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Diets of Spectacled and Black Caiman in the Anavilhanas Archipelago, Central Amazonia, Brazil

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ABSTRACT.—Stomach contents were collected from 213 *Caiman crocodilus* with snout-vent lengths (SVL) between 15 cm and 115 cm, and 25 *Melanosuchus niger* with SVLs from 15 cm to 95 cm, in the Anavilhanas Archipelago, Rio Negro, Central Amazonia. The prey types consumed by the two species were generally similar. However, fish were common in the diet of *C. crocodilus* but absent from the *M. niger*. Snails (*Pomacea*) occurred in 24% of stomachs of *M. niger*, but in only 2% of *C. crocodilus*. The mean mass of food and the mean proportion of fish consumed increased, while the mean proportion of terrestrial invertebrates decreased significantly with the size class of *C. crocodilus*. The mean proportion of molluscs consumed increased significantly with the size class of *M. niger*, but there was no relationship between the mean mass of food or the mean proportion of other prey categories and size class in this species. However, the sample included only subadults. The mean size of all prey consumed, and of fish, increased significantly with size of *C. crocodilus*. However, there was no relationship between the mean size of prey in the categories terrestrial invertebrates, shrimps, or crabs, and the size of *C. crocodilus*. The mean size of all prey consumed was positively related to the size of *M. niger*. The mean mass of food consumed by *C. crocodilus* varied with the water body type (lake or canal), but there was no effect of season as indexed by the water level of the Rio Negro. Seasonal variation in the proportion of fish, terrestrial invertebrates, and shrimps consumed by *C. crocodilus* differed among water body types. Empty stomachs occurred in 24% of the *C. crocodilus* and 20% of the *M. niger*. Individuals with food in the stomach had eaten small volumes, suggesting that the caiman are unlikely to impact fisheries in the region.

The majority of diet studies of the common caiman (*Caiman crocodilus crocodilus*) are from savanna habitats (Staton and Dixon, 1975; Gorzula, 1978; Seijas and Ramos, 1980; Ayarzaguena, 1983; Fitzgerald, 1988; Escalona, 1991; Thorbjarnarson, 1993), and there are few from the Brazilian Amazon (Vanzolini and Gomes, 1979; Magnusson et al., 1987). Knowledge of food habits of the black caiman (*Melanosuchus niger*) is limited to general reports (Medem, 1981, 1983), and a limited study in the Brazilian Amazon where only nine stomach contents of the species were obtained (Magnusson et al., 1987).

The Anavilhanas Ecological Station (AES), is one of the largest reserves in the lower Rio Negro, Central Amazonia, and the only protected area to include large areas of habitat seasonally inundated by black-water rivers (igapó). The Rio Negro is the largest black-water river system with rather unusual limnological characteristics (Goulding et al., 1988), and this may influence prey availability and the diet of top predators. Little is known of the diet of caimans in this habitat, though the popular press frequently contains claims that caimans consume large quantities of commercial fish and compete intensively with fishermen (e.g., Correio Braziliense, 8 December 1986; A Crítica, 25 July 1991). The Anavilhanas Archipelago is formed by thousands of islands which form a complex of lakes and canals (Brasil, 1984). Caiman distributions are not uniform within the AES, and may vary seasonally (Da Silveira et al., 1997), but it is not known whether caiman feeding success or prey availability differs among habitats or seasons.

This study was undertaken in the AES to answer the follows questions: (1) Which prey types are consumed by *C. crocodilus* and *M. niger* in the Anavilhanas Archipelago? (2) How does prey type, the mean mass of food, and the mean size of prey vary with ontogeny in these species? (3) What are the effects of seasonal variations in water level of the Rio Negro, type of water body and food availability on mean mass of food and on the prey types consumed by *C. crocodilus*?

MATERIALS AND METHODS

Capture and Stomach Contents Removal.—Caimans were captured throughout the Archipelago of the AES between 02°30′ and 03°00′S and 60°30′ and 61°00′W. Caiman are common throughout the Archipelago (Da Silveira et al., 1997). Captures were made by hand or with a

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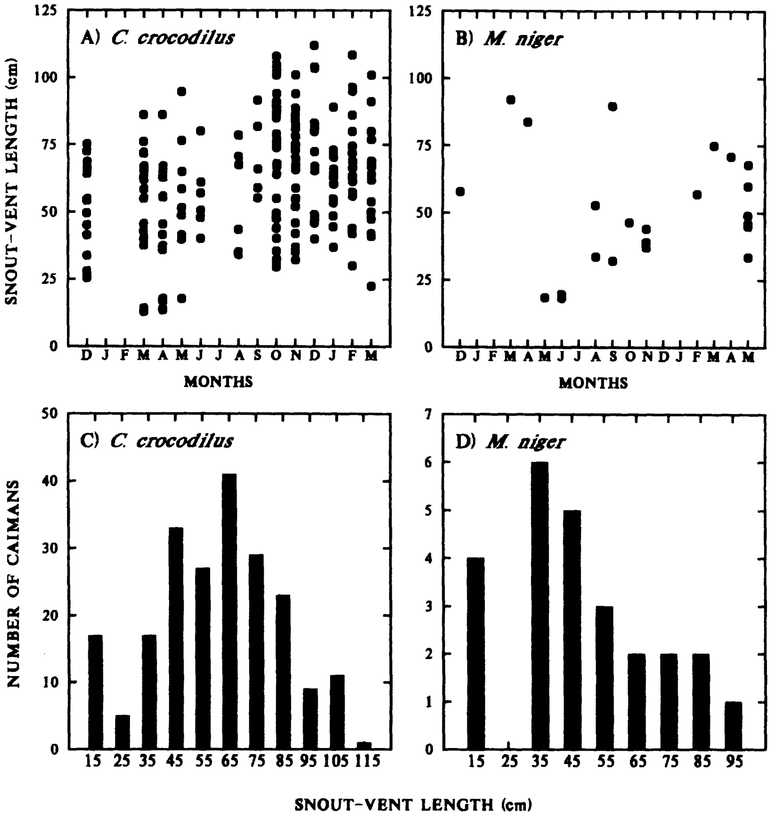

FIG. 1. Snout-vent length (cm) of *C. crocodilus* (A) and *M. niger* (B) captured in each month for stomach flushing, between December 1990 and May 1992. Overall size structures of *C. crocodilus* (C) and *M. niger* (D) captured for diet analyses. In parts C and D caimans are grouped in 10 cm SVL classes centered on the values shown.

noose in the lakes and canals of the Archipelago, between 2000 and 2200 h, in December 1990 and between March 1991 and May 1992. Only *M. niger* was captured in April and May 1992 (Fig. 1A and B).

