# **ECOTROPICA**

Volume 7 2001 No. 1-2

ECOTROPICA 7: 1-11, 2001 © Society for Tropical Ecology

# FEEDING ECOLOGY OF BLACK CAIMAN MELANOSUCHUS NIGER IN A WESTERN AMAZONIAN FOREST: THE EFFECTS OF ONTOGENY AND SEASONALITY ON DIET COMPOSITION

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Resumen. Entre 1992 y 1994 se capturaron 88 individuos del lagarto negro (Melanosuchus niger) en la laguna de Cocha Cashu en la Amazonia peruana, Parque Nacional de Manu. Las muestras de contenido estomacal se recolectaron sin matar a los animales. Queince categorias de presas, incluyendo vertebrados e invertebrados se encontraron en los estomagos. Caracoles (Pomatia spp.) y peces fueron los principales items en la dieta de adultos. Caracoles fueram mas abundante en los animales jovenes, mientras que los peces fueron mas abundantes en la dieta de los adultos. Batracios, pequenas aves, y mamiferos, tambien fueram comidos. Los resultados de estadisticas descriptivas y de analisis multivariado de ordenacion indican que existe un efecto significativo de la ontogenia en la composicion de la dieta. Se encontraron ademas, diferencias estacionales significativas en la composicion de la dieta, lo cual sugere que el lagarto negro tine que ajustar su comportamiento alimenticio de acuerdo a la abundancia y disponibilidad de alimento. A pesar del lagarto negro ser un predator primario, mismo adultos dependem tanto de vertebrados como de invertebrados para satisfacer sus necesidades energeticas. La conservacion de esta especíe, que ha sufrido fuertemente por caza indiscriminada, tiene que tomar en cuenta la protecion de areas naturales como lagunas y areas riberenas que presentan una alta diversidad de organismos de varios niveles troficos y son alimento para el lagarto negro.

Abstract. During 1992 and 1994, 88 individuals of black caiman (Melanosuchus niger) were captured in an oxbow lake in Manu National Park, Peruvian Amazonia. Stomach contents were collected without killing the animals. Fifteen prey categories including invertebrates and vertebrates were found in the stomachs. Snails (Pomatia spp.) and fish were the main items present in the diet. Snails were more abundant in the diet of juveniles and fish more abundant in that of adults. Frogs, birds, and mammals were also eaten. Results from both descriptive statistics and multivariate ordination analyses indicated that there was a significant effect of ontogeny on diet composition. There were also significant seasonal differences in diet composition, suggesting that in order to resist periods of food scarcity black caimans may adjust their feeding behavior according to changes in prey abundance and occurrence. Although black caimans are top predators, even adults apparently depend on both invertebrates and vertebrates to satisfy their energetic needs. Conservation of this heavily hunted species has to consider protection of natural areas such as lakes and rivers, principally those where a high diversity and abundance of organisms from various trophic levels occurs. Accepted 29 December 2000.

#### INTRODUCTION

An important issue in tropical ecology is the understanding of how complex ecological food webs in terrestrial and aquatic communities are composed and structured. Top predators feed on many prey species from different trophic levels. Therefore the analysis of stomach contents of predators may offer an opportunity to describe the composition of prey species they eat at a given site and verify how their diet composition changes through time.

The black caiman, Melanosuchus niger, is the largest alligatorid in South America. It is also the largest

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predator in the Amazon basin, growing to more than 5 m in body length (Medem 1983). The species has been intensively hunted because of its size, the quality of its skin, and recently for meat (Steward 1987, Da Silveira & Thorbjarnarson 1999), and also because it is considered a potential danger to humans and domestic animals (Plotkin *et al.* 1982).

Caimans are considered opportunistic and generalist in their feeding habits because they consume a wide variety of prey. Juveniles consume mainly insects, and adults include a large proportion of molluscs, fish, and other chordates (Fitzgerald 1988). Juvenile of spectacled caiman (*C. crocodiles*) feed almost exclusively on arthropods (Vásquez 1981), and that individuals larger than 1 m consume more vertebrates, crustaceans, birds, mammals, reptiles, and fish (Herrera & Perez 1986).

Although the black caiman occurs throughout the Amazon region, information on its food habits is scarce. The only available studies of feeding behavior and diet composition of this species are the nine stomach contents reported by Magnusson et al. (1987) and 25 stomach contents reported by Da Silveira & Magnusson (1999). In the Anavilhanas islands, central Amazon, the mean proportion of molluscs consumed increased significantly with the sizeclass of Melanosuchus niger (Da Silveira & Magnusson 1999). The same authors found no relationship between the mean mass of food or the mean proportion of other prey categories and size-class of this species. However, the mean size of all prey consumed was positively correlated with the size of M. niger (Da Silveira & Magnusson 1999). Vásquez (1981) reported the results from the stomach content of only one individual captured in Supay Cocha, Requena, in the Peruvian Amazon. Gorzula (1978) found that C. crocodilus in Venezuela had a more diverse diet composition during the wet season than during the dry season. In central Venezuelan Llanos, Thorbjarnarson (1993) analyzed a sample of 274 C. crocodilus (between October 1984 and June 1989) and found that fish, mammals, snails, and crabs were the most important prey. He also found that the diet of C. crocodilus shifted ontogenetically and seasonally. Fitzgerald (1988) recorded diet variation in C. crocodilus associated with changes in habitat, season, and age. At Cocha Cashu in Manu National Park, Peru, comparative studies were conducted on the biology and population status of black and spectacled caimans (Otte 1978, Herron 1985), but no information was given on diet composition.

The main objective of this three-year study was to analyze the diet composition of a population of black caiman in the Peruvian Amazon and determine whether it changes ontogenetically and seasonally.

# SITE AND METHODS

The study was conducted at Cocha Cashu Biological Station (11°51'S, 71°19'W) in Manu National Park, southeastern Peru. Cocha Cashu is an oxbow lake, which, during the highest floods, can be connected to the Manu River. The lake has an approximate area of 20 ha, a perimeter of 4 km, and a maximum depth of 2.95 m (Otte 1978, Herron 1985, Terborgh *et al.* 1985). The rainy season starts in October. Heavy period of rains occur between January and April (Terborgh *et al.* 1985), but precipitation is scarce between July and September. Annual mean precipitation for Cocha Cashu is about 2080 mm. Mean annual temperature is around 25° C.

