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DIET OF THE SPECTACLED CAIMAN (*CAIMAN CROCODILUS*) IN THE CENTRAL VENEZUELAN LLANOS

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ABSTRACT: Between October 1984 and June 1989, a sample of 274 spectacled caiman (189 dead on road, 85 sacrificed) was examined to study diet in the central Venezuelan llanos. I divided prey items found in the stomach into 10 categories and conducted analyses based on prey frequency and mass. Overall, fish, mammals, snails (*Pomacea*), and freshwater crabs were the most important prey. The diet of the caimans shifted ontogenetically and seasonally. The diet of the caimans during the dry season was composed largely of fish. Snails and crabs were consumed principally during the wet season. Mammals were most frequently encountered in the stomachs of the caimans during the late dry and early wet seasons. Vertebrate prey became more important with increasing size of caimans, with larger caimans consuming more fish and mammals. The consumption of insects was negatively correlated with the size of caimans, but snails and crabs were important in the diet of caimans of all size-classes. Caimans consumed food at a low rate, containing a mean of 15.6 g of recently ingested material; 25% of all stomachs that I examined were empty.

Key words: Crocodylia; *Caiman crocodilus*; Diet; Venezuela

A NUMBER of studies have examined the diet of crocodilians: e.g., *Alligator mississippiensis* (Chabreck, 1971; Delany and Abercrombie, 1986; Fogarty and Albury, 1967; McNease and Joanen, 1977), *Crocodylus porosus* (Taylor, 1979), *Crocodylus johnsoni* (Webb et al., 1982), *Crocodylus acutus* (Seijas, 1988; Thorbjarnarson, 1988), including several which have described the diet or feeding behavior of the spectacled caiman, *Caiman crocodilus* (Ayarzagüena, 1983; Fitzgerald, 1988; Gorzula, 1978; Magnusson et al., 1987; Schaller and Crawshaw, 1982; Seijas and Ramos, 1980; Staton and Dixon, 1975). Most previous investigations have examined diet over relatively short periods of time (principally during the annual dry season) and described ontogenetic shifts in utilization of prey. Other than the work by Gorzula (1978) and Ayarzagüena (1983), few dietary studies of *Caiman* have examined the nature of seasonal variation in diet.

This paper presents the results of a 4.5-yr study of dietary habits of caimans in the central Venezuelan llanos. The study addresses seasonal and ontogenetic dietary variation in terms of utilization of different categories of prey and the size of prey within each category. These results are then compared with reports on the diet of caimans in other parts of the llanos, as well as with those of a study conducted 10 yr previously at the same site (Staton and Dixon, 1975).

MATERIALS AND METHODS

Between October 1984 and June 1989 dead specimens of *Caiman* were collected from along a 44-km stretch of highway between Hato Masaguaral (8°33'N 67°37'W) and the Guárico River bridge near the town of Calabozo, Guárico state, Venezuela. Only caimans found dead on road (DOR) less than two days were collected. Caimans with ruptured stomachs infrequently had stomach contents strewn throughout the body cavity, and those individuals were not included in dietary studies. Additionally, from May 1986 to June 1987, a monthly sample ($n = 6$) of caimans from Masaguaral and an adjacent ranch (Flores Moradas) was killed for studies of diet and reproduction (MARNR Permit No. 001744 of 9 June 1986).

Caimans were classified into three size-classes (Ayarzagüena, 1983): II = 20–59.9 cm snout–vent length (SVL), III = 60–89.9 cm SVL, and IV ≥ 90 cm SVL. Because caimans are sexually dimorphic in size, size-class IV consisted entirely of adult males; size-class III contained adult females and subadult and small adult males. Size-class II was comprised of juveniles. The diet of hatchling caimans (size class I: <20 cm SVL) was studied as part of an examination of hatchling ecology (T. Escalona and J. B. Thorbjarnarson, unpublished data).