Caimans (213 *C. crocodilus* and 25 *M. niger*) were stomach flushed (Taylor et al., 1978), with modifications suggested by Webb et al. (1982), about 15 min after capture. The snout-vent lengths (SVL, cm) of the caimans were measured to the posterior border of the cloaca. Caiman were released at the site of capture. Stomach contents were preserved in 70% alcohol.

Stomach Content Identification.—Prey in stomach contents were identified to the level of order, family, or species, and then grouped in nine prey categories: terrestrial invertebrates (insects and spiders), shrimps, crabs, molluscs, snakes, mammals, fish, elongated terrestrial invertebrates (Diplopoda, Chilopoda and Oligochaeta), and other vertebrates. Items in each category in each stomach were weighed to the nearest 0.01 g, after draining off excess alcohol.

Variation in Prey Type with Caiman Size.—Regression analysis was used to examine changes in the mean mass of food and of the mean proportion of prey categories consumed in relation to caiman size. The proportion of the mass of each prey category, relative to total mass of food, was calculated for each caiman. However, the distribution of mass of prey categories was not normal and could not be transformed to meet the assumptions of most parametric statistical methods. Also, one prey category was responsible for most of the food mass in most caimans. Therefore, caimans were grouped into 10 cm SVL classes. The 15 cm class contained all caimans of SVL < 20 cm. The 25 cm class contained caimans for which 20 cm $\leq$ SVL $<$ 30 cm. The other classes followed successively. Thus, the degrees of freedom for analyses are associated with the number of size categories and not with the total number of stomach contents analyzed. The dependent variables in the analyses were the mean mass of food and mean proportion of each prey category in each SVL class.

Only those prey categories that occurred in

TABLE 1. Occurrence (N), relative occurrence (%N), mass in grams and percentage of mass (%M) of prey categories found in 213 stomach contents of *C. crocodilus* and 25 *M. niger.* Terrestrial invertebrates (TI) = insects and spiders; elongated terrestrial invertebrates (ETI) = Chilopoda, Diplopoda and Oligochaeta; other vertebrates (OV) = lizard, bird and caiman; empty = number of empty stomachs; plant = number of stomachs with plant material. %N is based on the number of stomachs with food.

	C. crocodilus				*M. niger*			
	Occurrence		Mass		Occurrence		Mass	
Categories	N	%N	g	%M	N	%N	g	%M
TI	74	46	56.0	3.9	17	85	18.8	29.4
Shrimps	13	8	4.7	0.3	2	10	0.2	0.3
Crabs	56	35	217.3	15.3	11	55	24.5	38.3
Molluscs	5	3	5.6	0.4	6	30	20.3	31.8
ETI	6	4	3.0	0.2	0	0	0	0
Snakes	5	3	10.9	0.8	0	0	0	0
Mammals	7	4	135.8	9.6	1	5	0.1	0.2
Fish	73	45	924.2	65.1	0	0	0	0
OV	3	2	62.7	4.4	0	0	0	0
Total			1420.2				63.9	
Empty	52	24			5	20		
Plant	96	45	158.6		11	44	24.0	

5% or more of the total number of stomachs with food were analyzed (Table 1). The consumption of shrimps and mammals by *M. niger* was not analyzed because these categories were present only in the 45 and 85 SVL classes, respectively. Empty stomachs were not included in the analyses.

Relationship Between Caiman Size and Prey Size.—Variation in the mean size of prey consumed in relation to the SVL of caimans was examined by regression analysis. Prey size was represented by the target-size index (Webb et al., 1982, as modified by Magnusson et al., 1987). The modified index is continuous, relatively independent of the shape of the prey, and consists of the square root of the product of the largest axis of the prey body and the largest axis orthogonal to the first, excluding appendages (Magnusson et al., 1987).

The analyses of target-sizes was based on 227 prey found in 82 stomachs of *C. crocodilus* and 25 prey from 11 stomachs of *M. niger.* Too few *M. niger* were collected to justify analyses within prey categories. Prey were measured with Vernier calipers accurate to 0.05 cm. The target-sizes of fragmented crabs (TSC, cm) and fish (*Plagioscon:* Sciaenidae) (TSP, cm) were estimated from lengths of claws (LC) and weights of otoliths (OTO), respectively, based on regression equations from samples of crabs (TSC = 0.38 + 1.34LC, $r^2 = 0.905$, $F_{1,67} = 635.7$, $P < 0.001$) and *Plagioscon* (TSP = 8.43 + 6.0OTO, $r^2 = 0.95$, $F_{1,26} = 454.7$, $P < 0.001$) collected in the study area.

Effects of the Type of Water Body, Season and Prey Availability on Diet.—Analysis of covariance (ANCOVA) was used to study the relationship between the mean mass of food and the mean proportion of each prey category consumed by 176 *C. crocodilus* in relation to the type of the water body (lake or canal) and season. Seasons were defined as high water (water level ≥ 26 m, $\bar{x}$ = 27.4 m), rising water (20 m ≤ water level < 26 m, $\bar{x}$ = 22.6 m), and low water (water level < 19 m, $\bar{x}$ = 17.6 m) depending of the level of the Rio Negro. Mean values for each season were used in analyses.

The proportion of each prey category was square-root arcsine transformed before analyses. The mean SVL of each size class was used as the covariate in the ANCOVA. Homogeneity of slopes was tested in all ANCOVAS using the interaction term (Wilkinson, 1990). However, interaction terms were not included unless significant ($P > 0.05$), or unless there was an a priori biological reason to expect an interaction. The small number (25) of stomach contents of *M. niger* obtained did not justify use of ANCOVA to investigate effects of water-body type and season on diet of this species.

