

Diets of Amazonian Crocodilians

WILLIAM E. MAGNUSSON, EDUARDO VIEIRA DA SILVA, AND
ALBERTINA P. LIMA

Departamento de Ecologia, Instituto Nacional de Pesquisas da Amazonia, Caixa Postal 478,
69000 Manaus Amazonas, Brasil

ABSTRACT.—Differences in diets among Amazonian crocodilians can largely be related to habitat selection. *Caiman crocodilus*, *Melanosuchus niger* and *Paleosuchus palpebrosus*, which occur around rivers and lakes have similar diets: small individuals eat invertebrates and large individuals eat invertebrates and fish. Juvenile *Paleosuchus trigonatus*, which live in small forest streams, eat larger numbers of terrestrial vertebrates than other similar-sized crocodilians. Large *P. trigonatus* eat many snakes and mammals but few fish. Mean, minimum, and maximum sizes of most prey types increase with crocodilian size for all species. There is an inverse relationship between the number of terrestrial invertebrates eaten and the number of fish eaten by different size classes of *Caiman crocodilus*, suggesting that mutually exclusive foraging modes are used for those prey categories.

Resource partitioning by reptiles and amphibians generally relates to partitioning of habitats rather than food types (Toft, 1985). Maiorana (1978) describes differences in diets among salamanders as an "epiphenomenon" because dietary overlap would be much greater if competition for space did not cause habitat segregation. Amazonian crocodilians appear to partition space, each species occurring most frequently in characteristic habitats (Magnusson, 1985), so it is to be expected that their diets will vary depending on the availability of different prey in each habitat.

In this paper we describe ontogenetic trends in types and sizes of prey taken by Amazonian crocodilians (*Caiman crocodilus*, *Paleosuchus trigonatus*, *P. palpebrosus*, *Melanosuchus niger*) and how these differ among species. Data were collected while studying habitat utilization by crocodilians (Magnusson, 1985) and the results complement that study.

METHODS

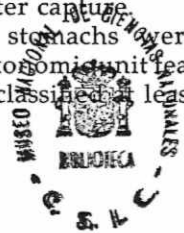
Crocodilians were captured by hand or by a short-penetration live-capture harpoon (Webb and Messel, 1977) during surveys of Lago Amanã (Lat. 2°30'S, Long. 64°40'W), Lago Calado (Lat. 3°15'S, Long. 60°40'W), the Manaus region (Lat. 3°05'S, Long. 60°00'W), Curuá-una Hydroelectric Dam (Lat. 2°45'S, Long. 55°20'W), Parque

Nacional de Amazônia (Lat. 4°30'S, Long. 56°30'W), and the Archipelago Anavilhanas (Lat. 2°30'S, Long. 61°00'W) between 1979 and 1983.

Each species occurred most frequently in characteristic habitats. Most *Paleosuchus trigonatus* were caught in small streams under closed-canopy rainforest. *Caiman crocodilus* were usually found in large rivers and lakes, adjacent to shallow shelving banks which are covered by dense grass mats during the season of high water. *Melanosuchus niger* and *P. palpebrosus* occurred most frequently adjacent to steep banks of rivers and lakes. Most of the areas with steep banks were associated with flooded forest, but had no grass mats during the season of high water. Details of the habitats and proportions of each species in each area are given by Magnusson (1985).

Most *Caiman crocodilus*, *Melanosuchus niger*, *Paleosuchus palpebrosus* and small *P. trigonatus* were captured between 2000 hours and 2400 hours and stomach contents were removed the next morning by the method of Taylor et al. (1977) with modifications suggested by Webb et al. (1982). Adult *P. trigonatus* were generally captured during the day by diving into their underwater caves and noosing them. Stomach contents were removed directly after capture.

Items retrieved from stomachs were identified to the lowest taxonomic unit feasible. Prey animals were classified at least



to the level of "order," while non-prey items were classified as "vegetation" or "stones." The volume and mass of each category in each stomach were determined, but, for reasons given in the Discussion, these results were not used in analyses. They are available on request from the authors. Instead, sizes of prey were ranked using an index based on the target-size (TS) concept of Webb et al. (1982). We calculated the "target-size" for each reconstituted prey item by taking the area of a rectangle with the two maximum linear dimensions of the prey item (excluding long thin appendages such as antennae). Our target-size therefore differs from that of Webb et al. (1982) in being a continuous variable. We analyzed these sizes in the form \sqrt{TS} to obtain a linear measure of prey size; this measure can be considered a "standard length" of prey that is independent of prey shape.

Prey were assigned to one of six major categories: crabs, shrimp, molluscs, terrestrial invertebrates, fish, and terrestrial vertebrates. "Crabs" contained only crabs of the families Trichodactylidae and Pseudohelphusidae. All shrimp were Palaemonidae (*Macrobrachium*, *Pseudopalaemon* and *Euryrhynchus*). The only molluscs eaten were pulmonate snails. Terrestrial invertebrates include Hemiptera, Coleoptera, Orthoptera, Hymenoptera, Diptera, Ephemeroptera, Odonata, Isoptera, Araneida, Diplopoda, Chilopoda, Scorpionida, and Isopoda. Fish were generally represented by only a few scales or vertebrae but included at least Characiformes and Siluriformes. Terrestrial vertebrates included all four tetrapod classes. Further subdivisions are discussed in the Results.

For the analysis of ontogenetic shifts in diet we calculated the mean number of each prey type per crocodilian for each of the six size classes of crocodilian considered (given in Table 1). The graphs of mean number of prey per crocodilian versus crocodilian size (Fig. 1) are therefore based on six points (the six size categories), but the number of individuals from which the mean numbers of prey per crocodilian were calculated varies among species and size classes (see Table 1).