Data were collected during August and October (dry season) of 1993. During this period, the river water level was low and the channel connecting it to the lake dried out, isolating the lake. The second part of the data collection was carried out between February and March (wet season) of 1994. During this period, the Cocha Cashu lake was directly connected to the river, which may have facilitated the movements of caimans of large size between the two aquatic systems.

Captures of black caimans. The caimans were captured using one of two methods, depending on the size of the animal. Small animals were grabbed by hand around their necks. Larger animals were caught with a lasso and a wooden handle placed around the neck of the animal and rapidly tightened (Vásquez 1981).

All black caiman individuals had complete tails, so we used their total length as a measure of size in the analysis. We also measured snout-vent length, head length, weight, and determined the sex of each individual. Sex was determined according by examining the genitals inside the cloaca (Chabreck 1965). Animals were marked by cutting off one of the caudal crest scales following the binary code of Vásquez (1981). Earlier marks were registered as well as information on natural injuries.

Collection of stomach contents. Caiman stomach contents were removed on the night of capture or the following morning. The method is a modification of the technique described by Taylor *et al.* (1978), and

consists of carefully inserting a transparent plastic tube into the caiman throat and filling the stomach with water. Tubes were lubricated with cooking oil and were of varying diameters depending on the size of the caiman. By gently pressing the ventral area near the stomach we were able to pump the water back with the stomach contents over a nylon mesh covering a plastic basin. The stomach contents were washed with water and preserved in 70% formal.

Statistical Analysis. For the analyses of diet, caimans were placed in the following eight size-class categories according to total body length: < 46 cm; 46-55 cm; 56-65 cm; 66-75 cm; 76-85 cm; 86-95 cm; 96-125 cm; > 125 cm. Caimans with empty stomachs were not included in the analysis. For the diet items we used the mean number of items/size-class of caiman to construct a raw matrix. The dissimilarity index was the mean of the differences in the proportions of each prey category in the diets, which gives the dissimilarity of the niche overlap formula (Winemiller & Pianka 1990). In this matrix the rows (objects) were the caiman size-classes, and the columns (attributes) were the mean proportions of each diet item. The mean values of prey items (in Table 1) were standardized by dividing them by their standard deviation. To give the same weight to each black caiman size-class, data were converted to proportions within size-classes. The prey categories were the following: molluscs (Pomatia spp.), fish, crabs, larvae, terrestrial beetles, aquatic beetles, centipedes, spiders, ants, and other insects. There was a great variety of species of coleopterans registered as prey items. However, identification was possible only to family in most cases and a few items were not identified.

The prey categories Coleoptera and other insects were placed in one category (insects), and because there was only one frog, one bird, and a few mammals they were all placed in one category (vertebrates). We used ordination analysis, which gives a test for the significance of the independent variables and shows the relationship between objects in two dimensions. Due to small number of items found in the black caiman stomachs, the category vertebrates was not included in the analysis.

The computer programs Systat (Wilkinson 1998) and PATN (Belbin 1992) were used to run the descriptive statistics and multivariate analysis respectively. Differences in diet composition in sample units from caiman of different ages were verified by using a semistrong hybrid non-metric multidimensional scaling ordination analysis (SSH-NMDS in PATN, Belbin 1992). We first used the Bray-Curtis index to construct a dissimilarity matrix. This index has been generally recommended for use in ecological studies (Minchin 1987, MacNally 1994). The multidimensional scaling SSH-NMDS was used to generate a single ordination of diet items within caiman sizes based on the Bray-Curtis distance matrix. The Bray-

TABLE 1. Diet items and size-classes of black caimans. Numbers are mean number of the diet items. The sample size (number of stomachs analyzed) is given within parenthesis (see methods for more explanations).

	Black caiman body length (cm)													
Diet items	< 46 (n = 3)	46-55 (n = 16)	56-65 (n = 12)	66-75 (n = 11)	76-85 (n = 15)	86-95 (n = 13)	96-125 (n = 11)	> 125 (n = 5)						
Snails	0.70	6.70	13.90	23.30	21.40	20.00	15.60	42.20						
Fish	0.00	0.17	0.00	0.17	0.32	0.33	0.40	0.60						
Crabs	1.57	4.00	2.60	0.17	0.58	0.88	0.00	0.00						
Larvae	8.00	6.00	13.30	4.25	1.84	0.78	0.40	0.60						
Terrestrial beetles <sup>1</sup>	3.00	8.10	3.50	2.00	2.10	0.40	0.60	2.40						
Aquatic beetles <sup>2</sup>	0.00	0.28	0.42	0.25	0.32	0.89	0.40	0.60						
Centipedes <sup>3</sup>	0.14	0.39	0.00	0.17	0.21	0.00	0.20	0.20						
Spiders	0.43	1.06	0.42	0.50	0.26	0.22	0.00	0.20						
Ants	3.40	1.70	0.08	0.33	0.68	0.22	0.20	0.20						
Other insects	0.00	0.06	0.00	0.17	0.05	0.11	0.00	0.00						

<sup>&</sup>lt;sup>1</sup> = Coleoptera; <sup>2</sup> = Belastomatidae; <sup>3</sup> = Myriapoda.

Curtis index is calculated according to the following formula:

$$D = \Sigma \mid Dik - Djk \mid / \Sigma (Dik + Djk)$$

Where Dik = the data value for the ith row and kth column of the data matrix; Djk = the data value for the jth row and kth column of the data matrix.

We also used SSH-NMDS ordination to verify whether there were seasonal changes in the diet composition of all black caiman individuals of considered separately and captured during the dry season of 1992 (28 individuals), dry season of 1993 (41 individuals),

and wet season of 1994 (19 individuals). In a multidimensional data matrix, individual black caimans were attributes and prey items the objects. The resulting vectors (SSH1 and SSH2) from the ordination were used as dependent variables in a multivariate analysis of variance (MANOVA), in which the categorical variable "individual" was used as an independent variable in the model. Finally, a multivariate test (Pillai Trace), available in Systat (Wilkinson 1998) was used to verify whether seasonal changes in diet composition were significant.