The availability of fish, terrestrial invertebrates (TI), shrimps, and crabs were estimated along 500 m sections of shoreline in 46 sites within the Archipelago, between June 1991 and March 1992. Fish were sampled with three gill nets, and TI, shrimps, and crabs were sampled with a dipnet (Da Silveira et al., 1997).

Bootstrap power analyses were done with SIMSTAT (Péladeau, 1996), and other all statistical procedures were done with SYSTAT (Wilkinson, 1990).

RESULTS

We removed stomach contents from 213 *C. crocodilus* and 25 *M. niger.* Almost all sizes of *C.*

TABLE 2. Frequency of occurrence of prey categories in different SVL classes of *C. crocodilus* and *M. niger.* N = number of stomach contents analyzed; terrestrial invertebrates (TI), elongated terrestrial invertebrates (ETI) = Chilopoda, Diplopoda and Oligochaeta; other vertebrates (OV) = lizard, bird and caiman.

	Snout–vent length classes (cm)										
Categories	15	25	35	45	55	65	75	85	95	105	115
					Caiman crocodilus						
N	17	5	17	33	27	41	29	23	9	11	1
TI	14	4	7	16	14	9	3	4	4	1	0
Shrimps	1	0	4	4	2	1	0	1	0	0	0
Crabs	5	2	3	12	6	16	4	6	1	1	0
Mollusc	0	0	0	1	1	0	1	1	0	1	0
ETI	1	0	1	3	0	1	0	0	0	0	0
Snakes	0	0	1	0	3	1	0	0	0	0	0
Mammals	0	0	0	1	3	3	0	0	0	0	0
Fish	0	0	4	15	8	14	12	10	10	5	1
OV	0	0	0	0	1	0	1	1	0	0	0
					Melanosuchus niger						
N	4	—	6	5	3	2	2	2	1	—	—
TI	4	—	4	4	1	1	2	1	1	—	—
Shrimps	0	—	0	2	0	0	0	0	0	—	—
Crabs	1	—	2	3	1	2	0	1	1	—	—
Mollusc	0	—	0	2	1	1	0	1	1	—	—
Mammals	0	—	0	0	0	0	0	1	0	—	—

crocodilus that occur in the Archipelago were captured each month for stomach flushing (Fig. 1A and C), but not for *M. niger* (Fig. 1B). All *M. niger* whose stomachs were flushed were less than 100 cm SVL (Fig. 1D).

Twenty four percent of the *C. crocodilus* and 20% of the *M. niger* that we flushed had empty stomachs. The total mass of stomach contents from 213 *C. crocodilus* was only 1420.2 g, and the 25 *M. niger* contained only 63.9 g of food. Plant material occurred in 45% of individuals of *C. crocodilus* and in 44% of *M. niger* (Table 1). Rocks are rare or absent from the Archipelago and no stones were found in stomach contents. Plant material found in stomachs was comprised of grasses (*Oryzia perennis* and *Paspalum repens*) and fragments of other plants.

Caiman crocodilus ate a variety of aquatic and terrestrial invertebrates and vertebrates in the Anavilhanas Archipelago. Terrestrial invertebrates, fish, crabs, and spiders were the categories of prey that occurred at highest frequencies. Other prey categories occurred in less than 10% of stomachs with food (Table 1).

Insects consumed were Coleoptera (nymphs and adults), Orthoptera, Hymenoptera, Homoptera, Odonata (larvae and adults), and Lepidoptera larvae. Shrimps consumed were palaemonids (*Pseudopalaemon, Palaemonetes,* and *Macrobachium*). Crabs were trichodactylids (*Sylviocarcinus pictus, Valdivia serrata,* and probably *Poppiana laevifrons*). Molluscs were ampularids (*Pomacea*) and all mammals were rodents. Only two specimens of snakes could be identified (*Hydrops martii* and *H. triangularis*—Colubridae). The fish identified were Characiformes, Perciformes, Siluriformes, Beloniformes, Synbranchiformes, and Osteoglossiformes. We encountered fragments of one teiid lizard (*Crocodilurus* or *Ameiva*), one bird (Columbidae), and the bones of an unidentified caiman, in three different *C. crocodilus.* Each type of vertebrate was found in only one caiman (Table 1).

Fish and crabs accounted for 65% and 15%, respectively, of the total mass of food present in stomachs of *C. crocodilus.* Mammals occurred in only 4% of stomachs with food. However, this category was the third largest in terms of mass (Table 1).

Caiman crocodilus in the 15 cm and 25 cm SVL classes ate only invertebrates, but those in the 35 cm class and larger had vertebrates in their diet. Terrestrial invertebrates and crabs occurred in the diets of all size classes, except for the 115 cm class, which was represented by one *C. crocodilus* which had eaten only fish (Table 2).

The *M. niger* had eaten mainly invertebrates. The only evidence of vertebrates in the stomach contents of this species was hairs in one 90 cm SVL individual. Terrestrial invertebrates, crabs, and molluscs were the most frequent categories of prey and were responsible for 99.5% of the total mass of *M. niger* stomach contents (Table 1). Terrestrial invertebrates occurred in all size classes examined, and crabs were absent only in the 75 cm class (Table 2).

The two species of caimans could be compared only in the sizes between the 35 cm and

95 cm classes. The occurrence of fish was significantly greater in *C. crocodilus* (X^2_1 = 13.2, P = 0.05) and the occurrence of molluscs was greater in *M. niger* (X^2_1 = 28.7, P = 0.05). The mean mass of food contained in the stomachs increased significantly with the size class of *C. crocodilus* (Fig. 2A). The mean proportion of the TI category consumed decreased (Fig. 2B), and that of fish increased with an increase in caiman size (Fig. 2C). There was no significant relationship between the mean proportion of crabs (r^2 = 0.142, $F_{1,9}$ = 1.486, P = 0.254) or shrimps (r^2 = 0.091, $F_{1,9}$ = 0.896, P = 0.369) consumed and size of *C. crocodilus*. However, the lack of relationship for shrimps could be due to an effect of habitat not included in this analysis (see below). The occurrence of other categories of prey was too infrequent (less than 5%) for statistical analysis.