Regressions were tested for statistical significance by Analysis of Variance (Zar, 1974:205). Comparisons between regressions were made by Analysis of Covariance using the Student-Newman-Keuls (SNK) procedure (Zar, 1974:233). All correlations (r) are Pearson correlations (Zar, 1974:236).

RESULTS

The frequencies of prey in each diet category differed among sizes and species of crocodilians. Differences among species may be due to habitat differences. However, because all sizes of each crocodilian species were collected in close proximity, ontogenetic differences probably relate more to differences in behavior.

Terrestrial Invertebrates.—Coleoptera represented 59%, 59%, 43%, and 61% of the total number of terrestrial invertebrates eaten by *Caiman crocodilus*, *Paleosuchus trigonatus*, *P. palpebrosus*, and *Melanosuchus niger*, respectively. Of the other taxonomic categories only Hemiptera (all Belostomatidae—19% in *C. crocodilus*), Araneida (19% in *M. niger* and 14% in *P. palpebrosus*), Hymenoptera (16% in *P. palpebrosus* and 11% in *P. trigonatus*) and Diplopoda (12% in *P. palpebrosus*) exceeded 10% of the terrestrial invertebrates eaten by any species of crocodilian. The relationship between the mean number of terrestrial invertebrates in the diet (TI) and size of crocodilian (SVL cm) for *C. crocodilus* ($TI = 11.33 - 0.17 SVL$, $N = 6$, $r^2 = 0.87$) was significantly different from the relationship for *P. trigonatus* ($TI = 3.68 - 0.05 SVL$, $N = 6$, $r^2 = 0.33$) (SNK test: slopes, $P < 0.05$; elevations, $P > 0.5$). The mean number of terrestrial invertebrates per crocodilian was high (10.5) for the smallest size class of *C. crocodilus*, but declined steadily with increase in crocodilian size before starting to level off in the size classes > 50 cm snout-vent length (SVL). The mean number of terrestrial invertebrates was low (< 6.0) in all size classes of *P. trigonatus* and showed no consistent trend with size of crocodilian (Fig. 1A). The data for *M. niger* show much greater similarity to that of *C. crocodilus* than to *P. trigonatus*. Data for *P. palpebrosus* are too few in the smaller size classes, where

TABLE 1. Total numbers of crocodilians in each size category and numbers of crocodilians in each size category which contained each prey type.

	Snout-vent length (cm)						Total
	10-19.9	20-29.9	30-39.9	40-49.9	50-59.9	>60	
<i>Caiman crocodilus</i>							
Total	13	33	21	16	14	8	105
Crabs	1	9	6	3	8	3	30
Shrimp	0	1	3	0	0	0	4
Molluscs	1	12	10	4	2	2	31
Terrestrial invertebrates	13	33	20	14	6	4	90
Fish	1	8	5	7	11	6	38
Terrestrial vertebrates	1	1	1	3	2	1	9
<i>Paleosuchus trigonatus</i>							
Total	8	6	5	9	5	22	55
Crabs	0	0	1	3	1	4	9
Shrimp	2	1	2	1	1	6	13
Molluscs	0	0	0	1	0	2	3
Terrestrial invertebrates	7	3	4	6	4	10	34
Fish	0	0	0	1	0	3	4
Terrestrial vertebrates	2	2	1	4	1	15	25
<i>Paleosuchus palpebrosus</i>							
Total	2	2	7	6	6	3	26
Crabs	0	0	5	1	3	1	10
Shrimp	1	1	0	1	0	0	3
Molluscs	0	0	2	1	0	1	4
Terrestrial invertebrates	1	1	5	3	4	2	16
Fish	0	1	2	4	2	2	11
Terrestrial vertebrates	0	0	0	0	0	0	0
<i>Melanosuchus niger</i>							
Total	0	4	1	0	2	2	9

largest differences among species occurred, for a valid comparison.

Fish.—The relationship between size of crocodilian (SVL cm) and mean number of fish (F) in the diet for *P. trigonatus* ($F = -0.04 + 0.002 \text{ SVL}$, $N = 6$, $r^2 = 0.44$) was significantly different from the combined relationship for *P. palpebrosus* and *C. crocodilus*, which did not differ from each other ($F = -0.03 + 0.1 \text{ SVL}$, $N = 12$, $r^2 = 0.32$). The pattern for *M. niger* was similar to that for *C. crocodilus* and *P. palpebrosus* (Fig. 1B). The general pattern of increase in number of fish in the diet with crocodilian size in *C. crocodilus*, *P. palpebrosus*, and *M. niger* may also occur in *P. trigonatus*, but even the largest *P. trigonatus* eat few fish (Fig. 1B). The mean number of fish per stomach closely reflects the proportion of crocodilians with fish (Table 1, but see caveats in Discussion).

Crabs and Shrimp.—Shrimp occurred only in the smaller size classes of *C. crocodilus*, and then in small numbers. They were

found in low numbers in most size classes of *P. trigonatus* (Fig. 1C). *P. palpebrosus* took shrimp but the small sample sizes do not allow detailed analysis of ontogenetic trends. The *M. niger* had not eaten shrimp. No general pattern in the number of crabs taken by different sized crocodilians is evident (Fig. 1D). Apart from the smallest size class, crabs appear in small numbers consistently in all size classes of all species for which adequate samples are available.