The habitat of the llanos savanna undergoes an extreme seasonal shift in availability of water from near drought conditions in the dry season (January–June) to extensive flooding during the rainy season (July–December) (Sarmiento, 1983). To examine seasonal variation of diet, I classified samples as early dry season (January–March), late dry season (April–June), early wet season (July–September), or late wet season (October–December).

Stomach contents of all caimans were first collected in a plastic basin, then rinsed with water in a fine sieve to remove mucous and gastric juices. I classified prey items as either freshly ingested, partly digested, or fragments. All fresh and partly digested items were weighed on an O-Haus triple-beam balance to the nearest 0.1 g. Prey were separated into one of 10 principal taxonomic categories: snails (Ampullaridae; *Pomacea doliodes*), arachnids, Coleoptera, other insects, crabs, fish, amphibians, reptiles, birds, or mammals. I identified prey to the lowest taxon possible. The lengths of all opercula of *Pomacea* were measured to the nearest 1 mm.

To reduce bias due to the differential digestibility of prey items (Garnett, 1985; Jackson et al., 1974), I analyzed ontogenetic and seasonal variation in the diet of caimans within categories of prey (Magnusson et al., 1987). In so doing, I assumed that the remains of different prey within any one prey category persisted in the stomach for similar periods of time. Most analyses were based on the overall incidence of the remains of prey. However, because the chitinous exoskeletons of certain invertebrates may remain in crocodilian stomachs for periods of up to several months (Garnett, 1985), seasonal variation in the consumption of snails, Coleoptera, and other insects was analyzed using recently ingested prey only (fresh and partly digested categories). My analyses of crabs were based on all remains, because freshwater crustaceans are digested relatively rapidly (Delany and Abercrombie, 1986; Magnusson et al., 1987).

I tested seasonal and ontogenetic variation of prey utilization using the Kruskal-Wallis analysis of variance by ranks. Size-related trends in the incidence of prey were analyzed using Spearman's rank correlation. I examined ontogenetic trends in prey size and mass using least-square regressions with the assumption that parametric statistics apply to the data sets. All statistical analyses were conducted using the CSS statistical package for microcomputers (Statsoft, Inc.).

RESULTS

I examined the stomach contents of 274 caimans: 85 were captured in the field and 189 were DOR. No significant differences were found between sexes in the utilization of any of the 10 principal prey categories (Mann-Whitney U test: $P > 0.05$). While the mean size of captured caimans was greater than that of DOR's ($F_{1,261} = 38.21$, $P < 0.001$: Table 1), no effect of season was apparent on the size of the caiman collected ($F_{3,269} = 1.78$, $P > 0.05$: Table 1). A comparison of DOR and captured caimans revealed no significant differences in any of the prey categories except for fish (Mann-Whitney U, $P < 0.01$), which comprised a significantly larger part of the diet of sacrificed caiman. An examination of the effects of size-class and season on the frequency of fish in the diet of DOR and captured caimans showed a similar seasonal pattern for both samples, with a peak in the dry season. However, utilization by size-class differs, with sacrificed size-class II ($\chi^2 = 33.0$, $P < 0.001$) and III ($\chi^2 = 10.6$, $P < 0.01$) caimans consuming more fish than similarly sized DOR individuals. I felt that these differences were not great

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TABLE 1.—Mean size of caimans (cm SVL) collected in diet-sample by season, including captured and DOR specimens. Values are presented ±SD, with ranges and sample sizes in parentheses.

Season	DOR	Captured	Overall
Early dry (Jan.–March)	68.0 ± 23.1 (25.7–118.0; n = 35)	83.8 ± 18.5 (61.6–118.5; n = 16)	73.0 ± 22.9 (n = 51)
Late dry (April–June)	71.0 ± 19.0 (34.0–114.0; n = 51)	81.1 ± 15.0 (58.0–120.9; n = 36)	75.2 ± 18.1 (n = 87)
Early wet (July–Sept.)	64.4 ± 18.6 (32.5–119.0; n = 42)	81.6 ± 14.9 (63.1–112.0; n = 18)	69.5 ± 19.3 (n = 60)
Late wet (Oct.–Dec.)	66.0 ± 16.7 (27.5–112.7; n = 61)	80.5 ± 17.8 (44.5–110.0; n = 15)	68.9 ± 17.9 (n = 75)
Overall	67.3 ± 19.2 (25.7–119.0; n = 189)	81.6 ± 16.2 (44.5–120.9; n = 85)	71.8 ± 19.5 (n = 274)

enough to warrant dividing DOR and sacrificed caimans into two separate categories for analyses, so all individuals were grouped together.

