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# Fishing Behavior of Paraguayan Caiman (*Caiman crocodilus*)

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**The diet of Paraguayan caiman consisted mainly of fish which they caught with various stratagems such as using themselves as weirs and herding prey with their tails. An average of 6.3 snaps or lunges were needed to catch a fish. On occasion most or all caiman in a pond fished at the same time and did so day and night for as many as 13 consecutive days. During the dry season, caiman crowded into certain ponds, almost to the exclusion of similar ones nearby. This behavior was possibly more dependent on social factors than on food availability.**

THE food habits of various crocodilians have been analyzed (Cott, 1961; Chabreck, 1971; Gorzula, 1978; Vanzolini and Gomes, 1979), but the literature contains little information on methods of prey capture and other aspects of feeding behavior (Guggisberg, 1972). While studying wildlife in the Pantanal, a swampy region of 100,000 km² in the Mato Grosso states of southwestern Brazil, we had an opportunity to observe large aggregations of





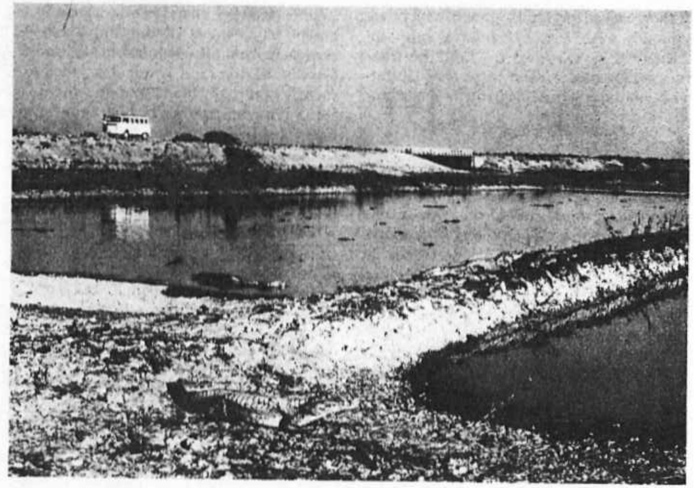

Fig. 1. A typical caiman pool along the Transpantanal Highway.

Paraguayan caiman (*Caiman crocodilus yacare*). Most observations were made on the Jofre Ranch (56°59′W, 17°16′S) which is bisected by the Transpantanal Highway. During construction of this highway in 1973–74, soil was excavated nearby to raise the roadbed above flood levels, creating depressions about 50 × 125 m in size which filled with water to become permanent pools that attracted many caiman during the dry season (Fig. 1). Most of our observations were confined to 14 km of road. In November 1979, a night count of eyes seen by spotlight revealed 2,368 caiman along this stretch. Repeated counts at certain pools showed that at least a quarter of the animals might be submerged or otherwise not visible at night, indicating a total population of about 3,000.

Climate in the Pantanal is seasonal with a cool period from June to September during which the air temperature may fall to 0 C. The lowest air temperature during the study was 7.7 C and the highest 41 C. Average monthly minima ranged from 18–24 C and maxima 28–34 C. About half of the annual precipitation of some 1.2 m fell between December and March. The terrain was so flat that during the rainy season the Paraguay River and its tributaries flooded the adjoining areas. From late January to early May the mosaic of pastures, thickets and strips of forest along the highway was almost completely inundated to a depth of 1 m or more. The floods receded by late May, and by October water persisted only in scattered pools. Our observations were largely confined to the dry season, from October to December 1978, and June to December 1979.

## STUDY METHODS

During the day, we observed caiman at all hours, most commonly between 0600 and 0900 h; at night we checked certain pools briefly at various times to ascertain caiman activity. Food habits were determined by observing predation directly and by examining stomach contents of animals killed by cars or shot by vandals. Usually fish in stomachs were too digested for easy identification, but it was often possible to determine the species of captured fish in the mouth of a caiman by direct observation. Fish numbers and species in six ponds were sampled by sweeping a 5 × 10 m area once with a seine. To learn how far caiman travel, we attached a numbered, colored tag to one of the dorsal crests of the caudal scales of 143 animals. Fiftyfive of these were resighted a total of 192 times. The animals were easy to noose around the neck when they traveled on land between ponds, and they were then measured (snout–vent and tail lengths, chest girth), weighed and tagged.