The mean mass of food consumed did not vary significantly with *M. niger* size. However, the general trend of the data suggests that this relationship may be significant with a larger sample (Fig. 3A). Bootstrap power analysis indicated that a sample of 15 stomachs would have a probability about 80% of detecting a relationship of the magnitude apparent in our data at an α = 0.05, and that it would require about 22 caimans to have a 95% chance of detecting a relationship of that magnitude. The mean proportion of molluscs consumed increased significantly with *M. niger* size (Fig. 3B), but there was no relationship between caiman size and the mean proportion of TI (r^2 = 0.346, $F_{1,6}$ = 3.173, P = 0.125) or crabs (r^2 = 0.017, $F_{1,6}$ = 0.101, P = 0.762) consumed.

Prey Size.—The mean sizes of all prey (Fig. 4A) and of fish (Fig. 4B) eaten were significantly and positively related to *C. crocodilus* size. Individuals greater than 50 cm SVL included larger prey in their diets, but also continued to eat small prey (Fig. 4A). However, there was no relationship between the mean size of prey in the TI category (r^2 = 0.063, $F_{1,27}$ = 1.830, P = 0.187), shrimps (r^2 = 0.008, $F_{1,8}$ = 0.064, P = 0.807), or crabs (r^2 = 0.050, $F_{1,26}$ = 1.360, P = 0.254) eaten and the size of *C. crocodilus*. However, when we excluded one *C. crocodilus* from the analysis, the relationship between mean size of shrimps and size of caimans approached significance (r^2 = 0.431, $F_{1,7}$ = 5.295, P = 0.055), indicating a possible type II error. The mean size of all prey consumed by *M. niger* was significantly and positively related to caiman size class (Fig. 4C).

Effects of Water Body Type, Season and Food Availability on Diet.—ANCOVA indicated that water body type (lake or canal) affected the mean mass of food consumed by *C. crocodilus*, but there was no effect of season, as indexed by water level (Table 3A).

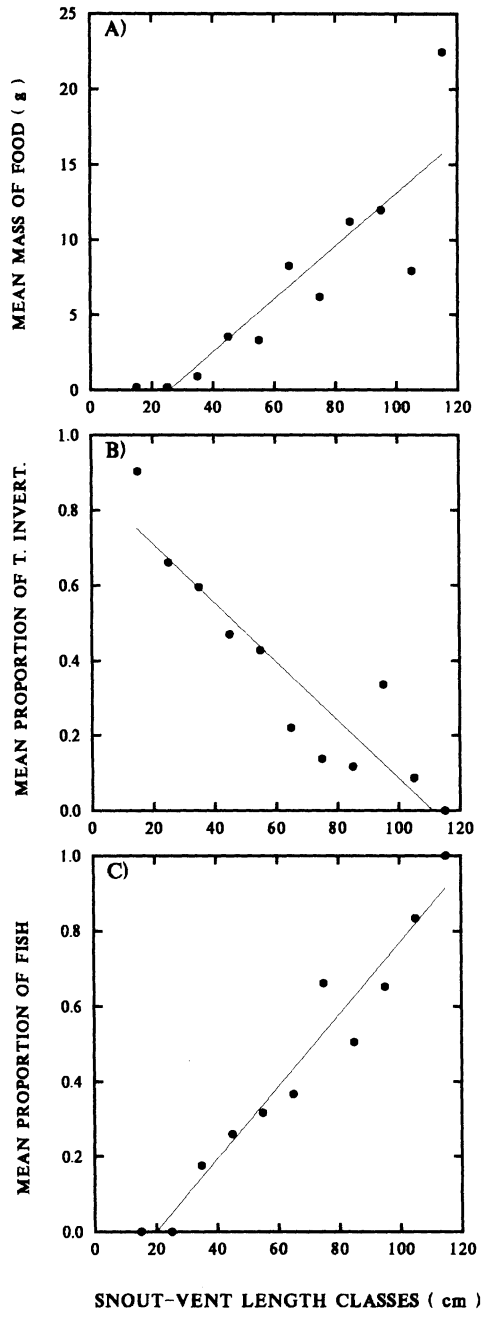

FIG. 2. A) Relationship between the mean mass of food in the stomach contents of *C. crocodilus* and snout–vent length class (SVLC) (mass = −4.525 + 0.176SVLC, r^2 = 0.776, $F_{1,9}$ = 31.117, P = 0.000). Relationships between the mean proportions consumed of B) terrestrial invertebrates (TI), and C) fish, and SVLC of *C. crocodilus*. (TI = 0.867 − 0.008SVLC, r^2 = 0.847, $F_{1,9}$ = 50.010, P = 0.000; fish = −0.192 + 0.010SVLC, r^2 = 0.949, $F_{1,9}$ = 166.213, P = 0.000). The SVL classes are in intervals of 10 cm. Each point in part A corresponds to the mean mass of food by SVL class. In parts B and C, each point corresponds to the mean proportion of a prey category in each SVL class.

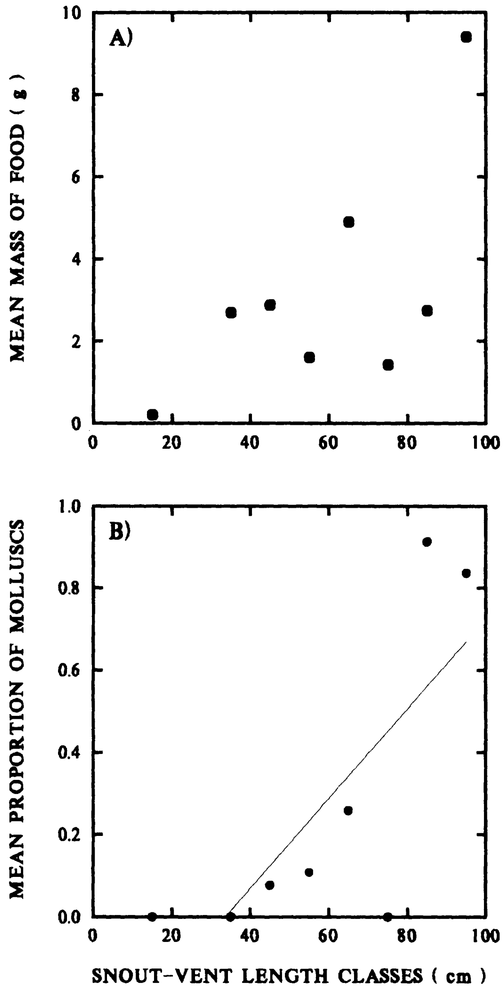

FIG. 3. A) Relationship between the mean mass of food in the stomach contents of *M. niger* and SVL class (SVLC) (mass = −0.866 + 0.070SVLC, $r^2 = 0.429$, $F_{1,6} = 4.517$, $P = 0.078$). B) Relationships between the mean proportion of molluscs and SVLC of *M. niger*. (molluscs = −0.367 + 0.011SVLC, $r^2 = 0.585$, $F_{1,6} = 8.441$, $P = 0.027$). SVL classes are in 10 cm intervals. Each point in part A corresponds to mean mass by SVL class. In part B, each point corresponds to mean proportion of molluscs in the diet in each SVL class.