Frequency of Prey Occurrence

The most commonly encountered prey-remains in stomachs of caimans were snails (*Pomacea doliodes*), freshwater crabs (*Dilocarcinus dentatus*), and Coleoptera (Table 2). Coleoptera were predominantly aquatic beetles of the family Hydrophilidae, with terrestrial scarab beetles being somewhat less common (Table 3). Other insects, primarily aquatic Hemiptera of the family Belastomatidae, were also frequently consumed. Fish were found in 17.5% of the stomachs of caimans examined, with the three most common species being *Synbranchus marmoratus* (an eel-like member of the Synbranchiformes), *Hoplosternum littorale* (an armored catfish: Callichthyidae), and *Hoplias malabaricus* (a predatory characoid). Remains of mammals were less commonly encountered and usually consisted of small, unidentified rodents. Remains of amphibians, reptiles, birds, and spiders were infrequently found.

Only 85 of the 274 (31.0%) caimans examined contained fresh or partly digested prey. A large percentage (24.5%) had no food remains at all in their stomachs (Table 1). Among all caimans (including those with empty stomachs), the mean mass of fresh and partly digested prey was 15.6 g.

TABLE 2.—Frequency of occurrence of prey categories, vegetation, gastroliths, and empty stomachs in caimans from Hato Masaguaral by size-class. No. = number of caimans that contained any remains of the indicated prey category.

	Size-class							
	II		III		IV		Total	
Prey category	No.	%	No.	%	No.	%	No.	%
Coleoptera	22	34.9	32	19.6	4	8.3	58	21.2
Other insects	16	25.4	30	18.4	3	6.3	49	17.9
Crabs	13	20.6	42	25.8	10	20.8	65	23.7
Snails	18	28.6	61	37.4	16	33.3	95	34.7
Arachnids	1	1.6	3	1.8	0	0.0	4	1.5
Fish	4	6.4	31	19.0	13	27.1	48	17.5
Amphibians	1	1.6	7	4.3	1	2.1	9	3.3
Reptiles	1	1.6	7	4.3	4	8.3	12	4.4
Birds	3	4.8	6	3.7	0	0.0	9	3.3
Mammals	2	3.2	24	14.7	4	8.3	30	11.0
Empty	12	19.1	38	23.3	17	35.4	67	24.5
Vegetation	9	14.3	49	30.1	15	31.3	73	26.6
Gastroliths	24	38.1	88	54.0	39	81.3	151	55.1

TABLE 3.—Prey items identified from stomachs of caimans on Hato Masaguaral. Values indicate the percentage of caimans with identified items from the indicated prey category that contained the identified prey item (e.g., hydrophilids were found in 75.6% of the caimans containing remains of coleopterans).

Prey category	Prey item	Percent of total
Coleoptera	Hydophilidae	75.6
	Scarabaeidae	12.2
	Unidentified	14.6
Other insects	Belastomatidae	82.1
	Orthoptera	10.3
	Unid. Hemiptera	5.1
	Mantidae	2.6
	Lepidoptera larvae	2.6
	Unidentified	2.6
Crabs	*Dilocarinus dentatus*	100.0
Snails	*Pomacea doliodes*	100.0
Arachnids	Unidentified	100.0
Fish	*Synbranchus marmoratus*	18.9
	Hoplosternum littorale	18.9
	Hoplias malabaricus	16.2
	Cichlidae	8.1
	Unid. Siluriformes	5.4
	Pimelodidae	5.4
	Pygocentrus notatus	5.4
	Unidentified	35.1
Amphibians	*Pseudis paradoxus*	42.9
	Leptodactylus sp.	14.3
	Pleurodema brachyops	14.3
	Unidentified	42.9
Reptiles	*Iguana iguana*	54.5
	Caiman crocodilus	16.7
	Chironius carinatus	9.1
	Unid. Ophidia	9.1
	Unidentified	9.1
Birds	*Porphyrula martinica*	28.6
	Dendrocygna sp.	14.3
	Icteridae	14.3
	Unid. Ciconiiformes	14.3
	Unidentified	28.6
Mammals	Unid. Rodentia	44.4
	Dasypus novemcinctus	5.6
	Didelphis marsupialis	5.6
	Unidentified	44.4