Molluscs.—Large *C. crocodilus* and *M. niger* contained large numbers of pulmonate gastropods, as did *C. crocodilus* and *P. palpebrosus* in the 20–40 cm size range (Fig. 1E). Only three *P. trigonatus* ate gastropods; those individuals were captured in a hydroelectric dam or the mainstream of the Tapajós River. *Caiman crocodilus* and *P. palpebrosus* in the 40–60 cm SVL size range were captured in the same habitats as the larger and smaller individuals so we have no explanation for the small number of

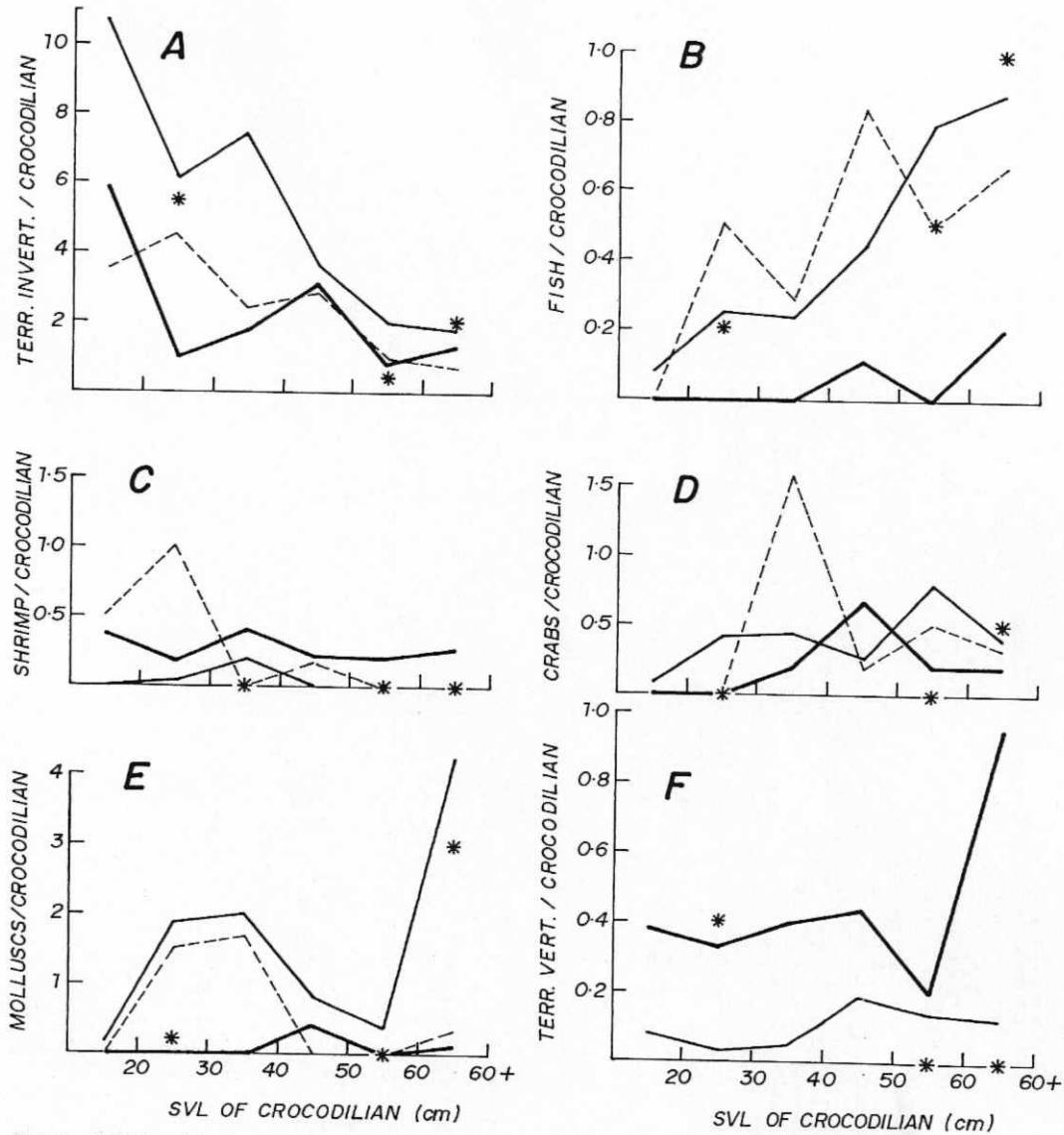


FIG. 1. Relationships between the mean numbers of (A) terrestrial invertebrates, (B) fish, (C) shrimp, (D) crabs, (E) molluscs, and (F) terrestrial vertebrates per individual versus length of crocodilian. Heavy solid lines—*Paleosuchus trigonatus*, broken line—*P. palpebrosus*, fine solid line—*Caiman crocodilus*, asterisks—*Melanosuchus niger*.

gastropods eaten by crocodilians in that size range.

Terrestrial Vertebrates.—No terrestrial vertebrates were found in *P. palpebrosus* and only two (snakes) were found in a single 27.0 cm SVL *M. niger*. Terrestrial vertebrates were eaten by all size classes of *C. crocodilus*, but the frequencies were much lower than for *P. trigonatus* (Fig. 1F). Of 104 *C. crocodilus*, two had eaten snakes, one a

lizard and one a mammal. Five *C. crocodilus*, one in each size class, had eaten birds. Small *P. trigonatus* (<60 cm SVL) ate roughly equal numbers of birds (3), lizards (3), frogs (3), and snakes (2). Larger *P. trigonatus* still ate birds (2) and frogs (1) but most vertebrate prey were mammals (7) or snakes (10). The types of terrestrial vertebrate prey taken will be discussed more fully under Prey Size.

