

DIETS OF *CAIMAN CROCODILUS YACARE* FROM DIFFERENT HABITATS IN THE BRAZILIAN PANTANAL

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The diet of *Caiman crocodilus yacare* was investigated during the dry season in different habitats of the Pantanal, Brazil. Stomach contents of 196 animals were analysed by prey class, the total number of prey, and the number of caimans eating each prey type. *C. c. yacare* ate mostly insects and fish. The caimans' diets differed significantly among habitats but not among caiman size classes.

INTRODUCTION

Caiman crocodilus yacare has an extensive South America distribution and occurs in high densities in the Pantanal region of Brazil (Mourao *et al.*, 1994). It is extensively harvested for its skin, illegally through direct hunting, and legally through ranching: collecting wild eggs, incubating them and raising the young in captivity. Several studies have been conducted in order to manage caimans on rangelands on a sustainable basis (Mourao *et al.*, 1994; Campos, 1993).

The Pantanal region contains a high diversity of aquatic habitats and species, and it seems likely that *C. c. yacare* is an important component of such systems. Information on food and feeding strategies is a first step towards evaluating their role, and it may also shed light on their management in captivity, where diet is known to influence growth rate and reproduction (Delany & Abercrombie, 1986).

Studies of the diet of *C. c. yacare* to date have been based on casual observations (Alvaro, 1945; Crawshaw & Shaller, 1980), or analyses of stomach contents (Aquino-Ortiz, 1988; Uetanabaro, 1989). Variation in the diet of crocodylians is thought to be related to both habitat and body size (Taylor, 1979; Webb *et al.*, 1982; Magnusson *et al.*, 1987; Thorbjarnarson, 1993; Allsteadt & Vaughan, 1994).

The present study reports the summer diet of *C. c. yacare* in relation to habitat and size.

MATERIAL AND METHODS

The Pantanal is situated in central western Brazil, between 16 and 22° and 55 and 58° (Fig. 1). It is a relatively flat region of alluvial accumulation, with an average altitude of 120 m above sea level (Brasil, 1974). Inundation is common and can be pluvial or fluvial in origin. Drainage occurs by rivers, streams and temporary channels and there are a great number of ponds. The extent of inundated areas varies seasonally (Carvalho, 1986; Vila da Silva & Kux, 1992).

For this study, 196 caimans were caught during the summer dry season, in brackish ponds, freshwater ponds, temporary channels and the Negro river in the Nhecolândia region, freshwater ponds and artificial roadside ponds in the Abobral region and the Miranda river in the Miranda region (Fig. 1).

In October 1987, 21 animals were caught in ponds in Nhecolândia. Between September and October 1989, 46, 45 and 27 caimans were caught in brackish ponds, temporary channels and the Miranda river, respec-

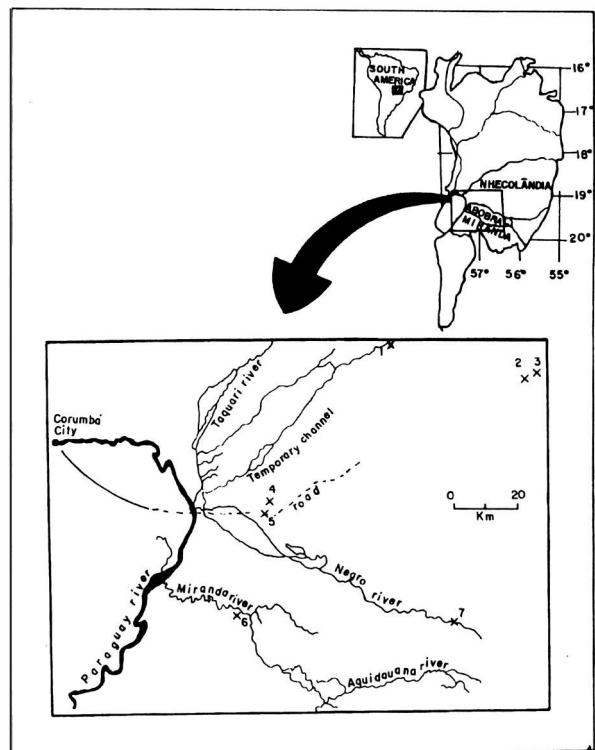


FIG. 1. The study area. Numbers indicate sampling sites. 1, temporary channels; 2, ponds of Nhecolândia; 3, brackish ponds; 4, ponds of Abobral; 5, artificial roadside ponds; 6, Miranda river; 7, Negro river.