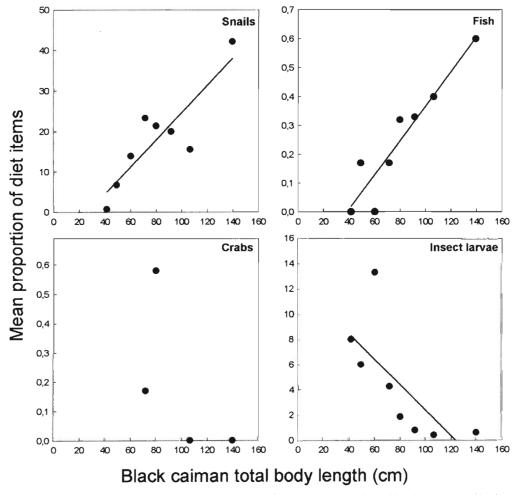
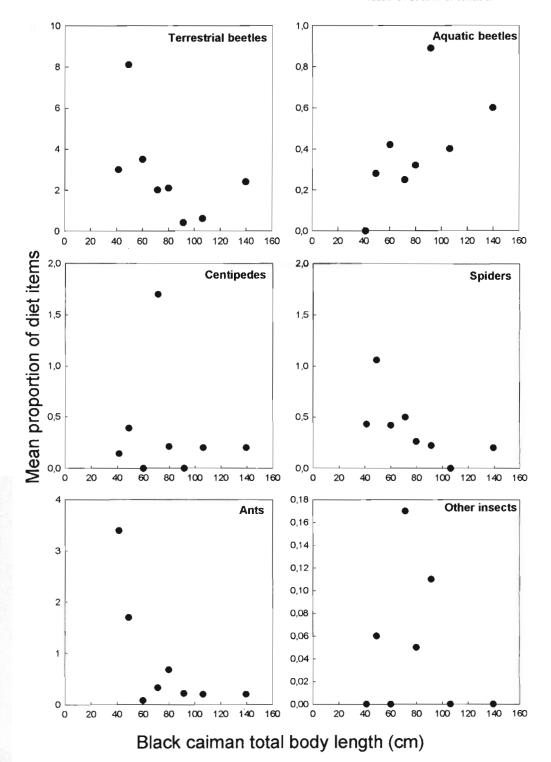


FIG. 1. Relationship between mean number of diet items found in the stomachs and black caiman total body length (cm). The equation for snails is  $y = 0.3369 \times -8.9448$ ; for fish  $y = 0.0060 \times -0.2284$ ; and for insect larvae  $y = -0.1012 \times +12.4852$ . Continued on page 5.



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# **RESULTS**

Diet composition and ontogenetic changes. Eighty eight black caimans were captured to remove the stomach contents. Two individuals had empty stomachs and therefore were not considered in the analysis. The proportions of prey in each diet category differed between different sizes of the black caimans (Table 1). The most numerous prey found in the diet, independent of caiman size, were snails, mainly *Pomatia* spp., which are very abundant at Cocha Cashu lake. As the caiman body size increased by a factor of four the mean number of snails in their stomach followed the same trend.

Snails and Coleoptera composed the most frequent and most abundant invertebrate prey items (Table 1). Other prey were frequent but not abundant were spiders, aquatic beetles, Myriapoda, crabs, and larvae. There were only one frog, one bird, and one mammal. A list of all the items found in the black caiman stomach contents at Cocha Cashu is available in appendix 1. In this appendix it can be seen that there is an impressive variation in diet composition among the 88 black caiman individuals.

The frequency of snails increased considerably with increasing black caiman body length. There was also a tendency to increase the frequency of fish with

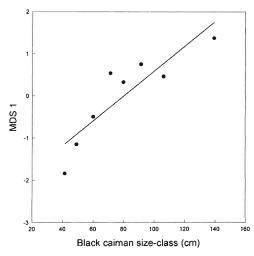


FIG. 2. Relationship between diet composition MDS1 (derived from multidimensional scaling analysis) and black caiman size-class (cm). The equation for this relationship is  $y = 0.0294 \times -2.3486$ .

increasing black caiman body size. The opposite tendency was observed for crabs. For the rest of the prey items there was no clear tendency (Table 1, Fig.1).

There was a positive and significant relationship between the mean proportion of snails in the diet and the black caiman size ( $r^2 = 0.875$ ; n = 8; P < 0.004, Fig. 1). A positive and significant relationship was also found between the mean proportion of fish in the diet and caiman size ( $r^2 = 0.939$ ; n = 8; P < 0.0005, Fig. 1). There was also a significant negative relationship between the mean proportion of insect larvae in the diet and caiman size ( $r^2 = 0.717$ ; n = 8; P < 0.045, Fig. 1). No significant relationships were found between the mean proportion of crabs, terrestrial beetles, aquatic beetles, centipedes, spiders, ants, other adult insects, and black caiman size (Fig.1). The number of opercula found in the stomach samples varied considerably, with a maximum of 202 in just one caiman. There was a great variety of species of coleopterans registered as prey items.

The results of a multiple dimensional scaling ordination analysis (SSH-MDS) summarized information on overlap of diet in one dimension, and explained a reasonable proportion of the variation between the categories of prey and caiman size-classes of caiman (stress = 0.10). The diet composition (MDS1 axis of the ordination) had a strong positive and significant relationship with size-classes of black caimans ( $r^2 = 0.887$ ; n = 8; P < 0.003, Fig. 2). Therefore the results of MDS analysis clearly suggest that diet composition changes as the black caiman grow larger (Table 1, Fig. 2).