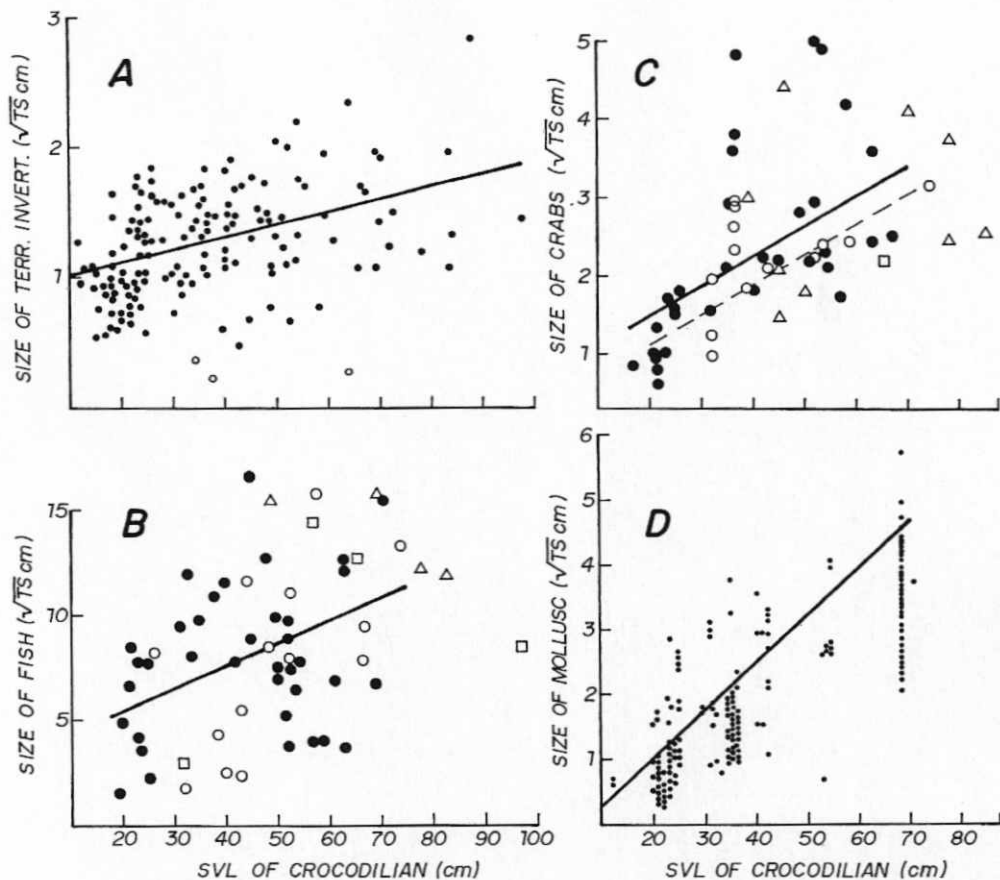


FIG. 2. (A)—Relationship between mean size of terrestrial-invertebrate prey per crocodilian and length of crocodilian (all species combined). Open circles represent means based on samples which contained only tiny Diptera. These were not included in the analysis. (B)—Relationship between mean size of fish prey per crocodilian and length of crocodilian. Regression line is based on means per individual for *Caiman crocodilus* and *Paleosuchus palpebrosus*. Points represent all individual prey. Open circles—*P. palpebrosus*, closed circles—*C. crocodilus*, triangles—*P. trigonatus*, squares—*Melanosuchus niger*. (C)—Relationships between mean size of crabs taken by each crocodilian and length of crocodilian. Regression lines for *C. crocodilus* (solid) and *P. palpebrosus* (dashed) are based on means per crocodilian. Points represent all individual prey, symbols as in part B. (D)—Relationships between mean size of molluscs eaten by *C. crocodilus* and length of crocodilian. Points show data for all individual molluscs.

The only crocodilian from which we recorded more than one individual prey item from any class of vertebrate was the *M. niger* mentioned above (but see Discussion). The only species in which we found more than one class of vertebrate per individual was *P. trigonatus*. The mean number of vertebrates per stomach therefore reflects the proportion of crocodilians that had eaten vertebrates (Table 1).

Relationships Among Prey Types.—There are no obvious relationships between the

numbers of any two types of prey taken except for an inverse relationship between fish and terrestrial invertebrates eaten by *C. crocodilus* ($r = -0.93$, $N = 6$, $P < 0.003$).

Vegetation.—The proportion of individuals with vegetation in the stomach did not vary significantly with size in *C. crocodilus* ($\chi^2_5 = 7.33$, $P > 0.1$). The mean for all size classes combined was 65%. The occurrence of vegetation in stomachs of large *P. trigonatus* (>30 cm SVL) was significantly more frequent (76% of individuals)

than in smaller individuals (29%) ($\chi^2_1 = 8.4$, $P < 0.005$).

Gastroliths.—Stones were retrieved from 6 of 14 (43%) small *P. trigonatus* (<30 cm SVL) and 35 of 41 (85%) larger *P. trigonatus*. Few (7%) of the *C. crocodilus* had stomach stones and there was no obvious trend with stones in this species. None of 11 small *P. palpebrosus* (<40 cm SVL) contained stones, but 5 of 15 (33%) larger *P. palpebrosus* contained stones. The *M. niger* examined did not contain stones.