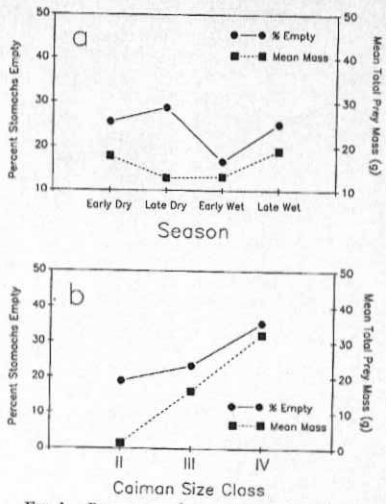
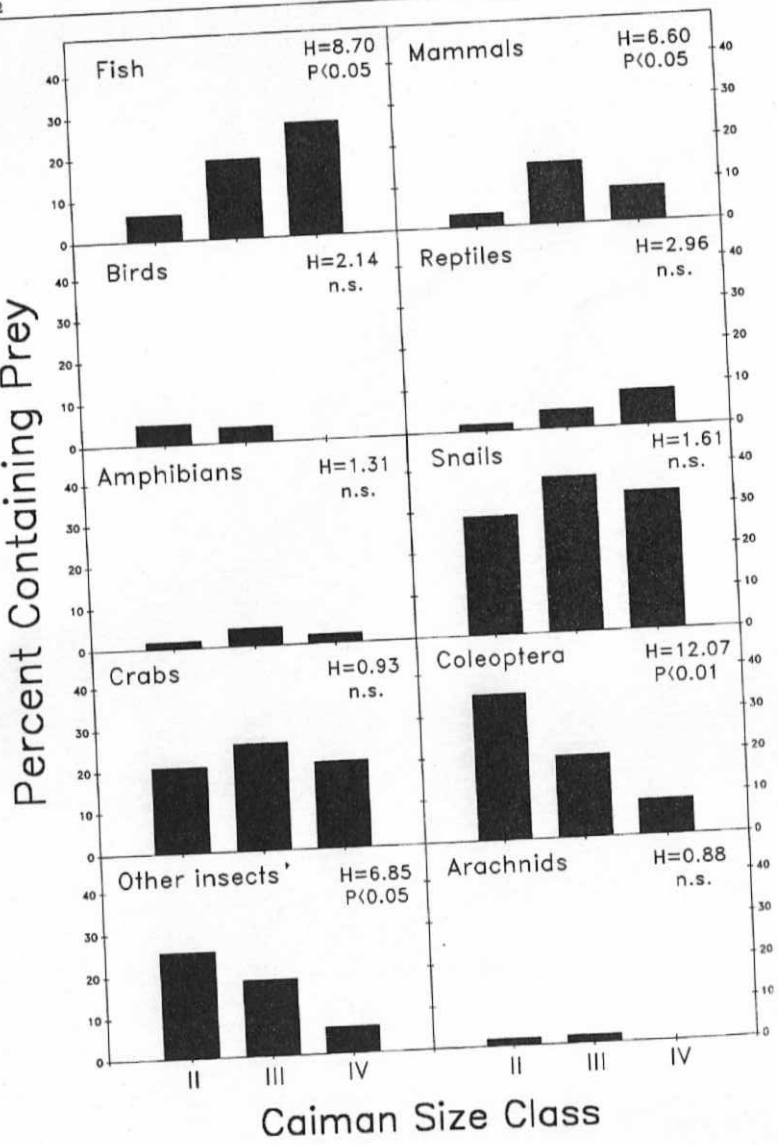


FIG. 1.—Percentage of empty stomachs and mean total mass of recently ingested prey by (a) season (early dry = January–March, late dry = April–June, early wet = July–September, late wet = October–December) and (b) size-class of caimans (II = 40.0–59.9 cm SVL, III = 60.0–89.9 cm SVL, IV ≥ 90 cm SVL).