The effects of seasonality on diet composition. The results of the SSH-MDS ordination to verify whether there were seasonal changes in diet composition, considering all black caiman individuals separately, indicated that there were differences in diet composition, since one group of individuals was very distinct in relation to the rest (see low right area of Fig. 3). The second dimension (MDS2 in Figure 3) of the ordination on caiman diet composition was significantly affected (Manova, F = 6.933; P = 0.002). The results of a (Manova) post-hoc multivariate test confirmed that there were significant seasonal differences in black caiman diet composition (Pillai Trace F = 3.736; df = 4, 166; P = 0.006) (Fig. 3). Some individuals had significantly more snails, spiders, aquatic beetles, and other insects in their stomachs during the wet season than during the dry season.

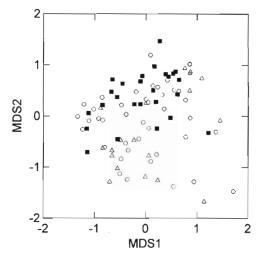


FIG. 3. Results of the ordination in two dimensions of the diet similarities of all individual black caimans captured during the dry season of 1992 (September – November) (filled squares), the dry season of 1993 (September – November) (open circles), and wet season of 1994 (February – March) (open triangles). The ordination was derived by multidimensional scaling analysis (see Methods).

#### DISCUSSION

The results on black caiman diet composition showed that fish were present in the stomachs of juveniles and adults. Even juveniles have the instinct to attack anything that moves on the water surface and below. Therefore they may feed on small fishes abundant among the roots and stems of floating aquatic plants. The same might be true for other prey such as spiders, ants, and beetles that often 'walk' on the water surface, producing waves that perhaps attract attention. The high incidence of *Pomacea* snails was also observed by Da Silveira & Magnusson (1999) at the Anavilhanas Archipelago in the Rio Negro, Central Amazonia.

An interesting finding of this study was the presence of vertebrates such as frogs, birds, and mammals in the black caiman diet. Frogs are abundant in the Cocha Cashu lake environment, principally during the beginning of the rainy season. The females of various frog species tend to move along the lake shore in shallow waters searching for sites to lay their

eggs. Black caimans, like most other caimans, are attracted to anything that moves on the water surface, and may take advantage of that to locate and capture swimming frogs. Birds were also found in the stomachs of some caimans. They probably represent young birds that have accidentally fallen from nests constructed in branches over the water. Terrestrial mammals walking along the lake shore too close to the water could also be promptly attacked by a caiman. Magnusson *et al.* (1987) also found mammals in the diet of forest dwarf caiman (*Paleosuchus trigonatus*), a species commonly occurring along streams in the Amazon forest.

Magnusson et al. (1987) recommended some important points to consider when interpreting crocodilian stomach contents, such as: (a) prey of different types will be digested at different rates; (b) prey of equivalent size are digested faster by large than by small caimans; (c) certain prey have body parts which are indigestible and accumulate in the caiman's stomach (e.g., snail opercula); (d) the various kinds of food items may pass at different rates through the caiman gut; and (e) nutritive value may be different for prey of equivalent mass. We agree with all these considerations, and any one of them might reflect what we found in this study. Our data suggest that there was accumulation of indigestible parts, such as molluscs opercula, that could reflect an increasing number of opercula with increasing caiman body size. However, there must be an anatomical limit of stomach size for each caiman size that can accumulate a given number of opercula, and eventually the Caiman must excrete them. Since black caimans of any age and at any time in Cocha Cashu lake are able to capture snails, the probability of any individual having an operculum in their stomachs must be high. Although we have not study the question, we think that the accumulation of opercula in the stomach may help black caiman to tear apart soft body meat of other prey animals such as vertebrates, so increasing the speed of digestion. However, experiments in feeding black caiman of different sizes with different prey types, and monitoring their rates of passage and digestion, were not available for the Amazon region. This method removes the problem of whether the items present in the stomachs were recently eaten or had already been in the stomachs for days or even weeks. As in our study, many of the published studies using stomach flushing cannot claim that it removes the entire stomach contents.

The ontogenetic changes in diet composition. Ontogenetic shift in the diet of crocodilians has been shown for species from other continents (McNease & Joanen 1977, Webb et al., 1982) and for a few from South America (Seijas & Ramos 1980, Magnusson et al. 1987, Uetanabaro 1989, Thorbjarnarson 1993, Da Silveira & Magnusson 1999). Diet samples for black caiman are scarce and are not available for the western part of the Amazon region. This is the first study to investigate the diet of black caiman in a pristine environment in western Amazonia.

The ontogenetic differences found in this study in the diet of black caiman from the Peruvian Amazon forest are probably related more to differences in foraging behavior of individuals of different ages, and to differences in the frequency of feeding in a given type of microhabitat used to capture prey. Juveniles tend to hunt in shallow waters at the lake margins with patches of grass, where snails and small fish are quite abundant. Although adults sometimes enter shallow waters to capture sedentary fish, they spend most of their time hunting in open waters or at the borders of grass patches.

In central Amazon, Da Silveira et al. (1997) found babies of black caiman in patches of grass, and they suggested that this microhabitat is a good place not only to forage but also to escape attack from conspecific adults and predators. This seems to be valid for other species of Alligatoridae such as Caiman yacare in the Pantanal (Cintra 1988). The juveniles of Caiman yacare, after hatching in March-April, which corresponds to the period of highest water level in the area, spend most of their time, at least during their first year after hatching, in areas with grasses and aquatic plants along the lake shore (Cintra 1989).

The effects of seasonality on the Black Caiman diet. Black Caimans are top predators and may feed on many different types of prey. To understand more about caiman feeding ecology and behavior in natural conditions, it is important to know which organisms constitute their food supply and whether their diet composition changes seasonally and with size.

Another finding in this study was that the diet composition of black caiman in Peru did change seasonally. This suggests that black caimans are able to feed on proportionally different kind of prey depending on the time of year. These results may help in planning future management activities for this species in the Amazon region. Gorzula (1978) found that *C. crocodilus* in Venezuela had a more diverse dier

composition during the wet season (29 items/caiman) than during the dry season (3 items/caiman). Fitzgerald (1988) recorded diet variation in *C. crocodilus* associated with changes in habitat, season, and age. However, Da Silveira & Magnusson (1999) did not find significant differences in mass of food consumed between seasons at Anavilhanas, Rio Negro.