Prey Size.—There was no significant relationship between the size class of *P. trigonatus* and the size of the shrimp they ate (ANOVA, $F_{1,11} = 2.86$, $P > 0.1$). The numbers of the other species eating shrimp were too small for analysis. The relationship between the size of terrestrial-invertebrate prey and crocodilian length did not differ significantly among species (Analysis of Covariance, $F_{6,138} = 0.96$, $P > 0.25$). The regression for all species combined (\sqrt{TS} TI [mm] = $0.90 + 0.01$ SVL Croc. [cm], $N = 146$) explained only 19% of the variance in the mean size of terrestrial-invertebrate prey per crocodilian. Three small Diptera (Fig. 2A) were not included in the analysis as we believe that they contaminated the stomach contents after collection, or less probably, that they represent secondary ingestion. Only mean sizes of terrestrial-invertebrate prey are presented in Fig. 2A. Individual prey sizes (\sqrt{TS}) ranged from 0.23 cm to 3.46 cm. For all the following analyses regression lines are based on the mean size of prey per crocodilian, but points on the graphs show sizes of all prey eaten.

The relationship between the size of fish eaten and length of crocodilian (\sqrt{TS} fish [cm] = $3.2 + 0.11$ SVL Croc. [cm], $N = 49$) was significant, but did not differ between *C. crocodilus* and *P. palpebrosus*, and it explained only 17% of the variance in size of fish eaten. The sizes of fish eaten by *P. trigonatus* and *M. niger*, relative to crocodilian size, were similar to those eaten by *C. crocodilus* and *P. palpebrosus* (Fig. 2B).

The relationships between size of crocodilian and mean size of crabs eaten were similar for *P. palpebrosus* (\sqrt{TS} Crab [cm] = $2.67 + 0.4$ SVL Croc. [cm], $N = 10$, $r^2 =$

0.61) and *C. crocodilus* (\sqrt{TS} Crab [cm] = $4.88 + 0.47$ SVL Croc. [cm], $N = 30$, $r^2 = 0.36$) but are presented separately because the variances differ significantly ($F_{9,28} = 4.68$, $P < 0.001$). Data for *M. niger* and *P. trigonatus* show similar trends (Fig. 2C).

Only *C. crocodilus* ate sufficient numbers of molluscs to justify analysis. There was a strong relationship between the mean size of molluscs taken by this species and the SVL of the individual (\sqrt{TS} molluscs [cm] = $-0.45 + 0.07$ SVL Croc. [cm], $N = 31$, $r^2 = 0.51$). The maximum and minimum sizes of molluscs eaten showed similar trends relative to crocodilian size as did the mean sizes (Fig. 2D).

The mean size of terrestrial vertebrate prey was significantly related to the size of crocodilian for *P. trigonatus* (\sqrt{TS} [cm] = $3.95 + 0.1$ SVL Croc. [cm], $N = 29$). However, the regression explains only 15% of the variance in prey size (Fig. 3). One feather found in the stomach of a recently hatched animal (17 cm SVL) was disregarded in the analysis as the probability of such a tiny crocodilian eating such a large bird, even as carrion, is remote. In contrast, the mean size of terrestrial vertebrates (\bar{x} $\sqrt{TS} = 8.1$, $S = 1.99$ cm) in the stomachs of *C. crocodilus* showed no significant relationship with SVL ($F_{1,8} = 0.79$, $P > 0.25$).

The increase in prey size with the size of *P. trigonatus* is mainly due to an increase in the size of birds taken and the inclusion of mammals in the diets of large animals (>65 cm SVL). Within mammals there was a consistent increase in prey size with crocodilian size. Two animals with SVLs of 65 cm ate rats (*Oryzomys* sp. and *Proechimys* sp.). A 70 cm animal ate an agouti (*Dasyprocta* sp.), 78 cm animals ate a small monkey (species not determined), a marsupial (*Metachirus nudicaudatus*), and a porcupine (*Coendou* sp.). An 84 cm animal ate an armadillo (*Dasyppus novemcinctus*). We have evidence of another *P. trigonatus* eating a porcupine. Signs of a struggle and spines and pieces of flesh were found on a mudbank in front of a hole occupied by a male with a SVL of 77 cm. The animal had obviously recently eaten a large meal, but we did not capture him for fear of causing internal damage by the porcupine quills.

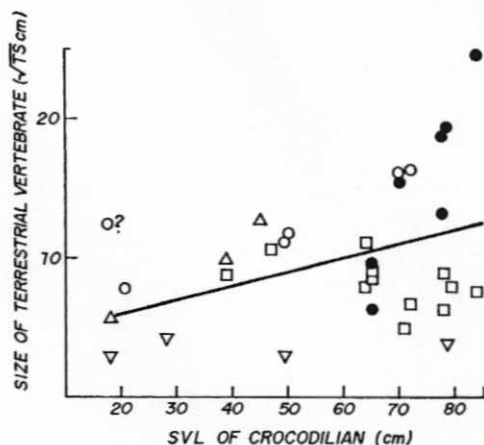


FIG. 3. Relationship between mean size of terrestrial-vertebrate prey in each *P. trigonatus* and size of *P. trigonatus*. Points represent all individual prey taken. Open circles—birds, up-pointing triangles—lizards, down-pointing triangles—frogs, squares—snakes, closed circles—mammals. The point for the bird in the animal less than 20 cm SVL was not included in the regression analysis (see text for explanation).

When captured 11 days later he still had porcupine quills imbedded in his jaws but these were gone two months later. The animal has been captured regularly in the same area over the following two years, so eating porcupines apparently is not hazardous for *P. trigonatus*. The sizes of the snakes and frogs eaten did not increase with crocodilian size and few lizards were taken (Fig. 3).