tively. Between October and November 1990, 24, 13 and four caimans were collected in brackish ponds, ponds of Abobral and artificial roadside ponds, respectively, and in October 1990, six and 10 animals were caught in artificial roadside ponds and the Negro river, respectively.

All animals were caught at night (between 20.00 hr and 23.00 hr). They were weighed, their snout-vent lengths (SVL) were measured and their stomach contents were removed from live caimans by the method of Taylor *et al.* (1977) with modifications suggested by Webb *et al.* (1982). This method enabled removal of stomach contents without harming the animal. Caimans were classified into three size classes: juveniles = < 50 cm SVL; sub-adults = 50.1-70.0 cm SVL; and adults = > 70.1 cm SVL. This set consisted of 196 animals, juveniles ranging from 19.2-50.0 cm SVL (mean = 33.1 cm, $n = 79$) and from 0.1-3.5 kg in weight (mean = 1.1 kg, $n = 79$); sub-adult ranging from 51.0-70.0 cm SVL (mean = 60.5 cm, $n = 52$) and from 1.8-11.5 kg in weight (mean = 5.4 kg, $n = 52$) and adults ranging from 71.0-111.0 cm SVL (mean = 86.7 cm, $n = 65$) and from 7.0-45.0 kg in weight (mean = 16.8 kg, $n = 65$). Stomach contents were preserved by formalin. After removal of vegetation and parasites from the stomach contents, all items were grouped into one of nine major classes: (1) Gastropoda; (2) Arachnida; (3) Crustacea; (4) Insecta; (5) Diplopoda; (6) Pisces; (7) Amphibia; (8) Aves and (9) Mammalia. Because of the wide variation in degree of food digestion, data are presented by numerical and occurrence percentages, rather than volumetric and weight measurements. The numerical method (% N) describes the number of items in a given prey class expressed as a percentage of the total number of items across all stomachs, while the frequency occurrence method describes the number of stomachs containing a particular item expressed as a percentage of all stomachs (Hyslop, 1980).

Samples of the main food items were collected for identification and chemical analysis. Fish were sampled in all habitats, except for brackish ponds, with a seine of 15 m long and with a 0.5 inch bar mesh. Aquatic insects were sampled with a screen (80 x 50 cm) only in brackish ponds at different depths (20, 30 and 40 cm).

Samples of the foods items were dried in the laboratory at 60°C and ground in a wiley mill. A portion of each sample was then dried at 105°C to determine mineral content. Crude protein was determined using the Kjeldahl method (AOAC, 1970), and crude energy was determined by a calorimetric bomb apparatus. Percentage concentration of phosphorus (P) was determined by colorimetry (Fick *et al.*, 1976) and calcium (Ca) by atomic absorption (Harris & Popat, 1954). Similarities among diet were quantified using the Bray-Curtis (Czekanowski) index of similarity.

Analyses of diets of generalist carnivores present many statistical problems. Firstly, eating one type of

prey excludes the eating of another, introducing spurious negative correlations. Secondly, 'diet' is a composite variable. In a comparison of 20 diet categories between two habitats the probability of finding at least one apparently significant difference approaches one, even if data are distributed randomly between the habitats. When many habitats are compared, the probability of a Type I error increases, unless some form of multiple comparison procedure is used. With many prey categories and many habitats to be compared, multiple comparison methods are almost guaranteed to result in Type II errors.