In order to generalize the results of this study it will be necessary to capture more of black caiman individuals of different sizes and in some other areas of the Amazon region, to verify whether ontogenetic shifts are a common pattern and occur elsewhere. Although black caiman can be found in large rivers in other parts of the Amazon, such as those in the Anavilhanas Islands in the Rio Negro in Brazil, they tend to concentrate their activity in large lakes (Da Silveira et al. 1997). Because of this habitat preference, the diet of Black caiman will probably be similar at different sites in the Amazon. However, future studies making regional comparisons in the Amazon region are needed to confirm this hypothesis.

### **ACKNOWLEDGMENTS**

We thank the Asociación para la Conservación de la Selva Sur (ACSS), Centro de Datos para la Conservación (CDC), and Consejo Nacional de Ciencia y Tecnologia for logistic support and funding. We appreciate the field assistance of Reiner Zimmermann, Juan Quispe, Julio Horna, Cecília Flores, Ricardo Sanches, and José Tello. We also want to thank John Terborgh for his support during our wonderful field seasons at Cocha Cashu. RC thanks Bill Magnusson for the teaching of the caiman stomach sampling technique. We appreciated the comments and sugestions made by Bill Magnusson on the manuscript and his advice on part of the multivariate statistical analyses. Suggestions by Guilherme Mourão and John Thorbjarnarson and editing by Karl-L. Schuchmann were also appreciated.

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APENDIX. Stomach contents of 88 black caiman individuals from the Peruvian Amazon.