The minimum and maximum sizes of prey appear to increase with crocodilian size as does the mean for terrestrial invertebrates (Fig. 2A), crabs (Fig. 2C) and probably fish (Fig. 2B). Only for terrestrial vertebrates (*P. trigonatus*) was there evidence to suggest that large individuals eat small prey as readily as large prey (Fig. 3).

The mass of gastroliths retrieved from *P. trigonatus* was proportional to the length of the individual (Mass [g] = 0 + 3.1 SVL Croc. [cm], N = 41, $r^2 = 0.45$). Too few stones were retrieved from other species (Fig. 4) to justify analysis.

DISCUSSION

Five important points must be considered when interpreting data on crocodilian stomach contents:

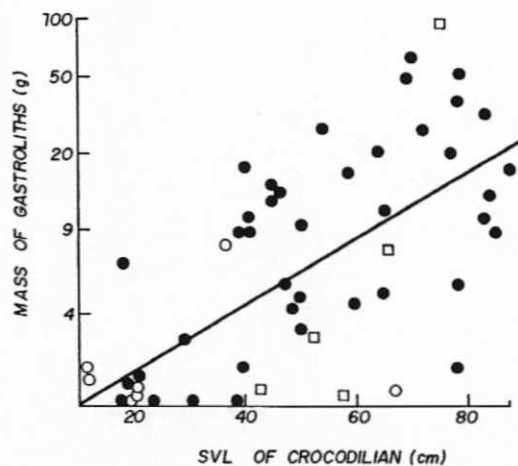


FIG. 4. Relationship between total mass of gastroliths retrieved from *P. trigonatus* and length of *P. trigonatus* based on data represented by solid circles. Open circles—*C. crocodilus*, squares—*P. palpebrosus*.

1. Different prey types are digested at vastly different rates. Jackson et al. (1974) discuss this in relation to secondary ingestion but a more important effect is that the frequency of occurrence of a prey type in stomach samples will be inversely proportional to its rate of digestion (Garnett, 1985).
2. Within prey types, larger items will take longer to digest, and larger crocodilians will digest equivalent sized prey faster than small crocodilians.
3. Some prey have indigestible parts that accumulate in the crocodilian's stomach allowing estimation of the total number of prey eaten (e.g., operculae of molluscs), whereas the least digestible parts of other prey types do not allow such estimation (e.g., mammal hair and fish or snake scales).
4. The retention of indigestible items may depend on the overall passage rate through the stomach, i.e., amount of other food eaten.
5. Different prey of equivalent mass, volume, or area may have vastly different nutritive value for a carnivore (e.g., Dimmitt and Ruibal, 1980; Lance et al., 1983).

By analyzing data only within prey types we minimize biases due to aspects (1), (3), and (5).

Various methods have been used to present data on stomach contents analysis of crocodylians (Webb et al., 1982). However, ontogenetic trends have generally been investigated using only two or three broad size categories of crocodylians. Although the results may appear precise because of the large number of individuals included in each category, the analysis is influenced by the size distribution within each category. We believe that it is more important to describe adequately the trends in the relationships between diet and crocodylian size than it is to make statistical comparisons between any two size classes.

Choice of prey categories can critically influence the interpretation of results. We have used categories that we believe may reflect different foraging modes used by the crocodylians, and we have grouped taxa which should have similar digestibilities. These decisions are largely subjective; except for Taylor (1979) no one has made any systematic attempt to observe the feeding behavior of small crocodylians. For instance, we have grouped belostomatids with terrestrial invertebrates even though the family is largely aquatic. Had we used terrestrial/aquatic prey categories the belostomatids would have been lumped with fish even though there was a strong negative correlation between the occurrence of the two groups ($r_s = -0.79$, $P < 0.05$). Also, the chitinous exoskeleton of belostomatids is likely to present problems of digestion more similar to those of terrestrial invertebrates than to crustaceans which have relatively easily digested calcareous exoskeletons (Garnett, 1985). The prey categories we have used have been used in most previous major studies of crocodylian diet (see review in Webb et al., 1982).

The diets of *P. trigonatus* and *C. crocodilus* are obviously very different. Young *Caiman crocodilus* eat mainly terrestrial invertebrates and gradually change over to fish and molluscs. *Paleosuchus trigonatus* consistently eat items from all categories except molluscs until they reach adult size (>65 cm SVL), when the number of snakes and mammals in the diet increases dramatically. We attribute differences between the species to differences in the habitats they

occupy. In areas of geographical overlap, despite the selection of different microhabitats (Magnusson, 1985), the diets of the two species are similar; *P. trigonatus* even eats molluscs which do not occur in its normal habitat.

Although the data for *P. palpebrosus* and *M. niger* are limited, the similarity of their diets to that of *C. crocodilus* is striking. It is likely that this is because the habitats they occupy are adjacent to those occupied by *C. crocodilus* (Magnusson, 1985). However, it is important to keep in mind that the size range of *M. niger* examined, although similar to those of the other species, did not include adults. Also, our study sites did not include savanna streams which are probably the primary habitat of *P. palpebrosus*. In such areas the diet of *P. palpebrosus* may differ more markedly from that of *C. crocodilus*. The high frequencies of gastroliths in large individuals and the relatively low frequency of terrestrial invertebrates in the diets of small individuals of *P. palpebrosus* suggest similarities to *P. trigonatus* which deserve further investigation.

The frequencies of most prey types in the diets remain roughly constant or increase with crocodylian size. As the sizes of these prey remain constant (shrimp only) or increase with crocodylian size, the volumes ingested must also increase with crocodylian size. Evaluation of the importance of these changes would require data on digestibility and size-dependent energetics that are not presently available.