One alternative is to reduce the diet to one or two dimensions and subsequently apply conventional statistical or Monte Carlo procedures. Many multivariate methods are available (James & McCulloch, 1990), and often, though not always, they produce similar results. All are based on a matrix of similarities, or dissimilarities, between the objects to be ordinated. In this paper, the objects were size classes within habitats and distances among them were based on diet category. All indices of similarity or dissimilarity have advantages and disadvantages. The Bray-Curtis (Czekanowski) index of similarity has been shown to be useful in a variety of ecological studies (Faith *et al.*, 1987), it is not affected by joint absences (Belbin, 1995) and is less affected by aliasing than most similarity indices (MacNally, 1994). However, several others could as easily be justified.

In this study, semi-strong multidimensional scaling (MDS - Belbin, 1995) was used to produce axes that reflect similarity among diets because the method is robust and essentially non-parametric. However, some other ordination techniques might also be applicable. Objects that are closer together on those axes are closer in terms of overall diet, taking into account all prey categories simultaneously.

The ordination techniques were chosen for reasons that are totally independent of the comparisons among data sets. The range of similarity indices and ordination techniques available is such that *post-hoc* selection from among them will almost certainly result in relationships concordant with any *a priori* prejudice. Therefore, to maintain the validity of the inferential statistics, only *a priori* selection of the similarity index and ordination technique was used. Use of an inappropriate similarity index or ordination might increase the probability of a Type II error but would not affect the probability of a Type I error.

Conventional statistics have assumptions that could not be met by these data. To test for the effects of size and habitat on each MDS axis, the sum of squares was calculated using the formula for analyses of variance with two factors and no replication (Zar, 1974). The significance of differences was tested with a Monte Carlo simulation devised by David Williams (100 random runs) on the RANUNI random number functions from SAS Inst., Inc. (1985)

TABLE 1. Summary of foods categories in the diet of 196 *C. c. yacare* from different habitats, expressed as percent by number (*N*) and frequency of occurrence (*O*).

	Brackish ponds		Miranda river		Negro river		Temporary channel		Ponds of Abobral		Ponds of Nhecolândia		Artificial roadside ponds	
	<i>N</i> %	<i>O</i> %	<i>N</i> %	<i>O</i> %	<i>N</i> %	<i>O</i> %	<i>N</i> %	<i>O</i> %	<i>N</i> %	<i>O</i> %	<i>N</i> %	<i>O</i> %	<i>N</i> %	<i>O</i> %
JUVENILES (< 50 cm SVL)														
	<i>n</i> =32		<i>n</i> =3		<i>n</i> =5		<i>n</i> =20		<i>n</i> =7		<i>n</i> =8		<i>n</i> =4	
Gastropoda	0	0	0	0	55.0	20.0	1.6	10.0	0	0	85.5	75.5	2.4	50.0
Arachnida	0	0	0	0	0	0	0.4	5.0	5.5	14.3	0	0	1.9	25.0
Crustacea	0	0	0	0	5.0	20.0	1.2	15.0	30.5	14.3	0	0	0	0
Insecta	99.4	96.8	93.7	100.0	25.0	40.0	95.6	90.0	27.8	100.0	14.5	100.0	64.2	100.0
Diplopoda	0	0	0	0	0	0	0.4	5.0	16.8	71.4	0	0	0	0
Pisces	0	0	6.3	66.6	15.0	60.0	0.4	5.0	19.4	100.0	0	0	9.4	75.0
Amphibia	0.2	6.2	0	0	0	0	0.4	5.0	0	0	0	0	0	0
Aves	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mammalia	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SUB-ADULTS (50.1 cm - 70.0 cm SVL)														
	<i>n</i> =11		<i>n</i> =10		<i>n</i> =2		<i>n</i> =13		<i>n</i> =3		<i>n</i> =2		<i>n</i> =11	
Gastropoda	0	0	4.8	10.0	14.3	50.0	9.1	7.7	0	0	88.0	100.0	52.2	50.0
Arachnida	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Crustacea	0	0	9.5	20.0	0	0	9.1	7.7	0	0	0	0	0	0
Insecta	99.5	100.0	66.7	50.0	71.4	50.0	9.1	7.7	33.4	33.4	12.0	50.0	21.7	100.0
Diplopoda	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pisces	0	0	19.0	40.0	14.3	100.0	63.6	53.8	66.6	66.6	6.0	0.8	26.1	100.0
Amphibia	0.5	36.4	0	0	0	0	9.1	7.7	0	0	0	0	0	0
Aves	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mammalia	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ADULTS (> 70.1 cm SVL)														
	<i>n</i> =24		<i>n</i> =15		<i>n</i> =3		<i>n</i> =7		<i>n</i> =3		<i>n</i> =11		<i>n</i> =2	
Gastropoda	4.2	7.9	0	0	0	0	0	0	0	0	92.3	81.8	0	0
Arachnida	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Crustacea	0	0	24.0	40.0	0	0	0	0	0	0	0.4	9.0	0	0
Insecta	88.9	87.5	16.0	20.0	60.0	100.0	61.1	28.6	40.0	66.0	6.5	45.5	20.0	50.0
Diplopoda	0	0	24.0	40.0	0	0	0	0	0	0	0	0	0	0
Pisces	0	0	48.0	73.3	40.0	66.6	38.9	61.1	40.0	66.0	0.4	9.0	80.0	100.0
Amphibia	3.2	58.3	0	0	0	0	0	0	0	0	0	0	0	0
Aves	0	0	0	0	0	0	0	0	0	0	0.4	9.0	0	0
Mammalia	0	0	0	0	0	0	0	0	20.0	33.3	0	0	0	0

