoology 74:1238–1245.

Pianka, E. R., and L. J. Vitt. 2003. Lizards: Windows of the Evolution of Diversity. University of California Press, Los Angeles.

Pires, J. M., and G. T. Prance. 1985. The vegetation types of the Brazilian Amazon. *In* G. T. Prance and T. E. Lovejoy (eds.), Key Environments: Amazonia, pp. 109–145. Pergamon Press, Oxford.

Preest, M. R. 1994. Sexual size dimorphism and feeding energetics in *Anolis carolinensis*: why do females take smaller prey than males? Journal of Herpetology 28:292–298.

Reeder, T. W., C. J. Cole, and H. C. Dessauer. 2002. Phylogenetic relationships of Whiptail lizards of the genus *Cnemidophorus* (Squamata: Teiidae): a test of monophyly, reevaluation of karyotypic evolution, and review of hybrid origins. American Museum Novitates 3365:1–61.

Rohlf, F. J., and F. L. Bookstein. 1987. A comment on shearing as a method for "size correction." Systematic Zoology 36:356–367.

Shine, R. 1980. "Costs" of reproduction in reptiles. Oecologia 46:92–100.

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

Sinervo, B., R. Hedges, and S. C. Adolph. 1989. Decreased sprint speed as a cost of reproduction in the lizard *Sceloporus occidentalis*: variation among populations. Journal of Experimental Biology 155:323–336.

Somers, K. M. 1986. Multivariate allometry and removal of size with principal component analysis. Systematic Zoology 35:359–368.

Strüssmann, C. 1997. *Dracaena paraguayensis*. Courtship. Herpetological Review 28:151.

Tabachnick, B. G., and L. S. Fidell. 1996. Using Multivariate Statistics. HarperCollins Publishers Inc., New York.

Taylor, H. L., C. R. Cooley, R. A. Aguilar, and C. J. Obana. 1992. Factors affecting clutch size in the Teiid Lizards *Cnemidophorus tigris gracilis* and *Cnemidophorus tigris septentrionalis*. Journal of Herpetology 26:443–447.

Tinkle, D. W., H. M. Wilbur, and S. G. Tilley. 1970. Evolutionary strategies in lizard reproduction. Evolution 24:55–74.

Traeholt, C. 1994. The food and feeding behaviour of the water monitor, *Varanus salvator*, in Malaysia. Malayan Nature Journal 47:331–343.

———. 1997. Effect of masking the parietal eye on the diurnal activity and body temperature of two sympatric species of monitor lizards, *Varanus s. salvator* and *Varanus b. nebulosus*. Journal of Comparative Psychology B 1997:177–184.

Trivers, R. L. 1976. Sexual selection and resource accruing abilities in *Anolis garmani*. Evolution 30:253–269.

Vanzolini, P. E. 1961. Notas bionômicas sobre *Dracaena guianensis* no Pará (Sauria: Teiidae). Papéis Avulsos do Departamento de Zoologia da Secretaria de Agricultura de São Paulo 14:237–241.

Vanzolini, P. E., and J. Valencia. 1965. The genus *Dracaena*, with a brief consideration of macroteiid relationships (Sauria, Teiidae). Arquivos de Zoologia, São Paulo 13:7–46.

Vitt, L. J. 1982. Reproductive tactics of *Ameiva ameiva* (Lacertilia: Teiidae) in a seasonally fluctuating tropical habitat. Canadian Journal of Zoology 60:3113–3120.

———. 1991. Ecology and life history of the wide-foraging lizard *Kentropyx calcarata* (Teiidae) in Amazonian Brazil. Canadian Journal of Zoology 69:2791–2799.

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 C. M. Carvalho. 1992. Life in the trees: the ecology and life-history of *Kentropyx striatus* (Teiidae) in the Lavrado area of Roraima, Brazil, with comments on tropical teiid life histories. Canadian Journal of Zoology 70:1995–2006.

———. 1995. Niche partitioning in a tropical wet season: lizards in the Lavrado area of Northern Brazil. Copeia 1995:305–329.

Vitt, L. J., and G. R. Colli. 1994. Geographical ecology of a Neotropical lizard: *Ameiva ameiva* (Teiidae) in Brazil. Canadian Journal of Zoology 72:1986–2008.

Vitt, L. J., and J. D. Congdon. 1978. Body shape, reproductive effort, and relative clutch mass in lizards: resolution of a paradox. American Naturalist 112:595–608.

Vitt, L. J., and W. E. Cooper Jr. 1985. The evolution of sexual dimorphism in the skink *Eumeces laticeps*: an example of sexual selection. Canadian Journal of Zoology 63:995–1002.

Vitt, L. J., and H. J. Price. 1982. Ecological and evolutionary determinants of relative clutch mass in lizards. Herpetologica 38:237–255.

Vitt, L. J., and P. A. Zani. 1996. Ecology of the lizard *Ameiva festiva* (Teiidae) in southeastern Nicaragua. Journal of Herpetology 30:110–117.

Vitt, L. J., P. A. Zani, J. P. Caldwell, and E. O. Carrillo. 1995. Ecology of the lizard *Kentropyx pelviceps* (Sauria: Teiidae) in lowland rain forest of Ecuador. Canadian Journal of Zoology 73:691–703.

Vitt, L. J., P. A. Zani, J. P. Caldwell, M. C. D. Araujo, and W. E. Magnusson. 1997. Ecology of Whiptail Lizards (*Cnemidophorus*) in the Amazon region of Brazil. Copeia 1997:745–757.

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

Vitt, L. J., S. S. Sartorius, T. C. Ávila-Pires, and M. C. Espósito. 2001. Life at the river's edge: ecology of *Kentropyx altamazonica* in Brazilian Amazonia. Canadian Journal of Zoology 79:1855–1865.

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

Wikramanayake, E. D., and G. L. Dryden. 1993. Thermal ecology of habitat and microhabitat use by sympatric *Varanus bengalensis* and *V. salvator* in Sri Lanka. Copeia 1993:709–714.

Wikramanayake, E. D., and B. Green. 1989. Thermoregulatory influences on the ecology of two sympatric varanids in Sri Lanka. Biotropica 21:74–79.

Zar, J. H. 1998. Biostatistical Analysis. 4th ed. Prentice-Hall, Inc., Englewood Cliffs, NJ.

Zug, G. R., L. J. Vitt, and J. P. Caldwell. 2001. Herpetology: An Introductory Biology of Amphibians and Reptiles. 2nd ed. Academic Press, San Diego, CA.

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