Seasonal and Ontogenetic Variation

The amount of recently ingested food found in stomachs of caimans remained relatively constant throughout the year, and no significant difference was found among seasons (Fig. 1a: Kruskal-Wallis, $H = 4.96$, $P = 0.17$). Likewise, the frequency of empty stomachs changed little throughout the course of the year (Fig. 1a: Kruskal-Wallis, $H = 2.86$, $P = 0.41$), or among the three size-classes of caimans (Fig. 1b: Kruskal-Wallis, $H = 4.22$, $P = 0.12$). However, the amount of recently ingested food was greater among larger caimans (prey mass $= -22.00 + 0.52$ SVL; $r = 0.17$, $P < 0.01$: Fig. 1b). The mean mass of recently ingested prey for each size-class was: II—1.4 g, III—16.2 g, IV—32.1 g.

Among the three size-classes of caimans, significant variation in the frequency of prey utilization was noted in four of the 10 categories of prey (Fig. 2). The consumption of fish increased (Spearman $r_s = 0.177$, $P < 0.01$) with the size of caimans, and decreased for Coleoptera (Spearman $r_s = -0.209$, $P < 0.001$) and other insects (Spearman $r_s = -0.154$, $P < 0.05$). The consumption of mammals tended to increase with size but was highest in caimans of size-class III. Among juvenile caimans (size-class II), four of the five most impor-



tant prey categories (based on mass of recently ingested prey) were invertebrates (Table 4). However, based on prey mass, fish were the most important prey of juveniles and caimans of size-class III (Table 4). Mammals and birds assumed greater importance among mid-sized caimans, and mammals, reptiles, and fish were the most important prey of large caimans.

Seasonally, the consumption of snails and crabs varied significantly (Fig. 3). Snails were eaten principally during the early wet season and crabs during the early and late wet season. Seasonal variation in the ingestion of fish and mammals was not at the formal level of significance statistically (Fig. 3), but the low probability values were considered to be indicative of trends in prey utilization, with peak consumption of fish during the early dry season, and mammals during the late dry and early wet seasons.

Prey Size

Regression analysis of prey mass (for each of the 10 prey categories) versus caiman SVL showed no significant correlations ($-0.43 < r < 0.71$, $0.98 < P < 0.08$), with the one exception of a slightly negative correlation between caiman SVL and amphibian mass ($r = -0.96$, $P = 0.04$), which was probably due to small sample size ($n = 4$). Sample sizes for most categories of prey were small due to the rarity of encountering recently ingested prey. Nevertheless, even among the three groups with relatively large samples (fish: $n = 22$; snails: $n = 25$; crabs: $n = 16$), no significant correlations were found.

The association between caiman-size and prey-size was investigated more thoroughly with snails by using length of operculum as an index of snail-size. In a sample of 52 caimans (containing 1–66 opercula), no correlations were found between caiman-size and either mean, minimum, or maximum operculum-length ($r = 0.10$–0.20, $0.16 < P < 0.48$).

TABLE 4.—The five most important categories of prey (based on mass of recently ingested prey) by size-class of caimans. Values in parentheses represent mean total mass (g) of items from that prey category.