Only terrestrial invertebrates decline in frequency in the diets of larger crocodylians. The mean frequency of terrestrial invertebrates eaten by *C. crocodilus* declines by a factor of 11 from the smallest to the largest size class, but, assuming that the shapes of the terrestrial invertebrates eaten remain roughly constant, the mean volume per prey item would increase only about three times. Therefore, on any scale, terrestrial invertebrates must be less important to large than to small crocodylians.

The inverse relationship between the frequencies of fish and terrestrial invertebrates in *C. crocodilus* diets (and probably *P. palpebrosus* and *M. niger*) suggests that

foraging modes used for these groups may be mutually exclusive. An interesting comparison can be made between *C. crocodilus* and *Crocodylus johnstoni*. They are crocodylians of similar size and both eat mainly fish and terrestrial invertebrates. However, using the same size categories as for *C. crocodilus* there is only a weak and statistically insignificant correlation between the size of *C. johnstoni* and the frequency of fish in the diet ($r = 0.63$, $0.1 > P > 0.05$), and between size and the frequency of invertebrates in the diet ($r = -0.61$, $0.1 > P > 0.05$; based on original wet-season data from their 1982 paper supplied by Grahame Webb, Charlie Manolis, and Rik Buckworth). The fish eaten by *C. johnstoni* are tiny ($47\% \sqrt{TS} < 2$ cm, $49.9\% \sqrt{TS} < 4$ cm, Webb et al., 1982). The mean \sqrt{TS} ; of fish taken by even the smallest size class of *C. crocodilus* was 5 cm. The mean \sqrt{TS} of the largest size class was 10 cm. It is likely that *C. johnstoni* can use the same foraging mode to catch insects at the water's edge and small fish in shallows (Grahame Webb, pers. comm.), but that the capture of larger fish taken by *C. crocodilus* requires a different foraging mode.

There were large differences among size classes of *C. crocodilus* in the mean frequencies of molluscs in the diet, but there was no consistent trend with crocodylian size. The interesting pattern shown presently defies explanation but indicates that further research could be fruitful. Snails are common in the diets of other species of crocodylians which live in areas with abundant aquatic macrophytes (Fogarty and Albury, 1968; Staton and Dixon, 1975; Diefenbach, 1979). Their absence from the diet of *P. trigonatus* probably relates to the lack of macrophytes, and hence snails, in small streams.

Several species of crocodylians include more terrestrial vertebrates, especially mammals, in their diets when they attain large sizes (Giles and Childs, 1949; Cott, 1961; Blomberg, 1977; McNease and Jonen, 1977; Taylor, 1979; Medem, 1981). *Paleosuchus trigonatus* is interesting because it regularly eats terrestrial vertebrates at all sizes, and includes large numbers of mammals in its diet at a relatively small

size (65–84 cm SVL). Data on movements of *P. trigonatus* in rainforest streams (Magnusson and Lima, unpubl.) indicate that *P. trigonatus* less than 65 cm SVL are vagrants, remaining little time in any one area. Large animals (> 65 cm SVL) have fixed and relatively small home ranges (500–1000 m of stream). The increase in mammals and snakes in the diets of larger *P. trigonatus* may reflect a change in foraging behavior associated with living in an area with which they are familiar. If the lack of mammals in the diet of small crocodylians were due simply to mechanical problems of handling relatively large and agile prey, one would expect all species to make the change at about the same size. It would be interesting to look for changes in the life styles of other species at the time when changes in diet occur. An alternative, and not necessarily exclusive, explanation is that mammals are an optimal diet for reproducing females (Lance et al., 1983).

Vertebrates were the only prey group for which there was no evidence that small items are avoided by larger crocodylians. Christian (1982) has described a similar shift in the minimum acceptable size of prey in frogs. The changes in behavior that lead to larger crocodylians rejecting or coming into contact less frequently with small items deserves further study.

Stomach stones occurred frequently only in *P. trigonatus* and larger *P. palpebrosus*. Individuals of the genus *Paleosuchus* may deliberately seek more stones than the other species. However, we think it more likely that stones were simply more available in the microhabitats where these species were collected. Likewise, we are hesitant to place any great biological importance on the higher incidence of vegetative debris in stomachs of *P. trigonatus*.

Young crocodylians eat mainly insects or crustaceans (see reviews in Taylor [1979], Medem [1981, 1983] and Webb et al., [1982]). Larger individuals may or may not continue to eat insects and crustaceans, but all supplement their diets with snails, fish or terrestrial vertebrates, depending on the habitat. Because of the variety of foods taken, crocodylians are usually referred to as "generalists" or "opportunistic." How-

ever, it is important to emphasize that this does not mean that they use a generalized foraging mode or that the prey they take depends on opportune encounters. Crocodilians have highly specialized foraging modes (e.g., Taylor, 1979; Whitfield and Blaber, 1979; Crawshaw and Schaller, 1980; Pooley, 1982) which they can change as the situation warrants. In this regard they are unusual among the reptilia which usually have fairly stereotyped food gathering behaviors. Unfortunately, because of the difficulty of observing animals at night in the wild, food gathering behavior of crocodilians has not been studied in detail as has their complex reproductive behavior. That the prey types available depend on the habitat occupied is trivially obvious, but to what extent habitat selection influences the foraging mode of Amazonian (or any other) crocodilians is completely unknown. The wide range of head shapes in the crocodilia can be related in broad terms to habitat (generally wide flat heads in swamp dwelling species, long thin snouts in riverine species). However, to what extent these morphologies reflect adaptive peaks in foraging mode is entirely unknown. Comparative studies of the efficiency with which different species of crocodilians handle the same species of prey under standardized conditions would appear to be a worthwhile avenue of future research.

