SHORTER COMMUNICATIONS

Feeding Behavior of Two Sympatric Caiman Species, *Melanosuchus niger* and *Caiman crocodilus*, in the Brazilian Amazon

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Abstract.—We studied the feeding behaviors of two sympatric species of caimans (*Melanosuchus niger* and *Caiman crocodilus*) during the dry season in the Mamirauá Sustainable Development Reserve, Amazonas State, Brazil. Observations were made in 50 × 13 m plots located along the land-water interface. We investigated the influence of interspecific density and the effects of temperature and water depth on the feeding behaviors of both species. We identified three principal categories of feeding behavior: trapping (with the body perpendicular to the shore, the caiman captures prey swimming close to the shore), active search (with the head under the water, the caiman searches for benthic prey), and jumping (leaping partially out of the water and capturing fish or other under water invertebrates prey). Using multiple linear regression, we found that water temperature had a negative effect on trapping by *M. niger*; and water depth did not affect feeding behaviors in either species. Density of *M. niger* did not affect either the density or the frequency of feeding by *C. crocodilus*. Results suggest that environmental factors have little influence on the feeding behaviors of the caimans we studied, and there is probably little interspecific competition for food during the dry season.

Caimans are abundant apex predators in the Neotropics and consume a variety of terrestrial and aquatic prey (Magnusson et al. 1987; Thorbjarnarson, 1993a; Da Silveira and Magnusson, 1999; Horna et al., 2001). The feeding behaviors of caimans have previously been studied in seasonally flooded savannas in the Venezuelan Llanos (Ayarzagüena, 1983; Thorbjarnarson, 1990a, 1993b) and the Brazilian Pantanal (Schaller and Crawshaw, 1982; Olmos and Sazima, 1990). However, little is known about the feeding behavior of caimans in the forested parts of the Amazon basin. *Melanosuchus niger* is the largest Amazonian predator (Ross and Magnusson, 1989), and males of this species can exceed 4 m in length (Ross, 1998). Males of *Caiman crocodilus* can reach 2.5 m of total length (Ross, 1998), but individuals of this size are rare in the Brazilian Amazon (Da Silveira and Thorbjarnarson, 1999; Da Silveira, 2001). In many parts of the Amazon basin, these two species are broadly sympatric, and studies of feeding behavior may help us understand the ecological relationships between these caimans.

Our study was undertaken during the dry season and examined feeding behaviors of Black Caiman (*M. niger*) and Spectacled Caiman (*C. crocodilus*) in the Mamirauá Sustainable Development Reserve in the western Brazilian Amazon. Highest densities of these species in the Amazon basin are found in this reserve. Large and sympatric populations have been effectively protected from hunting for the past 10 years offering a unique opportunity to study the behavior of these species without significant human interference (Da Silveira, 2002).

The specific questions addressed in this study were (1) Does the abundance of *M. niger* affect density and the feeding behaviors of *C. crocodilus*? and (2) do air and water temperature or water depth affect the feeding behavior of either species?

Materials and Methods

The study was carried out during the annual dry season (24 September and 2 November 2001) in the southeastern portion (03°08′S to 64°45′W and 02°36′S to 67°13′W) of the Mamirauá Sustainable Development Reserve (MSDR), Brazilian Amazon. The MSDR covers 1,124,000 ha of seasonally inundated varzea forest at the confluence of the Solimões (Amazon) and Japurá Rivers (Ayres, 1993). Caiman feeding behavior was observed in 42 plots located along the shores of the Lago Mamirauá, which is one of the largest water bodies in the MSDR. During the wet season, it is approximately 10 km long and 400 m wide (Ayres, 1993). Further observations were made along the shores of Cano Mamirauá, a 10-km long channel that connects the lake to the Solimões River. Additional information on the MSDR is available from its management plan (Mamirauá, 1996, available at www.mamiraua.org.br).

We carried out general ad libitum observations (Altman, 1974) for 20 h to define categories of feeding behavior. After that, we classified them into three categories: trapping, active searching, and jumping. Trapping is a passive behavior with the caimans remaining immobile, body oriented perpendicular to the shore, with the head and most of the body in shallow water and usually with at least a portion of tail on land. In this position, the caimans' body will block underwater moving prey along the shore, and caimans

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can capture them with a rapid lateral movement of the head and the tail. Searching is an active foraging technique with caiman moving slowly in shallow water along the shoreline and periodically submerging the head and moving it in sweeping motions from side to side in search of submerged prey. Jumping is also an active feeding behavior with caimans using their hind legs and tail to propel their body forward and partially out of the water. As observed sometimes, submerged prey (e.g., fish, crab) was captured as the caiman splashes back down into the water.