1	item ind.	S	С	L	ТЬ	Aq	F	В	М	b/w	Ac	Ot	Fg	Α	Oi	Ma	P	Caiman size*
33         -         -         4         1         -				1														
44         -		/																
5         1         3         2         3         -         1         -					4	ı												
66         59         1         1         1         1         4         1         4         5         4         5         5         1         4         5         45,5         5         9         45,5         39,2         39,2         39,2         39,2         39,2         39,2         39,2         10         45,4         45,4         46,4         46,4         46,4         46,4         46,5			_	_	_	_	_	_	_	_	-	_	_	_	_	_	_	
7       61       4       1       8       4       1       2       5       1       4       1       3       2       2       2       39.2       39.2       39.2       39.2       1       45.4       45.4       46.5       39.2       45.4       46.5<						2	3											93
8       4       1       2       5       1       45.5       39.2       39.2       39.2       39.2       39.2       39.2       39.2       75       11       8       13       1       45.4       45.4       46.5       13       1       45.4       46.5       46.5       46.5       46.5       46.5       46.5       46.5       46.5       46.5       46.5       57.4       46.5       57.4       46.5       57.4       46.5       57.4       46.5       57.4       57.4       55.7       57.4       55.7       56.5       56.5       56.5       56.5       56.5       56.5       56.5       60.0				I				1										_
9         3         2         2         39.2         39.2         39.2         75         75         75         75         75         75         45.4         46.5         46.5         46.5         46.5         46.5         46.5         46.5         46.5         46.5         63         77.4         57.4         57.4         57.4         57.4         57.4         57.4         57.4         57.4         57.4         57.4         57.4         57.4         57.4         57.4         57.4         57.4         57.4         57.7         16         28         3         3         1         2         1         1         2         57.4         57.7         16         28         3         3         1         2         1         1         2         56.5         56.5         10         9         66.5         66.5         66.5         66.5         66.5         66.5         66.5         64.5							1											
10       1       8       13       1       45.4         11       8       13       1       45.4         12       6       3       46.5         13       35       1       2       57.4         15       28       7       3       57.4         16       28       3       3       1       2       57.4         17       22       1       1       2       56.5         18       19       6       1       0       60       60         19       60       4       0       1       1       60         20       6       1       1       0       60       60         19       60       4       0       1       1       79.8         22       47       2       1       1       2       80.6         23       48       2       1       1       9       2       89.4         24       27       1       1       1       9       2       42         21       1       1       1       9       2       42         33       1 <td< td=""><td></td><td>4</td><td>l</td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td></td<>		4	l															
111       8       13       1       45.4         12       6       3       46.5         13       35       1       2       57.4         15       28       7       3       57.4         15       28       7       3       57.4         16       28       3       3       1       2         17       22       1       1       56.5         18       19       6       1       6       1       6         19       60       4       56.5       60         19       60       4       56.5       66.5         20       6       1       1       79.8         24       27       1       1       79.8         24       27       1       1       1       2         23       48       2       1       1       2       89.4         25       5       2       3       1       2       89.4         25       5       2       3       1       2       89.4         27       1       4       5       1       9       2       42 <td></td> <td></td> <td></td> <td>3</td> <td></td>				3														
12       6       3       46.5         13       35       1       2       57.4         15       28       7       3       5       57.4         15       28       7       3       1       2       55.7         16       28       3       3       1       2       55.7         16       28       3       3       1       2       54.5         17       22       1       1       0       60       60       60         19       60       1       1       1       2       54.5       56.5         20       6       1       1       1       2       1       1       79.8         22       47       2       1       1       2       1       1       79.8         23       48       2       2       3       1       1       2       89.4         25       5       2       3       1       1       2       89.4         25       5       2       3       1       1       2       9       2       42         29       3       1       1 <td></td>																		
13       35       1       2       63         14       2       3       2       57.4         15       28       7       3       55.7         16       28       3       3       1       2       55.7         17       22       1       1       56.5       56.5         18       19       6       1       1       60       60         19       60       4       56.5       79.8       64.5         20       6       1       1       79.8       64.5         21       6       1       1       79.8       64.5         23       48       2       1       1       1       79.8         24       27       1       1       1       1       2       89.4         25       5       2       3       1       1       2       89.4         27       1       1       1       1       1       2       89.4         27       1       1       1       1       1       1       1       1         28       1       2       1       1       1					13													
144       2       3       2       57.4         15       28       7       3       1       2       55.7         16       28       3       3       1       2       55.7         17       22       1       1       56.5       60         18       19       6       1       1       1       56.5         20       6       1       1       1       79.8       60         20       6       1       1       1       79.8       64.5         20       6       1       1       1       79.8       64.5         21       6       2       1       1       2       64.5       66.5         23       48       2       1       1       2       89.4       64.5       68.8         24       27       1       1       1       1       2       89.4       81.8       1       138.8       81.2       81.8       1       74.8       82.2       99.2       42.2       1       1       82.2       99.5       30.0       1       11       4       5       1       1       1       1       7 <td></td>																		
15       28       7       3       1       2       55.7         16       28       3       3       1       2       56.5         17       22       1       1       1       56.5         18       19       6       1       1       1       60         19       60       4       3       1       2       54.5         20       6       1       1       1       2       66.5         21       6       2       1       1       2       64.5         22       47       2       1       1       2       64.5         23       48       2       1       1       1       2       89.4         25       5       2       3       1       1       2       89.4         25       5       2       3       1       1       2       89.4         27       1       1       1       2       3       1       3       7       1       82         29       3       3       7       1       3       7       1       82       82         29						2												
16       28       3       3       1       2       54       56.5         17       22       1       1       1       56.5       56.5         18       19       6       1       1       54.5       56.5         20       6       1       1       1       79.8       54.5         20       6       1       1       1       79.8       64.5         22       47       2       2       1       1       2       2       3       64.5         23       48       2       1       1       1       2       89.4       68.         24       27       1       1       1       1       2       89.4       81.       81.       81.       81.       81.       81.       81.       81.       81.       81.       81.       81.       82.       99.       2       42.       42.       82.       99.       2       42.       42.       82.       99.       2       42.       42.       42.       42.       42.       42.       43.       42.       42.       42.       43.       42.       43.       42.       43.       42.<																		
17       22       1       1       1       56.5         18       19       6       1       54.5       60         19       60       4       54.5       54.5         20       6       1       1       1       1       101.1         21       6       1       1       2       1       1       79.8         22       47       2       1       1       2       64.5       68         24       27       1       1       1       2       89.4         25       5       2       3       1       2       89.4         25       5       2       3       1       3       89.4         25       5       2       3       1       3       89.4         25       5       2       3       1       4       5       1       3       74.8       81         27       1       4       5       1       1       4       5       1       1       4       4       4       4       4       4       4       4       4       5       1       1       4       4 <t< td=""><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td></t<>																		
18         19         6         1         4         54.5         54.5           20         6         1         1         1         54.5         101.1           21         6         1         1         1         1         1         79.8           22         47         2         1         1         2         1         1         79.8           23         48         2         1         1         2         1         2         89.4           24         27         1         1         1         2         89.4         89.4           25         5         2         3         1         1         2         89.4           25         5         2         3         1         1         2         89.4           27         1         4         5         1         1         1         2         89.4           28         1         2         4         3         3         1         1         4         5         1         1         4         5         1         1         4         1         1         4         4         1 <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td>1</td> <td></td> <td>2</td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td>							1		2									
19         60         4         54.5           20         6         1         1         1         1         1         1         101.1           21         6         1         1         1         1         1         79.8           22         47         2         1         1         2         1         64.5           23         48         2         1         1         2         89.4           24         27         1         1         1         2         89.4           25         5         2         3         1         1         2         89.4           25         5         2         3         1         1         2         89.4           25         5         2         3         1         1         2         89.4           25         5         2         3         1         1         2         4         3           27         1         4         5         1         1         1         9         2         42           31         1         1         1         1         1         1					1													
20       6       1       1       1       1       1       79.8         21       6       2       1       1       2       64.5         23       48       2       1       1       2       89.4         24       27       1       1       1       2       89.4         25       5       2       3       1       3       81         26       11       2       4       3       81         27       1       4       5       1       2       4       3         27       1       4       5       1       1       4       5       1       81         27       1       4       5       1       1       9       2       42         31       1       1       3       7       1       9       2       42         31       1       1       3       7       1       1       82       9       2       42         31       1       1       3       7       1       1       8       1       1       8       1       1       1       8       1 <td></td> <td></td> <td></td> <td>6</td> <td></td> <td></td> <td></td> <td></td> <td></td> <td>1</td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td>				6						1								
21       6       1       1       1       1       79.8         22       47       2       1       1       2       64.5         23       48       2       1       1       1       2       89.4         25       5       2       3       1       1       2       89.4         26       11       2       4       3       1       1       2       89.4         27       1       4       5       1       1       1       74.8       82         29       3       3       1       1       1       9       2       42         31       1       1       4       5       1       1       9       2       42         31       1       1       3       7       1       1       9       2       42         31       1       1       3       7       1       1       82       9       2       42         31       1       1       3       7       1       1       82       1       1       82       1       1       1       82       1       1 <td< td=""><td></td><td></td><td></td><td></td><td>4</td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td>54.5</td></td<>					4													54.5
22       47       2       1       1       2       64.5         23       48       2       1       1       1       1       2       89.4         24       27       1       1       1       1       2       89.4         25       5       2       3       1       1       2       89.4         26       11       2       4       3       81       74.8       81         27       1       4       5       1       1       1       82       95       95         30       1       11       4       5       1       9       2       42         31       1       1       3       7       1       9       2       42         31       1       1       3       7       1       82       9       2       42         31       1       1       3       7       1       1       82       12       80.6         32       19       1       12       3       1       1       7       1       82.2         34       5       1       12       3       1 </td <td>20</td> <td></td> <td></td> <td></td> <td>1</td> <td>1</td> <td></td> <td>101.1</td>	20				1	1												101.1