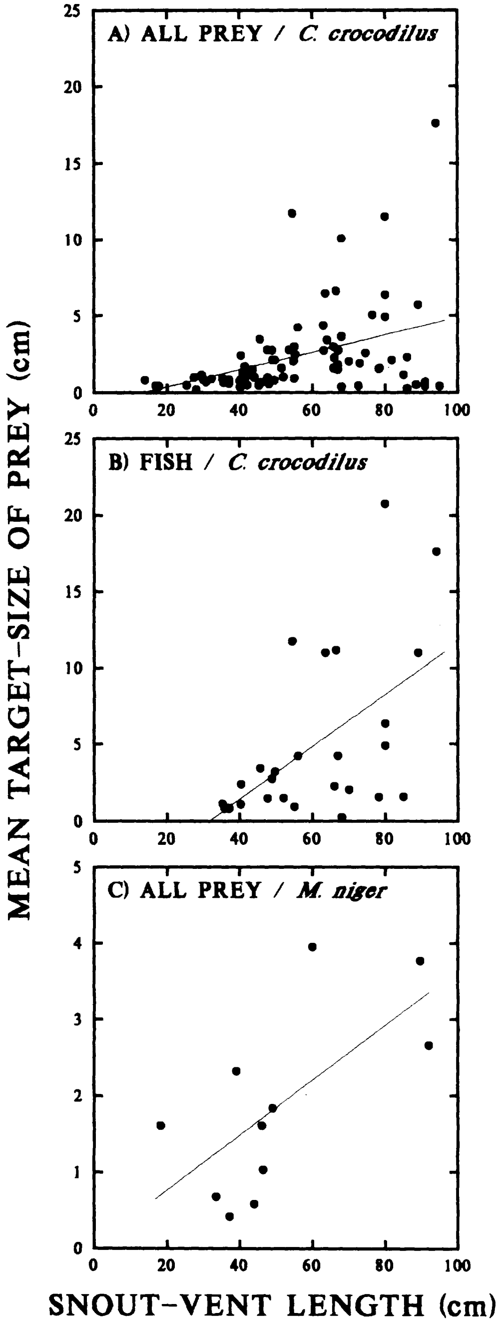

FIG. 4. Relationships between A) the mean target size of all prey (MTS, cm) and B) the mean target size of fish (MTSF, cm) and SVL class (SVLC, cm) for 82 *C. crocodilus*. (MTS = −0.753 + 0.056SVL, $r^2 = 0.157$, $F_{1,79} = 14.726$, $P = 0.000$; MTSF = −5.406 + 0.171SVL, $r^2 = 0.229$, $F_{1,24} = 10.224$, $P = 0.004$). C) Relationship between the mean target-size of all prey (MTS, cm) and (SVLC) of 11 *M. niger* (MTS = 0.046 + 0.036SVL, $r^2 = 0.045$, $F_{1,9} = 7.203$, $P = 0.025$).

There was an interaction between the effects of water body type and season on the mean proportion of fish consumed by *C. crocodilus* (Table 3B). In lakes, the mean proportion of fish consumed (Fig. 5A) and the availability of fish (Fig. 5C) decreased with an increase in the level of the Rio Negro. In canals, the proportion of fish in the diet increased with an increase in river level (Fig. 5B), while fish availability remained relatively constant with water level changes (Fig. 5D). However, we collected only two sam-

TABLE 3. Summary of analyses of covariance: The effects of the covariate snout–vent length (SVL, grouped in 10 cm intervals), type of water body (lake or canal) and season, as indexed by the water level of the Rio Negro (low, rising and high) on A) mean mass of food, B) mean proportion of fish, C) terrestrial invertebrates (TI), D) shrimps and E) crabs consumed by *C. crocodilus.*

Variables	Sum of squares	DF	Mean square	F	P	r^2
A) Mean Mass of Food						
SVL	721.560	1	721.560	6.771	0.013	0.256
Season	86.926	1	86.926	0.816	0.372	
Type	420.925	1	420.925	3.950	0.054	
Type*Season	376.719	1	376.719	3.535	0.067	
Error	4369.349	41	106.569			
B) Mean Proportion of Fish						
SVL	2.783	1	2.783	35.100	0.000	0.672
Season	0.035	1	0.035	0.446	0.509	
Type	1.354	1	1.354	17.075	0.000	
Type*Season	1.666	1	1.666	21.016	0.000	
Error	2.775	35	0.079			
C) Mean Proportion of TI						
SVL	2.391	1	2.391	19.444	0.000	0.530
Season	0.253	1	0.253	2.054	0.160	
Type	1.172	1	1.172	9.531	0.004	
Type*Season	1.263	1	1.263	10.273	0.003	
Error	4.426	36	0.123			
D) Mean Proportion of Shrimps						
SVL	0.028	1	0.028	6.523	0.015	0.400
Season	0.032	1	0.032	7.397	0.010	
Type	0.034	1	0.034	7.774	0.009	
Type*Season	0.025	1	0.025	5.862	0.021	
Error	0.152	35	0.004			
E) Mean Proportion of Crabs						
SVL	0.007	1	0.007	0.072	0.790	0.061
Season	0.016	1	0.016	0.170	0.683	
Type	0.012	1	0.012	0.135	0.716	
Type*Season	0.032	1	0.032	0.349	0.558	
Error	3.230	35	0.092			

ples of food availability in the canals at high water.