A total of 42 observational plots (50 m long and 13 m wide [10 m into the water and three meters on land]) was marked with wooden sticks placed two or three days before observation began, so caimans would become accustomed to them. We carried out observations of caiman feeding behaviors from a blind 20–50 m from the plots (mostly on the same shore) and covered by a green plastic mosquito net. We undertook two observation sessions of 20 min each in each of 34 plots, with a 40-min interval between the end of the first and the beginning of the second. We used means of two sessions in each plot in the statistical analyses. Only one observation session was made in eight plots because only one or two individuals were found during the first observation session. The 76 observation sessions totaling 25 h of data collection were carried out between 0700 and 800 h. We carried out 36 observation sessions between midday and 1600 h. We did not performed nocturnal observations because artificial light·would be needed and could potentially affect caiman behavior (Santiago et al., 1998). We measured air temperature at the beginning and end of observations at each plot and water temperature at 0.3 m depth and 10 m from the shore at the end of the data collection in each plot. We measured water depth at 10 m from the shore in six equidistant points along the 50-m extension of the plot, and in 69% of the plots mean depth was less than 50 cm. We used mean depth and air temperature of each plot in the statistical analyses.

The SVL of approximately 50% of the individuals present in each plot was visually estimated before each observation session based on the field experience of the authors (Magnusson, 1983; Da Silveira et al., 1997). Throughout all sessions, the number of individuals of each species was counted every 2 min. Immediately after each count, the number of feeding (jump and search) attempts by each species was recorded for each 2-min period. The large number of caimans in some plots did not permit quantification of individuals' feeding attempts. Also, we were unable to accurately determine the prey captured or the percentage of successful fishing attempts for any of the behaviors. The number of individuals in the characteristic trapping position along the shoreline was also noted during each 2-min period.

Multiple regression analysis was used to investigate the influence of M. niger density, water and air temperatures, and depth on the feeding behavior of each species. The effect of M. niger density on C. crocodilus feeding was also investigated. Density was indexed as the maximum number of individuals counted in each plot during the 40-min observation. All analyses were carried out in the Systat 8.0 package (L. Wilkinson, SPSS Inc. Chicago, 1998).
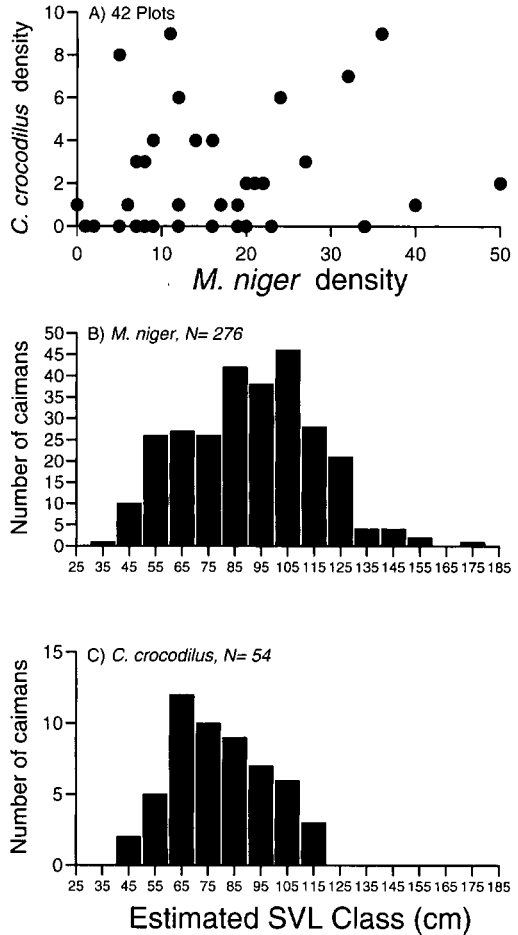

FIG. 1. Observed density (A) and size structure of *Melanosuchus niger* (B) and *Caiman crocodilus* (C) in 42 sampled plots in the Mamirauá Reserve.