TABLE 2. Number and numerical percentage of the main families of fish encountered in different habitats in the Pantanal in October 1991.

	Brackish ponds	Miranda river (n=70)	Negro river (n=176)	Temporary channel (n=312)	Ponds of Abobral (n=635)	Ponds of Nhecolândia (n=402)	Artificial roadside ponds (n=431)
FISH							
Characidae	0.0	12.8	39.8	42.0	0.0	74.4	55.0
Cichlidae	0.0	28.6	21.0	0.0	69.3	1.7	16.9
Curimatidae	0.0	14.3	21.6	45.8	0.0	0.0	0.0
Erythrinidae	0.0	10.0	0.0	11.5	0.0	1.2	22.7
Loricariidae	0.0	21.4	0.0	0.3	30.3	0.0	0.7
Pimelodidae	0.0	12.8	16.5	0.3	0.2	0.0	3.9
Doradidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Others	0.0	0.1	1.1	0.1	0.2	22.7	0.8
INSECTS							
Belostomatidae	25.0	-	-	-	-	-	-
Hydrophilidae	62.0	-	-	-	-	-	-
Odonata larvae	13.0	-	-	-	-	-	-

RESULTS

DIET COMPOSITION

Table 1 summarizes the diet composition of different sized *C. c. yacare* from different habitats, as represented by nine classes of prey. The most commonly encountered prey in stomachs were insects and fish.

Insects were encountered in all sized caimans in all sites and were most frequent in the diet of juveniles. Insects were mainly of Coleoptera, Diptera and Hemiptera. Insects were the major foods of caimans in brackish ponds which consisted mainly of Belostomatidae and Naucoridae (Hemiptera - Heteroptera), Anisoptera (Odonata) and Hidrofilidae (Coleoptera). Insects were the only food available in brackish ponds during time that the collections were made (Table 2).

Fish was an important food item for all size classes and habitats, except in brackish ponds and ponds of Nhecolândia. Few fish remains could be identified because of their degree of digestion, but these that could were from the family Loricariidae, Erythrinidae

(*Hoplias malabaricus*) and Doradidae (*Trachydoras* sp). Table 2 shows the number and percentage occurrence of fish, by family, in different habitats of the Pantanal.

Snails (*Pomacea* sp.) were common in the diets of caimans caught in the ponds of Nhecolândia, artificial roadside ponds and the Negro river. Snails were not found in the stomachs of caimans caught in ponds of Abobral, an only one adult caiman from brackish ponds had snails in its stomach.