Size-class		
II ($n = 65$)	III ($n = 163$)	IV ($n = 48$)
Fish (0.66)	Fish (4.75)	Mammals (12.41)
Snails (0.53)	Mammals (4.06)	Reptiles (11.34)
Crabs (0.18)	Birds (3.94)	Fish (7.17)
Other insects (0.03)	Crabs (1.55)	Crabs (1.29)
Coleoptera (0.03)	Amphibians (0.84)	Snails (0.12)

Other Stomach Contents

Vegetation was found in the stomachs of 26.6% of the caimans examined. Grasses were the most commonly encountered vegetation (76.2% of stomachs with vegetation), followed by leaves (19.0%), woody material (14.3%), and seeds (14.3%). Vegetation was usually found in small amounts, although in some cases large boluses of grass (to 183 g) were ingested.

Stones were encountered in more than one-half of the caimans examined (Table 2). The presence and total mass of stomach stones (MSS, in grams) were clearly related to size of the caiman (SVL, in centimeters) ($MSS = -31.95 + 0.57$ SVL, $r = 0.44$, $P < 0.001$, $n = 274$). The frequency of occurrence of stomach stones increased from 38.1% in caimans of size-class II to 81.3% in individuals of size-class IV (Table 1). The greatest mass of stones found in one caiman was 255.2 g in a male of 110 cm SVL.

Ascarids (*Sebekia* sp.) were encountered in 24.6% of the caiman stomachs examined.

DISCUSSION

The principal species of prey and ontogenetic trends in the diets of caimans in this study are similar to those reported in other studies in the Venezuelan llanos (Ayarzagüena, 1983; Fitzgerald, 1988; Seijas

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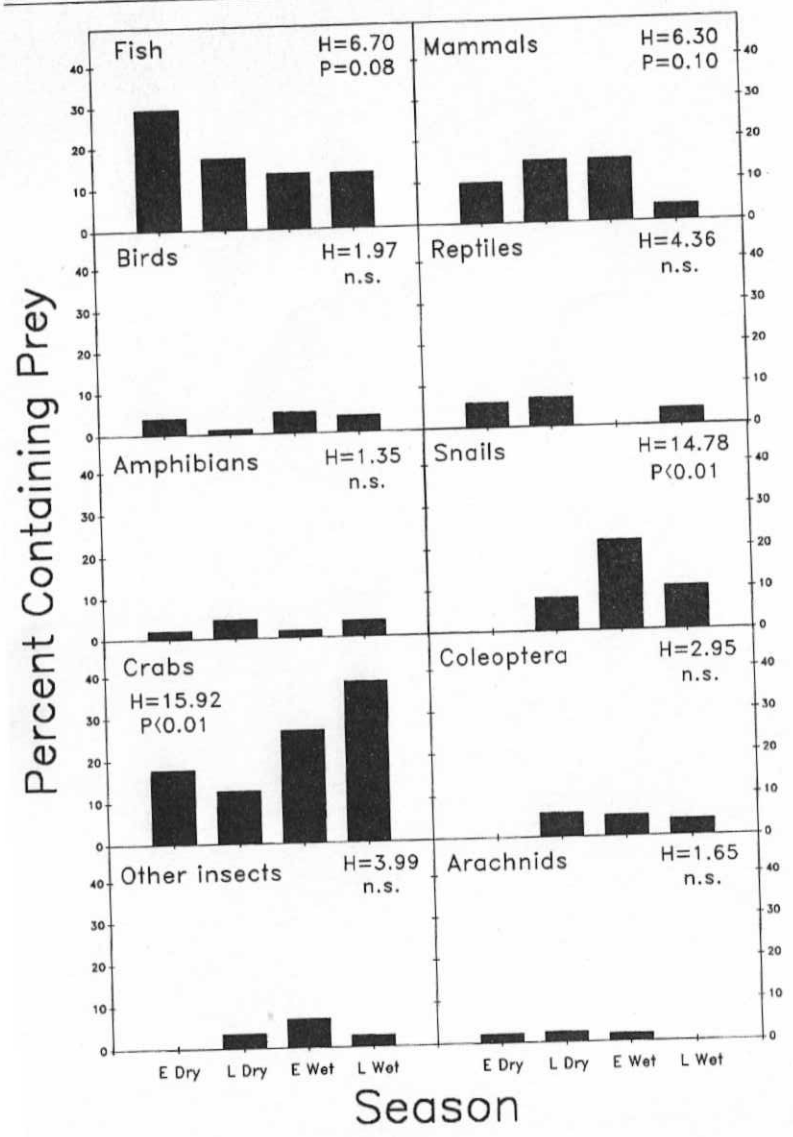
FIG. 2.—Incidence of prey found in stomachs as a function of size-class of caimans for each of the 10 prey categories. Size-classes as in Fig. 1b.