23       48       2       1       1       2       89.4         24       27       1       1       1       2       89.4         25       5       2       3       1       389.4         26       11       2       4       3       81         27       1       4       5       1       3       1       74.8         28       1       2       1       1       3       9       2       42         30       1       11       4       3       1       3       9       2       42         31       1       1       3       7       1       3       7       1       82         29       3       3       1       3       7       1       3       1       3       1       3       1       4       <	21											1						79.8
24       27       1       1       1       1       2       89.4         25       5       2       3       1       81       81         26       11       2       4       3       74.8       81         27       1       4       5       1       1       1       74.8       82         28       1       2       1       1       1       9       2       42         30       1       11       4       1       4       9       2       42         31       1       1       3       7       1       1       9       2       42         31       1       1       3       7       1       7       1       82.2       2       80.6       32       12       1       12       80.6       32       1       1       82.2       1       12       80.6       32       1       1       82.2       1       1       82.2       1       1       82.2       1       1       82.2       1       1       1       1       1       1       1       1       1       1       1       1       1 </td <td>22</td> <td></td> <td></td> <td></td> <td></td> <td>1</td> <td>1</td> <td></td> <td></td> <td></td> <td>2</td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td>64.5</td>	22					1	1				2							64.5
25       5       2       3       1       138         26       11       2       4       3       1       81         27       1       4       5       1       0       1       1       74.8         28       1       2       1       1       0       0       1       95       2       42         30       1       11       4       0       1       1       9       2       42         31       1       1       3       7       1       0       0       12       80.6         32       19       0       0       0       0       0       0       0       12       80.6         32       19       0        0       0       0       0       0       0       0       0       0       0       0 <td< td=""><td>23</td><td>48</td><td></td><td></td><td>2</td><td></td><td></td><td></td><td></td><td></td><td>1</td><td></td><td></td><td></td><td></td><td></td><td></td><td>68</td></td<>	23	48			2						1							68
26       11       2       4       3       1       74.8         27       1       4       5       1       1       1       74.8         28       1       2       1       1       1       1       82         29       3       3       5       1       11       4       4       5       1       1       9       2       42         31       1       1       3       7       1       1       9       2       42         31       1       1       3       7       1       7       1       80.6         32       19       2       2       2       80.5       2       2       80.5         33       1       12       3       7       1       82.2       1       1       82.2       1       1       82.2       1       1       82.2       1       1       82.2       1       1       82.2       1       1       82.2       1       1       1       1       1       1       1       1       1       1       1       1       1       1       1       1       1       1	24	27			1		1						1	2				89.4
27       1       4       5       1       1       74.8         28       1       2       1       1       1       82         29       3       9       2       42         30       1       11       4       9       2       42         31       1       1       3       7       1       12       80.6         32       19       1       3       7       1       82.2       80.5         33       1       1       1       3       7       1       82.2         34       5       1       12       3       61.3       62.2         34       5       1       12       3       1       7       1       82.2         34       5       1       12       3       1       7       80.6       14       79.7       14       79.7       14       79.7       14       79.7       14       79.7       14       79.7       14       79.7       17       10       10       10       10       10       10       10       10       10       10       10       10       10       10       10 </td <td>25</td> <td>5</td> <td></td> <td></td> <td>2</td> <td>3</td> <td></td> <td></td> <td>1</td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td>138</td>	25	5			2	3			1									138
28       1       2       1       1       1       95       95         30       1       11       4       1       9       2       42         31       1       1       3       7       1       12       80.6         32       19       2       80.5       2       2       80.5         33       1       1       12       3       61.3         35       35       2       2       2       61.3         35       35       2       2       1       1       7       80.6         37       1       2       1       1       7       80.6       14       79.7         36       45       1       2       1       1       1       7       80.6         37       1       2       1       1       1       7       80.6         37       1       2       1       1       1       7       80.6         38       32       1       1       1       1       1       45.5         40       2       3       27       1       1       1       9       43.9 <td>26</td> <td>11</td> <td></td> <td></td> <td>4</td> <td>3</td> <td></td> <td>81</td>	26	11			4	3												81
29       3       1       11       4       1       9       2       42         30       1       11       4       1       9       2       42         31       1       1       3       7       1       12       80.6         32       19       2       80.5       2       2       80.5         33       1       12       3       61.3       61.3         34       5       1       12       3       61.3         35       35       2       2       2       14       79.7         36       45       1       2       1       1       7       80.6         37       1       2       1       1       1       7       80.6         37       1       2       1       1       1       7       80.6         37       1       2       1 <td>27</td> <td>1</td> <td></td> <td>4</td> <td>5</td> <td>1</td> <td></td> <td></td> <td></td> <td></td> <td>1</td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td>74.8</td>	27	1		4	5	1					1							74.8
30       1       11       4       1       9       2       42         31       1       1       3       7       1       12       80.6         32       19       2       80.5       2       2       80.5         33       1       12       3       61.3       61.3         35       35       2       2       2       14       79.7         36       45       1       2       1       1       7       80.6         37       1       2       1       1       1       7       80.6         37       1       2       1       1       1       7       80.6         37       1       2       1       1       1       7       80.6         37       1       1       1       1       7       80.6         37       1       1       1       1       1       1       1       1       1       1       1       4       1       1       4       55.8       1       1       4       55.8       4       3       4       4       4       3       4       4 <td< td=""><td>28</td><td>1</td><td>2</td><td></td><td>1</td><td>1</td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td>82</td></td<>	28	1	2		1	1												82
30       1       11       4       1       9       2       42         31       1       1       3       7       1       12       80.6         32       19       2       80.5       2       2       80.5         33       1       1       12       3       61.3         34       5       1       12       3       61.3         35       35       2       2       2       14       79.7         36       45       1       2       1       1       1       7       80.6         37       1       2       1       1       1       7       80.6         37       1       2       1       1       1       7       80.6         37       1       2       1       1       1       7       80.6         37       1       3       1       1       1       1       7       80.6         38       32       1       1       1       1       1       45.5       1       4       55.8         41       1       4       3       4       3       4	29	3																95
31         1         1         3         7         1         1         2         80.6           32         19         1         2         80.5         30.5         30.5         1         12         30.5         30.5         1         12         30.6	30			1	11	4					1				9		2	
32         19         2         80.5           33         1         1         7         1         82.2           34         5         1         12         3         61.3         61.3           35         35         2         2         2         14         79.7           36         45         1         2         1         1         7         80.6           37         1         2         1         1         1         7         80.6           37         1         2         1         1         1         7         80.6           37         1         3         1         1         1         7         80.6           37         1         3         1         1         1         62.1         1         13         104           39         1         3         1         1         1         4         55.8         1         4         55.8           41         1         4         3         4         3         49.1         4           43         4         1         4         4         3         4         <	31	1					1											
33       1       1       1       7       1       82.2         34       5       1       12       3       61.3         35       35       2       2       2       14       79.7         36       45       1       2       1       1       1       7       80.6         37       1       2       1       1       1       7       80.6         37       1       2       1       1       1       7       80.6         37       1       2       1       1       1       62.1       1       13       104         39       1       3       1       1       1       4       55.8       1       4       55.8         41       1       4       3       4       3       49.1         43       -       -       -       -       -       -       -       -       -       -       37.1         44       1       1       1       1       1       1       10       73																		
34       5       1       12       3       61.3         35       35       2       2       2       14       79.7         36       45       1       2       1       1       7       80.6         37       1       2       1       1       1       7       80.6         37       1       2       1       1       62.1       13       104         39       1       3       1       1       1       45.5       1       45.5         40       2       3       27       1       1       4       55.8       9       43.9         42       3       2       5       4       3       49.1         43       -       -       -       -       -       -       -       -       -       -       -       -       37.1       2       109         45       79       4       17       1       1       1       1       10       73							1							7				
35       35       2       2       2       14       79.7         36       45       1       2       1       1       7       80.6         37       1       2       1       1       1       62.1         38       32       1       1       1       1       13       104         39       1       3       1       1       45.5       1       45.5       4       45.8         41       1       4       9       43.9       49.1         42       3       2       5       4       3       49.1         43       -       -       -       -       -       -       -       -       -       -       37.1         44       1       1       1       1       1       2       109         45       79       4       17       1       1       1       1       10       73				1	12	3												
36     45     1     2     1     1     7     80.6       37     1     2     1     1     1     62.1       38     32     1     1     1     1     13     104       39     1     3     1     1     45.5       40     2     3     27     1     1     45.5       41     1     4     9     43.9       42     3     2     5     4     3     49.1       43     -     -     -     -     -     -     -     -     -     -     -     37.1       44     1     1     1     1     1     1     2     109       45     79     4     17     1     1     1     1     10     73						2											14	
37       1       2       1       1       62.1         38       32       1       1       1       13       104         39       1       3       1       1       45.5         40       2       3       27       1       1       45.5         41       1       4       9       43.9         42       3       2       5       4       3       49.1         43       -       -       -       -       -       -       -       -       37.1         44       1       1       1       1       1       10       73				1						1					1			
38     32     1     1     1     1     13     104       39     1     3     1     1     45.5       40     2     3     27     1     1     455.8       41     1     4     9     43.9       42     3     2     5     4     3     49.1       43     -     -     -     -     -     -     -     -     37.1       44     1     1     1     1     10     73		.,				1				•	1				Ŷ		,	
39     1     3     1     1     45.5       40     2     3     27     1     1     4     55.8       41     1     4     9     43.9       42     3     2     5     4     3     49.1       43     -     -     -     -     -     -     -     -     37.1       44     1     1     1     10     73		32		•	-		1			1	•						13	
40     2     3     27     1     1     4     55.8       41     1     4     9     43.9       42     3     2     5     4     3     49.1       43     -     -     -     -     -     -     -     -     37.1       44     1     1     1     10     73		22		1	3					•								
41 1 4 9 43.9 42 3 2 5 4 3 49.1 43 37.1 44 17 1 1 10 73		2									1							
42 3 2 5 4 3 49.1 43 37.1 44 17 1 1 10 73		2			27						1				0		4	
43 37.1 44 1 2 109 45 79 4 17 1 1 10 73					2					4	3				,			
44     1     2     109       45     79     4     17     1     10     73				5		,				4	9							
45 79 4 17 1 10 73			_	_	_	_	1	_	_		_	_	_	-	_	_		
		70		/	17		ſ				1							
1 / 8.2			1	4		6					I					,		
	40	10)	1		)	U										1	/	/8.2