RESULTS

The total number of both species of caimans in the 42 plots was 696; 88% were M. niger and 12% were C. crocodilus. The number of M. niger in the plots varied between zero ($N = 2$) and 50 individuals (Fig. 1A). In 45% of the plots, more than 15 M. niger were present. Estimated SVL (ESVL) of 276 M. niger varied between 30 and 170 cm. Forty-five percent of the observed M. niger ($N = 126$) were between 85 and 105 cm ESVL (Fig. 1B) size-classes, which are principally male and female subadults (Da Silveira, 2001).

The number of C. crocodilus in the plots varied between zero ($N = 14$) and nine individuals (Fig. 1A). ESVL of 54 C. crocodilus ranged between 40 and 110 cm. Fifty-seven percent of the C. crocodilus ($N = 31$) observed were between 65 and 85 cm ESVL (Fig. 1C), which corresponds to adult females and subadult males (Thorbjarnarson, 1994). No hatchlings (SVL < 20 cm) of either species were observed.

In total, we observed 10 jumps and 16 active searches by C. crocodilus and 252 jumps and 244 active searches by M. niger, suggesting these two feeding

TABLE 1. Summary of the multiple regression analyses: effect of three independent variables on (A) *Melanosuchus niger* and (B) *Caiman crocodilus* feeding behaviors and (C) *C. crocodilus* density in the 42 plots observed in the Mamirauá Reserve.

Dependent Variables	Water depth	Water temperature	*M. niger* density	Sum of squares	*P*	R^2
(A) *M. niger*						
Jump	$P = 0.820$	$P = 0.399$	$P = 0.001$	1,824.58	0.002	0.331
Search	$P = 0.725$	$P = 0.325$	$P = 0.000$	877.63	0	0.464
Trapping	$P = 0.796$	$P = 0.006$	$P = 0.004$	14.57	0.001	0.464
(B) *C. crocodilus*						
Jump	$P = 0.488$	$P = 0.553$	$P = 0.766$	0.869	0.883	0.029
Search	$P = 0.710$	$P = 0.838$	$P = 0.765$	1.029	0.927	0.02
Trapping	$P = 0.955$	$P = 0.145$	$P = 0.687$	0.498	0.398	0.12
(C) *C. crocodilus* density	$P = 0.303$	$P = 0.996$	$P = 0.281$	27.089	0.284	0.099

behaviors are used in similar proportion by both species. The density of *M. niger* significantly affected the frequency of the three feeding behaviors observed for this species (Table 1A). The relationship between this variable and the three feeding behaviors was linear, and more *M. niger* number in a plot resulted in more feeding attempts recorded. However, density of *M. niger* did not significantly affect any of the three feeding behaviors carried out by *C. crocodilus* (Table 1B) or the number of *C. crocodilus* present in each plot (Table 1C).

Air temperature varied between 25 and 37°C (mean = 30.8°C, SD = 3.3) and water temperature varied from 29–38°C (mean = 32.8°C, SD = 2.4). Air temperature was highly correlated to mean water temperature ($r = 0.7$) and was not included in the models. Water depth varied between almost zero and 220 cm (mean = 46 cm, SD = 42.2). The only environmental factor found to influence feeding behavior was water temperature, which was negatively correlated with trapping behavior of *M. niger* ($P = 0.006$; Fig. 2). Water depth did not significantly affect any of the three feeding behavior of either species (Table 1).
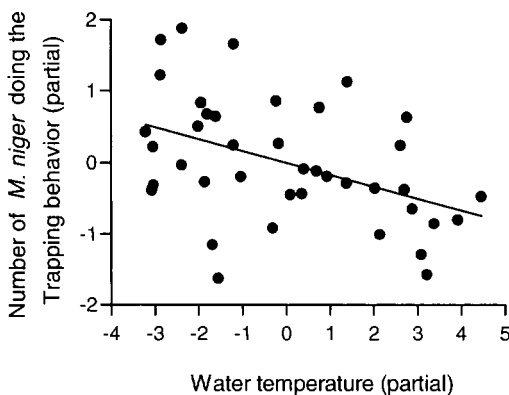

FIG. 2. Partial regression between the water temperature and the number of *Melanosuchus niger* carrying out the trapping behavior. Some numbers of the axes are negatives because the partial regression represents deviations from the expected result if all others variables were held constant at their observed means.