and Ramos, 1980), as well as those reported for the same site 10 yr previously (Staton and Dixon, 1975). The prey of juvenile caimans consists largely of invertebrates: Coleoptera, Belastomatidae, snails (*Pomacea*), and crabs. However, fish were an important part of the diet of juvenile caimans in this and other studies of diet (Ayarzagüena, 1983; Seijas and Ramos, 1980). Seijas and Ramos (1980) were the only ones to find shrimp (*Macrobrachium* sp.) to be important in the diet of caimans. Hatchling caimans (<20 cm SVL) on Masaguaral subsist principally on aquatic beetles (Carabidae, Hydrophilidae, Dytiscidae) (Staton and Dixon, 1975; T. Escalona and J. Thorbjarnarson, unpublished data). Fish were the principal prey of large caimans in all of the studies except for that of Ayarzagüena (1983). However, because Ayarzagüena ranked prey by percent occurrence, his data over-represented the importance of the slow digesting snails and crabs. Besides fish, other vertebrate prey were important in the diet of large caimans in this study. This differs from other investigations conducted in the llanos, none of which found mammals, birds, or reptiles to figure significantly in the diet. This, in part, reflects the tendency of previous studies to rely on frequency of occurrence as an index of relative importance (Ayarzagüena, 1983; Seijas and Ramos, 1980), underestimating the importance of large or quickly digested prey items (Garnett, 1985). Nevertheless, two studies that did incorporate prey-ranking based on volumetric analyses (Fitzgerald, 1988; Staton and Dixon, 1974) found vertebrates other than fish to comprise a minor part of caiman diet. Among studies that were not restricted to the dry season, crabs and snails were important in the diet of caimans of all sizes except hatchlings (Ayarzagüena, 1983; Fitzgerald, 1988; my study), and did not show any ontogenetic trends in the frequency of consumption.

Similar ontogenetic shifts in diet have been noted in studies of crocodilian diets among several species (e.g., Cott, 1961; Delany and Abercrombie, 1986; Magnusson et al., 1987; Thorbjarnarson, 1988; Webb et al., 1982). Dietary shifts are evident in both size and the type of prey (Webb et al., 1982). Ontogenetic shifts in diet presumably reflect the ability of larger individuals to capture larger prey (Fitzgerald, 1988; Magnusson et al., 1987) and are not unexpected in a species that undergoes a 500-fold increase in mass during its lifetime. However, habitat selection and foraging mode may also play crucial roles in determining diet (Magnusson et al., 1987; Seijas, 1988). In my study, the lack of correlation between caiman-size and prey-size within prey-categories, and the apparent shifts in the utilization of prey-categories with caiman ontogeny, suggest that growing caimans meet their increased energy requirements principally by switching to prey-categories of larger mean size.

Seasonal shifts in the consumption of certain prey items were found during this study, but the mean mass of recently ingested prey, and the percentage of empty stomachs, did not vary during the year, suggesting that certain prey items replaced others on a seasonal basis. The diet of caimans during the dry season in this and similar studies in the Venezuelan llanos is composed largely of fish (Fitzgerald, 1988; Seijas and Ramos, 1980; Staton and Dixon, 1975). On Masaguaral during the late dry season, the consumption of mammals and snails increased. Crabs were most commonly eaten during the wet season.