Amphibians were found in the stomach of caimans from temporary channels and brackish ponds. *Pseudis paradoxus* (Anura - Pseudidae), especially tadpoles were eaten in one of three brackish ponds sampled in 1989. Crabs (*Dilocarcinus pagei* and *Trichodactylus borellianus*) were encountered in the stomachs of caimans from the Miranda river, temporary channel ponds of Abobral and the ponds of Nhecolândia. Arachnida, Diplopoda, Aves and Mammalia were found in small numbers in the diets of caimans from most areas. Parasites (Nematoda) were encountered in the stomach of all caimans.

TABLE 3. Composition and energy values of some food items ingested by *C. c. yacare* in the Pantanal, based on dry matter.

	Dry matter (%)	Crude protein (%)	Gross energy (Kcal/kg)	Calcium (%)	Phosphorus (%)	Ca:P ratios
Hemiptera (Belostomatidae)	29.6	64.1	5.4	0.25	0.60	1:2.4
Coleoptera (Hydrophilidae)	37.9	65.4	5.1	0.25	0.5	1:2.0
Odonata (Larvas)	19.6	61.1	5.8	0.30	0.45	1:1.5
Snail (<i>Pomacea</i> sp.)	39.2	18.8	1.3	24.90	0.06	415:1
Crustacea (Trychodactylidae)	22.7	65.9	4.5	0.30	1.20	1:4.0
Fish (Loricariidae)	25.6	61.0	4.2	14.2	3.4	4.2:1
Amphibia (Pseudidae)	15.3	67.1	4.5	4.6	3.2	1.4:1

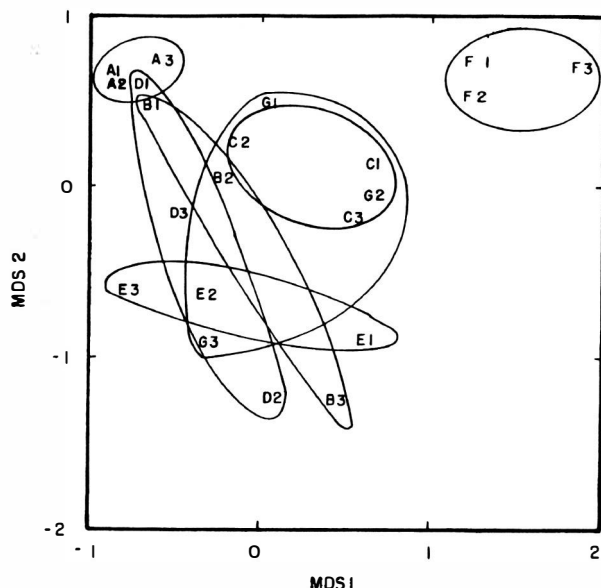


FIG. 2. Multidimensional scaling (MDS) analyses representing variation in diet among three size classes (1, juveniles; 2, subadults; 3, adults) and seven sites (A, brackish ponds; B, Miranda river; C, Negro river; D, temporary channels; E, ponds of Abobral; F, ponds of Nhecolândia; G, artificial roadside ponds)

Composition and energy values of some food items ingested by caimans are listed in Table 3. Mean crude protein and crude energy were generally high, except for snails (*Pomacea* sp.). Insects showed low levels of calcium and phosphorus. Ca to P ratios were 1:2.4, 1:2.0 and 1:1.5 for Belostomatidae, Hydrophilidae and Odonate larvae, respectively. Molluscs, crabs, fish and amphibians had Ca to P ratios of 415:1, 1:4, 4.2:1 and 1.4:1, respectively.

HABITAT AND CAIMAN SIZE VS. DIET

The diets of caimans from the same habitat tended to occupy similar regions of multidimensional space but there was no tendency for similar-sized caimans to be grouped together (Fig. 2). This was reflected in the Monte Carlo analyses which indicated significant grouping by habitats (MDS1, $P=0.02$; MDS2, $P=0.095$) but no significant grouping by size (MDS1, $P=0.992$; MDS2, $P=0.33$).