The type of water body significantly affected the mean proportion of TI category consumed by *C. crocodilus,* and there was an interaction between water body type and season (Table 3C). In lakes, the mean proportion of TI category consumed increased with an increase in river level (Fig. 5A), while TI availability was similar among seasons (Fig. 5C). In canals, the proportions consumed tended to decrease with an increase in water level (Fig. 5B), while availability of TI was generally similar among seasons, in spite of two canals with high TI availability when the water was rising (Fig. 5D).

There was a significant interaction between water-body type and season on the mean proportion of shrimps consumed by *C. crocodilus* (Table 3D). With the inclusion of water body type and season, ANCOVA indicated that the mean proportion of shrimps consumed also varied significantly with the caiman size (Table 3D). This relationship was not detected in analyses that did not include habitat variables, which reduced the residual variance. However, we have insufficient data to explore this relationship further. In lakes, the mean proportion consumed (Fig. 6A), and the availability of shrimps (Fig. 6C), decreased with an increase in river level. In canals, shrimp consumption (Fig. 6B) and shrimp availability (Fig. 6D) were less than those in lakes and were similar among seasons.

Water body type and season did not affect the mean proportion of crabs consumed by *C. crocodilus* (Table 3E). In lakes and canals, crab availability was similar among seasons (Figs. 6G and H).

DISCUSSION

The size structure of *C. crocodilus* from which stomach contents were sampled was similar to that we observed during spotlight surveys in the Anavilhanas Archipelago. However, some

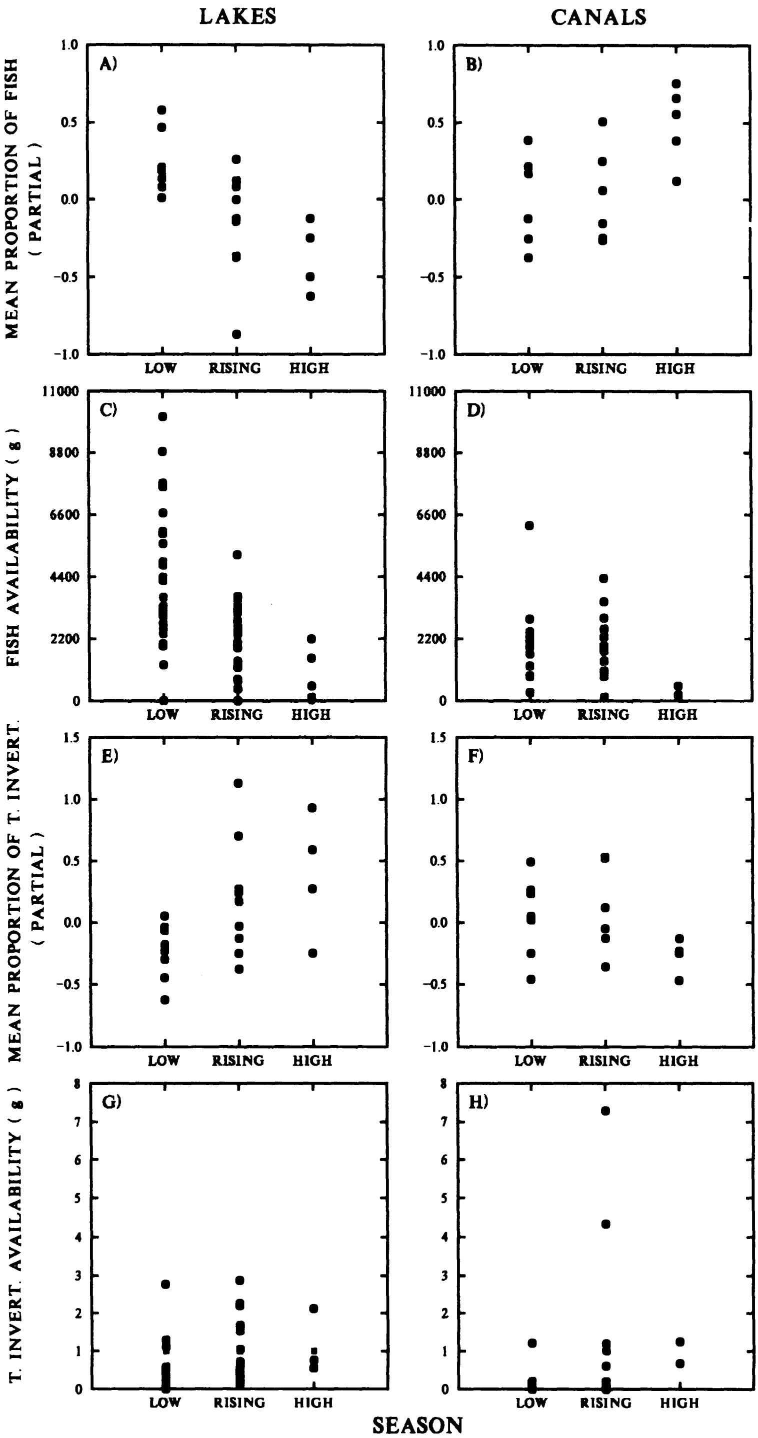

FIG. 5. Mean proportion of fish in the stomach contents of 176 *C. crocodilus* captured in A) lakes and B) canals, during low, rising and high-water seasons. Relative Fish availability (mass in grams) in C) lakes and D) canals, in the same seasons. Mean proportion of terrestrial invertebrates (TI) in the stomach contents of the same caimans, captured in E) lakes and F) canals and TI availability (mass in grams) in G) lakes and H) canals, in the same seasons. In parts A, B, E and F, each point corresponds to the mean proportion (square-root arcsine transformed) of fish and TI, respectively, (independent of caiman size) in each SVL class. In parts C, D, G and H, each point corresponds to fish and TI availability respectively, in one site in the Archipelago.