DISCUSSION

Crocodilians are generalist feeders, eating a wide variety of animal prey (Lang, 1987). Black Caiman and Spectacled Caiman principally feed on insects (coleoptera), spiders, crabs, snails, fishes, and rarely other vertebrates as birds, mammals, and reptiles (Magnusson et al. 1987; Thorbjarnarson 1993a; Da Silveira and Magnusson 1999; Horna et al. 2001). Although some crocodilians, such as the Narrow-Snouted Gharial (*Gavialis gangeticus*) or the Australian Freshwater Crocodile (*Crocodylus johnsoni*), have morphological specializations for the capture of aquatic prey; the Broad-Snouted Caiman (*Caiman latirostris*) depends largely on behavioral specializations (Thorbjarnarson, 1990b, 1993b; Olmos and Sazima, 1990).

Crocodilians, including *C. crocodilus*, have been reported to use a fish trapping technique that uses the body and tail to trap prey against the shore (Pooley and Gans, 1976; Schaller and Crawshaw, 1982; Thorbjarnarson, 1993b). We never observed this trapping technique being used by *M. niger* in the Mamirauá Reserve; and occasionally we saw a similar behavior in *C. crocodilus*, when the caiman was swimming parallel to the shore and used a very slow movement of the tail to drag water throughout its open mouth obviously trying to catch small fish. However, we did not quantify this foraging technique because it was not observed during the initial ad libitum observations.

Water temperature was the only environmental factors that influenced *M. niger* trapping behavior in the Mamirauá Reserve. During this feeding behavior, the individuals stay immobile with the whole dorsal part of the body exposed to the sun, and probably during the hottest hours of the day, it becomes difficult to maintain an ideal body temperature. Thus, caimans stop this behavior and submerge most of their body to regulate their body temperature, as it was already observed in *C. crocodilus* (J. W. Lang, Thermal ecology and social behaviors of *Caiman crocodilus* in the Llanos of Venezuela. Progress Report to the National Zoological Park, Smithsonian Institution, unpubl. data, 1977). Water temperature does not have any effects on jumping and searching behaviors of both species. Probably overheating is easier to avoid because during these behaviors caimans' body surface were mostly submerged.

Water depth did not affect any of the behaviors we investigated. However, the study was undertaken

during the dry season, and water depth in our study plots was shallow and varied little. Probably the three feeding behaviors described in this study can only be performed in shallow water. When water levels rise more than 10 m during the annual wet season, shallow habitats are very rare in the MSDR, and we presume the caimans change their foraging techniques or may simply stop eating during this period of the year, as apparently happens in the Anavilhanas Archipelago (Da Silveira and Magnusson, 1999).

We did not observe caiman fishing while floating on the water surface as observed in Venezuela and the Brazilian Pantanal (Schaller and Crawshaw, 1982; Thorbjarnarson, 1993b; Olmos and Sazima, 1990). Also the weir fishing technique (Schaller and Crawshaw, 1982; Thorbjarnarson, 1993b) used in narrow canals to capture fish swimming upstream was not seen in the MSDR.

Other studies have found that jumping has a very low success rate in capturing fish (M. A. Staton and J. R. Dixon, Breeding biology of the Spectacled Caiman, *Caiman crocodilus crocodilus*, in the Venezuelan Llanos, Wildlife Research Report Vol. 5, unpubl. data, 1977; Thorbjarnarson, 1993b). How jumping may help capture prey is not well understood, but it may serve to disorient aquatic prey and facilitate anticipation of prey perception by other caimans. We periodically observed that, when one *M. niger* jumped, the behavior appeared to be contagious and nearby individuals would also start jumping, and this may be some form of social facilitation or group feeding behavior.

In Venezuelan Llanos, M. A. Staton and J. R. Dixon (Breeding biology of the Spectacled Caiman, *Caiman crocodilus crocodilus*, in the Venezuelan Llanos, Wildlife Research Report Vol. 5, unpubl. data, 1977) considered jumping behavior as a sexual display that was part of the reproductive behavior in *C. crocodilus* and that it could have an alimentary function too. The present study was not carried out during the caimans mating period (Da Silveira, 2001); thus, we did not consider jumping as part of the reproductive behavior in the Mamiraá Reserve but primary as a feeding behavior.

Preliminary research suggested that *M. niger* can affect the ecology of *C. crocodilus* (Magnusson, 1982; Magnusson and Rebelo, 1983). In our study, *M. niger* density did not affect either the density or feeding behavior of *C. crocodilus*, suggesting there may be little interspecific competition for food during the dry season in the Mamiraá Reserve and probably most of the Amazonian flooded forests.

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