DISCUSSION

The diet of crocodylians has been shown to shift ontogenetically (e.g. Jackson *et al.*, 1974; Blomberg, 1977; McNease & Joanen, 1977; Seijas & Ramos, 1980; Webb *et al.*, 1982; Delany & Abercrombie, 1986; Magnusson, 1987; Uetanabaro, 1989). In this study, diet did not differ statistically between the size classes, but this was partly because of the strong habitat effects. As in previous studies, juveniles ate mainly insects while adults ate mostly fish: perhaps large samples from any one habitat would show significant differences.

Diet did differ significantly among habitats. Santos *et al.* (1994) found that the condition also differed be-

tween habitats, but not among size classes. Juvenile caimans were in the best condition in brackish ponds, while adults caimans were in the best condition in the Miranda river and artificial roadside ponds. These differences may be related to the interaction of food availability and ontogenetic trends in the diet. Juveniles consumed mainly insects which were most abundant in brackish ponds. Adults consumed mainly fish, which were available in all habitats, except brackish ponds.

Caimans caught in the ponds of Nhecolândia ate a diversity of foods such as small fish, crabs, snails and insects. Similar results were found by Uetanabaro (1989). He observed qualitative and quantitative differences in the diet of *C. c. yacare*. This may be explained by larger animals selecting items with larger net energy/feeding time ratios to satisfy energy requirements (Schoener, 1971). Depending on the habitat, larger animals use less time to catch prey than smaller animals, because they can eat food items of larger nutritive value, such as fish.

Caimans ate mainly aquatic animals despite abundant terrestrial fauna (mammals and birds). However, in Caño Negro, Costa Rica, *Caiman crocodilus fuscus* frequently ate aquatic birds (Allsteadt & Vaughan, 1994). Mammals were frequently encountered in the diet of *Caiman crocodilus crocodilus* in the Central Venezuelan Llanos (Thorbjarnarson, 1993).

Adult caimans probably eat fish throughout the year, except in brackish ponds. The fish community is not stable with time because of changes in water volume (Lowe-McConnel, 1975), but they are available throughout the year. Most of the fish that could be identified are slow moving bottom dwellers such as *Hoplias malabaricus*. This fish has a wide distribution and it generally lives in black water and marginally vegetated sites, where water flows slowly (Ueida, 1984; Kirovsky, 1994). According to Thorbjarnarson (1993), these fish are facultative air breathers that can tolerate the low levels of oxygen found during the dry season in most llanos water bodies.

Insects were the major food item during the dry season in brackish ponds, although caimans captured in brackish ponds in 1989 had eaten large number of amphibians. In that year, hundreds of caimans congregated in one of the three brackish ponds sampled, and it coincided with a bloom of algae and tadpoles. However, tadpoles were not encountered in significant number in other brackish ponds and habitats in other years. High occurrence and numeric frequency of insects for all sizes of animals caught in brackish ponds suggest the population feeds mainly on this form of prey.

Items such as fish and amphibians are difficult to identify due to rapid digestion. Delany & Abercrombie (1986) studied digestion rate of *Alligator mississippiensis* and observed that fish and amphibians are quickly digested. Magnusson (1987) suggested that when interpreting data on crocodylians stomach contents the following points should be considered: different prey

types are digested at different rates; larger crocodilians digest equivalent sized prey faster than small crocodilians; some prey have indigestible parts that accumulate in the crocodilian's stomach (e.g. operculum of snails); different passage rates may occur for various kinds of food, and different prey of equivalent mass, volume or area may have different nutritive value.

Caimans have a low and variable metabolic rate. Therefore, they may survive long periods of low food availability. It is common to observe hundreds of caimans concentrated in small natural and artificial ponds during the dry season. Therefore, other factors besides food availability may effect the habitat use by caimans. Similar observations were reported by Allsteadt & Vaughan (1994).

In overview, caimans appear to be opportunistic predators, that ingest the prey which is most abundant. Because of this, habitat is more important in determining prey type than caiman size. However, larger samples may indicate that significant ontogenetic or seasonality variation does exist in some if not all habitats.

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