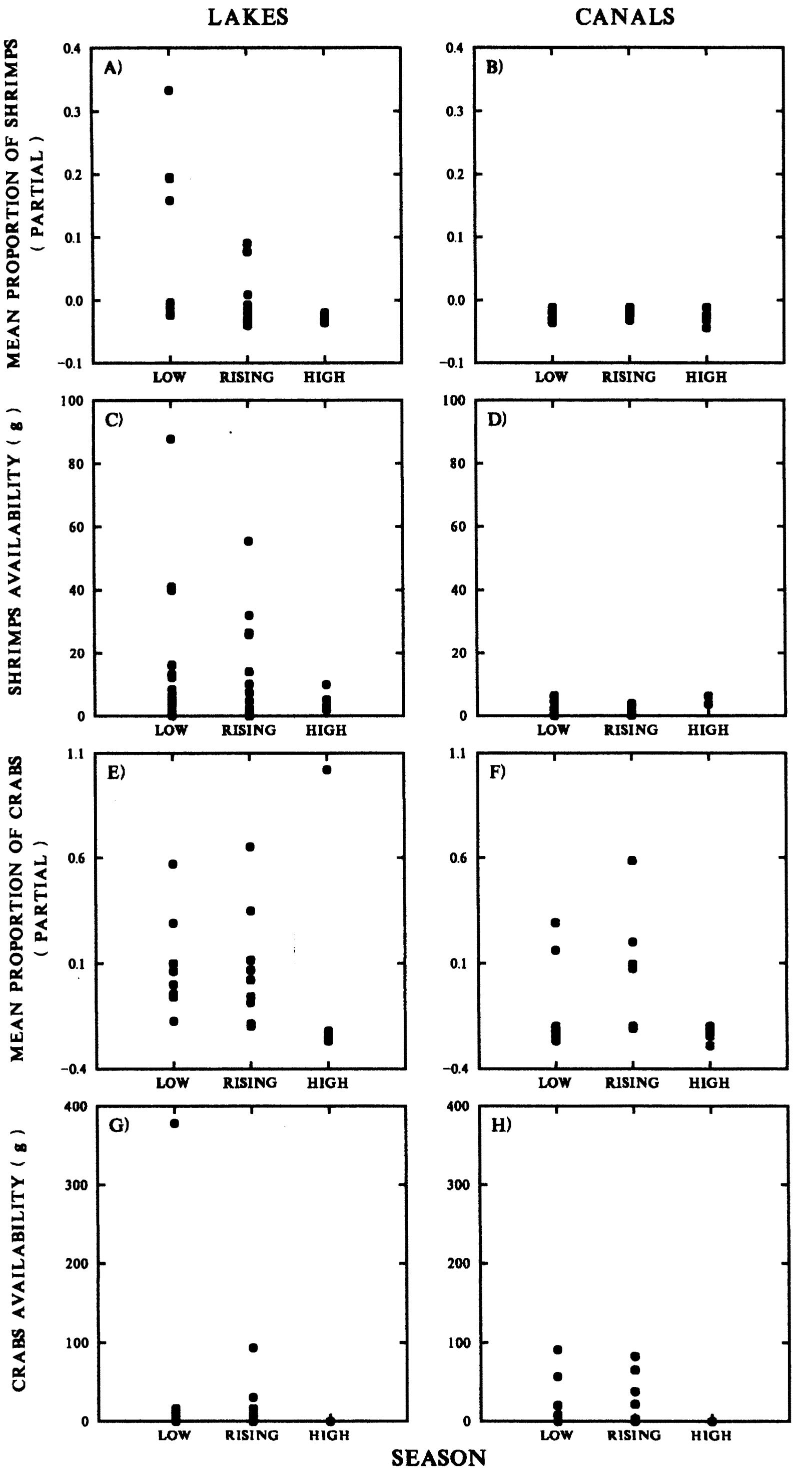

FIG. 6. Mean proportion of shrimps in the stomach contents of 176 *C. crocodilus*, captured in A) lakes and B) canals, during low, rising and high-water seasons. Relative shrimp availability (mass in grams) in C) lakes and D) canals, in the same seasons. Mean proportion of crabs in the stomach contents of 176 *C. crocodilus*, captured in E) lakes and F) canals, during low, rising and high-water seasons. Crab availability (mass in grams) in G) lakes and H) canals, in the same seasons. In parts A, B, E and F, each point corresponds to the mean proportion (square-root arcsine transformed) of shrimps and crabs consumed (independent of caiman size) in each SVL class. In parts C, D, G and H, each point corresponds to shrimps and crabs availability respectively, at one site in the Archipelago.

M. niger adults we observed in the study area (Da Silveira et al., 1997) were not captured. The total amount of food recovered from the caimans was low. Given the relatively slow rates of digestion of reptiles in general (Pough, 1983) and crocodilians in particular (Delany and Abercrombie, 1986), this indicates that the caiman populations are likely to have only a small impact on the rich and varied fish fauna of the Archipelago (Goulding et al., 1988), and does not support the claims in the popular press that caimans are competing with local fishermen.

The diets of crocodilians can vary with age, size, habitat, season, year, and prey availability (Webb et al., 1982; Delany and Abercrombie, 1986; Lang, 1987; Magnusson et al., 1987; Gorzula and Seijas, 1989). The relationships between changes in prey types and size of *C. crocodilus* in the Anavilhanas were similar to those encountered in other studies. Hatchlings eat mainly invertebrates, principally insects (Staton and Dixon, 1975; Escalona, 1991). Subadults and adults eat vertebrates, principally fish (Seijas and Ramos, 1980; Ayarzaguena, 1983; Magnusson et al., 1987; Fitzgerald, 1988; Thorbjarnason, 1993).

The types of prey consumed by *C. crocodilus* and *M. niger* in the Anavilhanas Archipelago were similar as they are in many other areas of the Brazilian Amazon (Magnusson et al., 1987). However, the occurrences of fish and molluscs of the genus *Pomacea* in the diets of these species in the Anavilhanas were statistically different. Fish were common in the diet of *C. crocodilus* in this study, but the *M. niger* investigated had not consumed fish. *Pomacea* occurred in 24% of *M. niger*, but only 2% of *C. crocodilus*. Although the sample size of *M. niger* was small, these differences could reflect different foraging modes or feeding microhabitats, and should be investigated in future studies.

Ingestion of plants by caimans in the Anavilhanas Archipelago was probably accidental, since plant protein is not digested or assimilated by crocodilians in the wild (Coulson and Hernandez, 1983; but see Staton et al., 1990). Previous studies did not find relationships between the occurrence of plant material and the size of *C. crocodilus* (Magnusson et al., 1987; Fitzgerald, 1988).