Although seasonal variation in the consumption of fish was not statistically significant ($P = 0.08$), I consider the observed variation to be biologically significant. In the hyperseasonal llanos habitat, water levels that drop during the early dry season concentrate both caimans and fish in a small number of waterholes. Most bodies of water in the llanos are relatively shallow and levels of fish biomass peak during the early dry season (Taphorn and Lilyestrom,

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FIG. 3.—Incidence of prey found in stomachs as a function of season for each of the 10 prey-categories. Seasons as in Fig. 1a. Snails, other insects, and Coleoptera include only recently ingested prey.

1984). Observations of fishing activity by caimans on Masaguaral also noted a peak during this period (January–February: Thorbjarnarson, 1991). Fitzgerald (1988) reported an increase in the consumption of fish on a nearby ranch during the late wet season and the early dry season. Many of the fish that are found in stomachs of caimans in this and other studies are facultative air breathers (e.g., *Hoplosternum, Hoplias*) that can tolerate the low levels of oxygen that prevail during the dry season in most llanos bodies of water. In contrast, on Masaguaral, few fish were consumed between May and August, when caimans move from their dry season concentrations and disperse across the freshly flooded savannas (Thorbjarnarson, 1991). Fish biomass in diked modules in Apure state reach their lowest levels during this period (Taphorn and Lilyestrom, 1984).

Few crabs or snails were seen on Masaguaral during the dry season (personal observation), when they would apparently aestivate. Densities of crabs on Masaguaral peak in August, but mean crab-size increased throughout the wet season (T. Donnay and S. Beissinger, personal communication). Dietary studies carried out during the dry season (Seijas and Ramos, 1980; Staton and Dixon, 1974) report lower incidences of these two prey items. Fitzgerald (1988) also reported a sharp decline in the consumption of both crabs and snails at the onset of the dry season.

Fewer than one third of the caimans examined in this study had more than fragments of prey in their stomachs, and on average they had only 15.6 g of recently ingested prey, representing only 0.2% of the caiman's body mass. One quarter of all stomachs of caimans contained no food at all. Studies on passage rates of prey items in *Alligator mississippiensis* suggest that remains of food items such as crustaceans, snails, mammals, birds, and turtles may remain in the stomach for five or more days after ingestion (Delany and Abercrombie, 1986). Certain relatively undigestible items, such as opercula of snails, may remain for considerably longer periods. Only 31% of the caimans examined in this study had fresh or partially digested prey, indicating that caimans were not eating small quantities of food on a continual basis. These results are in accord with the low metabolic demands of crocodilians (Coulson and Hernandez, 1983) and low-energy lifestyle of vertebrate ectotherms (Bennett, 1982; Pough, 1980). One of the obvious benefits of the low metabolic requirements of caimans is the ability to survive periods of low food availability. This is especially important in the hyperseasonal llanos habitat where, in some areas, juvenile caimans may have to live through an annual period of 3–5 mo with very little food.

Resumen

En los llanos centrales de Venezuela entre octubre 1984 y junio 1989 se examinó una muestra de 274 babas (*Caiman crocodilus*) (189 atropelladas, 85 sacrificadas). Los análisis fueron basadas en frecuencia y peso. En general, las presas más importantes fueron peces, mamíferos, caracoles *Pomacea*, y cangrejos de agua dulce. Se encontró que la dieta de las babas cambio entre estaciones, y con el tamaño de la baba. La dieta de la baba durante la estación de sequía consistió príncipalmente de peces. En cambio, durante la estación de lluvia, el consumo de caracoles y cangrejos aumentó. Mamíferos fueron encontrados en los estómagos de babas príncipalmente durante el final de la sequía y comienzo de la estación de lluvia. Babas juveniles se alimentaron principalmente de peces, caracoles, insectos (la mayor parte Coleoptera) y cangrejos. A medida que las babas van creciendo los vertebrados se convierten en presas más importantes. El consumo de insectos fue correlacionado negativamente con el tamaño de babas, pero caracoles y cangrejos formaron un importante parte de la dieta de babas de todos las clases de tamaño. Babas ingerieron pequeñas cantidades de comida, con un promedio de 15.6 g de presas frescas, y 24.5% de los estomagos vacios.

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