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item ind.	S	С	L	ТЬ	Aq	F	В	М	b/w	Ac	Ot	Fg	Α	Oi	Ma	Р	Caiman size*
47	35		. 3	6		1										5	69.2
48	33			3	3					2			2	1	1	13	68.3
49	3			1	1											2	95
50	5		1	6	5	1										19	64.5
51	31		1	6	2	1		1								7	78.4
52	14			1		1		1								2	76.6
53	4		1	11	3									1			39.5
54	1			5	1									2		2	37.2
55			3	16	2					2						1	43.6
56			2	11	5			1					1	2		6	44.5
57	27		2			1										15	86.2
58			3.	102		1											63
59	16			4	7											4	73.2
60	15			3	1											6	84.3
61				3	4			2						1			48.7
62	1		2	19	2			1									46.4
63	2					1		1								3	71.7
64				10	2	2		1						3		1	53.9
65	1	1	3	1	2	1		1						2		1	75.1
66		1	2	1	2					3						6	76.5
67			3			1				2							93
68	6		1	3													84.2
69	9			3	7			1		1						10	79.4
70		1			5	1					1					1	78.7
71		1		1	1			1								1	100.6
72	1			8	24			1		9 2				5 2			52.7
73	3	1		4	22									2	1		54.5
74	1	1	1	5	4					2							47.6
75			59	7	24	1				3				2		5	46.1
76				5	9						1			12		1	51.7
77	40	1														1	117
78	10	1															91.6
79	1					1											137.2
80	48	2		1	1	1											91.5
81						1								1		7	140
82	202	2		1		1										1	127.6
83	107				2											4	80.5
84	3	1			9					1						3	154.7
85	7		l		3												68.7
86	2		5	1	29	2				1							57.4
87				5	39	1								1		1	47
88		2	1	8	1	1		1		1	1						72.8

S = snails; C = crabs; L = larvae; Tb = terrestrial beetles; Aq = aquatic beetles; F = fish; B = birds; M = Myriapoda; b/w = bees/wasps; Ac = Arachnida; Ot = Orthoptera; Fg = frogs; A = ants; Oi = other insects; Ma = mammals (marsupials); P = parasites.