Stones are common in the stomachs of *C. crocodilus* in the Venezuelan Llanos, and their occurrence and mass is related to caiman size (Ayarzaguena, 1983; Fitzgerald, 1988; Thorbjarnarson, 1993). We did not find stones in the stomachs of *C. crocodilus* or *M. niger* in the Anavilhanas. Stones are generally absent in the Anavilhanas Archipelago, but are common on the Rio Negro shoreline, that borders the Archipelago. This suggests that caimans did not forage outside the Archipelago. In previous studies in the Amazon, the occurrence of stones was low and not related to *C. crocodilus* size (Vanzolini and Gomes, 1979; Magnusson et al., 1987). Magnusson et al. (1987) did not find stones in the stomachs of juvenile *M. niger*. One *C. crocodilus* of 75 cm SVL class had a fish hook in its stomach.

Crocodilians eat larger prey as they grow in size but they also continue to consume small prey (Valentine et al., 1972). In this study, the majority of prey consumed by caimans were small (target-size < 5 cm). However, the mean size of prey consumed increased with the size of *C. crocodilus* and *M. niger*. A similar relationship was found by Magnusson et al. (1987). Those authors also found a relationship between the mean sizes of insects, spiders, and crabs which were consumed, and the size of *C. crocodilus*. However, we did not find such relationships in this study.

Most food consumption by *Crocodylus johnsoni* in Australia (Webb et al., 1982) and by *Caiman crocodilus* in the Venezuelan Guayana (Gorzula, 1978) occurs in the wet season. In the Anavilhanas, the mean mass of food consumed by *C. crocodilus* varied between lakes and canals, but did not vary seasonally with river level. However, there was seasonal variation in the mean proportion of prey categories consumed. Similarly, Thorbjarnarson (1993) showed that the amount of recently ingested food found in the stomachs of *C. crocodilus* in the Venezuelan Llanos did not vary among seasons, but that the types of prey consumed did.

Fish and crabs represented 80% of the total mass of food consumed by *C. crocodilus* in this study. The differences in the mean proportion of fish consumed by *C. crocodilus* between lakes and canals in the Anavilhanas Archipelago could be related to differences in availability and/or to differences in prey vulnerability between these types of water bodies. The greater proportion of fish found in the diets of *C. crocodilus* caught in lakes, compared to those caught in canals during low water, is probably related to greater fish availability and lesser depths and currents in lakes (Da Silveira et al., 1997), which probably increase prey vulnerability to crocodilians.

We attempted to sample food availability of most types of prey consumed by caimans in the Anavilhanas. However, what is available to sampling methods and what is available to caimans could be very different. Without data on movements of caimans between habitats, it is difficult to determine if most caimans in the Anavilhanas are subjected to variations in the availability and consumption of prey. Future studies should attempt to combine more detailed information on caiman behavior with information on diet, and this could involve an intensive radio-telemetry study.

In lakes, the mean proportion of fish consumed decreased with an increase in river level, while in canals, the proportion of fish increased. This is probably because the Rio Negro inundates a greater proportion of flooded forest around the lakes than along the canals, where the banks are steeper (Da Silveira et al., 1997). In the canals, fish remained in the main water body longer than in the lakes, where they migrated into the vegetation and may have become more difficult for caimans to catch.

In the Venezuelan Llanos, crabs are an important prey of *C. crocodilus* during the wet season (Fitzgerald, 1988; Thorbjarnarson, 1993). In this study, the mean proportion of crabs consumed by *C. crocodilus* did not vary between lakes and canals, or with seasonal changes in river level. Shrimps are not generally considered important in the diet of *C. crocodilus* (see Seijas and Ramos, 1980 for an exception), and the results here (3% of total mass of food consumed) support this generality. However, shrimp consumption varied between lakes and canals, and with season.

Caiman crocodilus and *M. niger* are generalist opportunistic predators, and some of the generalizations that have been made in previous diet studies of these species (Vanzolini and Gomes, 1979; Seijas and Ramos, 1980; Magnusson et al., 1987; Fitzgerald, 1988; Thorbjarnarson, 1993) have application in the Anavilhanas Archipelago. However, this study showed that habitat structure and seasonality affect the diet of the caimans. Therefore, these generalizations must be used with caution.

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Comparative Phenology and Demography of *Triturus boscai* from Portugal

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ABSTRACT.—**The population structure and ecology of *Triturus boscai* were studied during eight years in northern (high and low altitudes) and central Portugal. Newts were censused monthly by dip-netting aquatic habitats. Annual activity cycles and reproductive phenologies varied among populations. Northern newts enter into winter dormancy and Central newts into summer dormancy. Individual age was assessed by skeletochronology using lines of arrested growth in the humeri. Females were larger than males in each population, but there was no difference between the sexes in age frequency distribution. The youngest mature newts were three years old. A higher growth rate in females, both before and after maturity, was responsible for the sexual size dimorphism. The growth curve showed a strong inflection after maturity in newts from Central Portugal; these were the smallest newts although mean age and longevity (7–8 yr) were greater than in the two northern populations (6–7 yr). Interpopulation differences in phenology are explained by differences in local climatic conditions, although differences in demographic parameters did not follow expected trends.**

Triturus boscai is a small newt endemic to the Iberian Peninsula and widely distributed in Portugal. This species inhabits small lakes, streams, and peat bogs but prefers small ponds with abundant vegetation (Caetano, 1982a). *Triturus boscai* is one of the most aquatic European newts and, like some *T. cristatus* (Thorn, 1968), may spend a large portion of the year in water. Apart from biogeography (Crespo, 1971; Salvador, 1974), morphological descriptions (Caetano, 1982b), and analysis of sexual behavior (Rafinski and Pecio, 1992; Faria, 1993), the only life history account of Bosca's newt is that of Barbadillo (1987). Caetano (1990) provided preliminary information on the application of skeletochronology for age estimation of this species. No demographic studies have been published on *T. boscai.*

Intraspecific plasticity in phenology and demographic traits may be expected and has been demonstrated for a variety of salamander species (e.g., Tilley, 1980; Dolmen, 1983; Bruce and Hairston, 1990; Caetano and Leclair, 1996). In *Triturus marmoratus* from Portugal, specimens from southern regions have earlier maturity, a markedly shortened life-span, and do not reach the same large size compared with specimens from northern regions (Caetano and Castanet,