Acknowledgments.—Many people helped with field work, including Lyn Branch, Gene Montgomery, Louise Emmons, and Peter Harlow. Crispiniano Carvalho provided stomachs of crocodilians killed by Indians on the upper Rio Negro. Data from Lago Amanã were collected while accompanying expeditions organized by Robin Best. Other trips were largely due to the administrative efforts of Maria de Nazaré Góes Ribeiro and she has our sincere thanks. Grahame Webb, Charlie Manolis, and Rik Buckworth kindly provided data on *C. johnstoni*. Célio Magalhães identified the crustaceans. Jorge Soares Dácio prepared the figures and Hygia Pimenta Carmo typed the manuscript. Part of this study was financed by grant number 40.5055/83 from the Brazilian Conselho Nacional de

Desenvolvimento Científico e Tecnológico to W. E. Magnusson.

LITERATURE CITED

- BLOMBERG, G. E. G. 1977. Feeding ecology, nesting ecology and habitat preference of Okavango crocodiles. Botswana Notes and Records, Spec. Ed. (2) (Okavango Delta Symposium):131-139.
- CHRISTIAN, K. A. 1982. Changes in the food niche during postmetamorphic ontogeny of the frog *Pseudacris triseriata*. Copeia 1982:73-80.
- COTT, H. B. 1961. Scientific results of an enquiry into the ecology and economic status of the Nile crocodile (*Crocodylus niloticus*) in Uganda. Trans. Zool. Soc. Lond. 29:211-357.
- CRAWSHAW, P. G., AND G. B. SCHALLER. 1980. Nesting of Paraguayan caiman (*Caiman yacare*) in Brazil. Papéis Avulsos Zool., São Paulo 33:283-292.
- DIEFENBACH, C. O. C. 1979. Ampullarid gastropods—staple food of *Caiman latirostris*. Copeia 1979:162-163.
- DIMMITT, M. A., AND R. RUIBAL. 1980. Exploitation of food resources by spadefoot toads (*Scaphiopus*). Copeia 1980:854-862.
- FOGARTY, M. J., AND J. D. ALBURY. 1968. Late summer foods of young alligators in Florida. Proc. Southeast. Assoc. Game and Fish Comm. 21:220-222.
- GARNETT, S. T. 1985. The consequences of slow chitin digestion on crocodile diet analyses. J. Herpetol. 19:303-304.
- GILES, L. W., AND V. L. CHILDS. 1949. Alligator management on the Sabine National Wildlife Refuge. J. Wildl. Manage. 13:16-28.
- JACKSON, J. F., H. W. CAMPBELL, AND K. E. CAMPBELL. 1974. The feeding habits of crocodilians: validity of the evidence from stomach contents. J. Herpetol. 8:378-381.
- LANCE, V., T. JOANEN, AND L. MCNEASE. 1983. Selenium, vitamin E, and trace elements in the plasma of wild and farm-reared alligators during the reproductive cycle. Canadian J. Zool. 61:1744-1751.
- MAGNUSSON, W. E. 1985. Habitat selection, parasites and injuries in Amazonian crocodilians. Amazoniana 9:193-204.
- MAIORANA, V. C. 1978. Difference in diet as an epiphenomenon: space regulates salamanders. Canadian J. Zool. 56:1017-1025.
- MCNEASE, L., AND T. JOANEN. 1977. Alligator diets in relation to marsh salinity. Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies 31:36-40.
- MEDEM, F. 1981. Los Crocodylia de Sur America vol. 1. Los Crocodylia de Colombia. Colciencias, Bogotá. 354 pp.
- . 1983. Los Crocodylia de Sur America vol. 2. Venezuela-Trinidad-Tobago-Guyana-Suriname-Guyana Francesa-Ecuador-Perú-Bolivia-Brasil-Paraguay-Argentina-Uruguay. Colciencias, Bogotá. 270 pp.
- POOLEY, A. C. 1982. Discoveries of a crocodile man. William Collins and Sons, London. 213 pp.
- STATON, M. A., AND J. A. DIXON. 1975. Studies on the dry season biology of *Caiman crocodilus crocodilus* from the Venezuelan Llanos. Memoria de la

- Sociedad de Ciencias Naturales La Salle 35:237-265.
- TAYLOR, J. A., G. J. W. WEBB, AND W. E. MAGNUSON. 1977. Methods of obtaining stomach contents from live crocodilians (Reptilia Crocodylidae). *J. Herpetol.* 12:145-417.
- . 1979. The foods and feeding habits of subadult *Crocodylus porosus* Schneider in northern Australia. *Aust. Wildl. Res.* 6:347-359.
- TOFT, C. A. 1985. Resource partitioning in amphibians and reptiles. *Copeia* 1985:1-21.
- WEBB, G. J. W., AND H. MESSEL. 1977. Crocodile capture techniques. *J. Wildl. Manage.* 41:572-575.
- , S. C. MANOLIS, AND R. BUCKWORTH. 1982. *Crocodylus johnstoni* in the McKinlay River area, N.T. 1. Variation in the diet, and a new method of assessing the relative importance of prey. *Aust. J. Zool.* 30:877-899.
- WHITFIELD, A. K., AND S. J. M. BLABER. 1979. Predation on striped mullet (*Mugil cephalus*) by *Crocodylus niloticus* at St. Lucia, South Africa. *Copeia* 1979:266-269.
- ZAR, J. H. 1974. *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs. 620 pp.

Accepted: 10 March 1986.