### Food Habits

Schmidt (1928) inspected 21 caiman stomachs from the Pantanal, and of these eight were empty, eight contained fish, six crabs, five snails and one a snake. Our findings were similar (Table 1). Thirty-one stomachs were examined between May and December and 35% of these were empty. In terms of frequency and bulk, the most important food was fish followed by snails, crabs and insects; no gastroliths were found. Sampling with a seine indicated at least 45 fish species in the ponds along the road. Direct observations showed that among the larger fish, those of about 100–600 g as determined by weighing fish of similar size. *Plecostomus* c.f. *plecostomus*, *Aequidens* sp., *Hoplias malabaricus*, *Astronotus ocellatus*, *Serrasalmus* c.f. *spilopleura*, *Rhamdia* sp., and *Brycon hilarii* were most often captured. Among smaller fish, those weighing less than 100 g, *Corydoras* sp., *Trachycorystes* sp., *Hoplosternum* sp., and *Platydoras costatus* were consumed. We once saw a caiman eat *Symbranchus marmoratus*, an eel-like fish. Caiman captured other vertebrates too, among them birds (1 *Egretta thula*, 1 *Aramus guarauna*), reptiles (1 *Dracaena paraguayensis*, 1 *Eunectes notaeus*, 2 *Caiman crocodilus*) and mammals (1 *Hydrochoerus hydrochaeris*).

### Fishing Behavior

Caiman characteristically waited for fish to come within snapping distance, using ambush rather than pursuit. They lay motionless in the shallows or on the bottom of ponds, or floated on the surface, either with eyes and nostrils showing or with head entirely under water. Ponds were seldom more than 2 m deep, and these fishing positions enabled caiman to waylay prey at all levels of their three-dimensional habitat. When sensing a fish, the caiman either snapped sideways or lunged ahead with half-open mouth, and the tail's sculling action combined with pushing of the feet sometimes propelled the animal's forequarters out of the water. Fish occasionally leaped into the air to escape, and the caiman then sometimes repeated its lunge.

The sideways snap was occasionally accompanied by a sweep of the tail. Brehm (1925) reported that R. Schomburgk noted that *Caiman crocodilus* in Guyana first killed fish with such a sweep and then snapped them up. We could not confirm this, but Paraguayan caiman had a fishing technique which involved using the tail. Facing land at right angles, a caiman moved almost imperceptibly sideways for 2–3 m, as if herding fish, and then slowly arced its body shoreward, gently wiggling its tail while advancing into the shallows (Fig. 2A). Fish trapped between land and caiman often tried to escape past the waiting jaws. In a somewhat simpler technique, a caiman curved its body and moved toward shore, pushing itself closer with its legs when grounded in shallow water. Such behavior involved only large caiman (snout–vent > 75 cm). It was observed 17 times by one of us (GBS) and several additional times by the other (PGC). Adjoining ponds sometimes had connecting channels, and in these the caiman used their bodies as weirs as if to guide fish to their mouths. Caiman placed themselves at right angles to the flow, obstructing the passage (Fig. 2B). Usually only one or two caiman occupied a particular passage, but once, when heavy rain created a wide riffle between ponds, 7–15 caiman fished in it all day. Caiman used yet other fishing techniques. One caiman lay with its body on land and head in the water at the edge of a rivulet and snapped at fish that passed its open mouth. Once a single caiman and once two caiman were at the base of a small waterfall, lunging at the occasional fish that descended.

We counted each snap or lunge as one fishing attempt. Of 5,267 attempts observed in three ponds, an average of 6.3 were needed to catch a fish, a success rate of 15.9%. The rate was relatively constant in the three ponds regardless of caiman density and water condition (turbid or clear, deep or riffle) (Table 2). Caiman in daytime fished most actively between 0600 and 0900 and least actively from 1000–1500 h, as shown in Fig. 3 for Pool C. The data from Pool C are based on 27.5 hours of observation over a period of 9 days, and they are corrected for a variable number of animals sunning themselves on land, the largest number usually doing so between 0900–1000 and 1500–1700 h. The drop in fishing activity is associated with a rise in air and water temperatures. Air temperatures are indicated in Fig. 3, and water temperatures, taken about 10 cm below the surface near shore, increased from 20–24 C in the



Table 1. Stomach Contents of Paraguayan Caiman, Expressed in Percent Frequency of Occurrence.

| Contents | Snout–vent length 41–80 cm n = 18 | Snout–vent length 80+ cm n = 13 |
|---|---|---|
| Empty | 28 | 46 |
| Fish | 33 | 54 |
| Snail (mainly *Pomacea*) | 22 | 31 |
| Crab (*Dilocarcinus*) | 6 | 15 |
| Insect (mainly *Coleoptera*) | 22 | 0 |

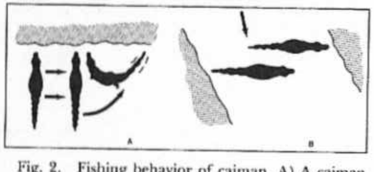


Fig. 2. Fishing behavior of caiman. A) A caiman herds fish toward shore with its body and tail; B) Two caiman use their bodies as a weir across a stream. The arrow indicates direction of stream flow.

morning to 27–30 C by mid-afternoon. By contrast, captive subadult *Alligator mississippiensis* and *Crocodilus niloticus* are disinclined to eat when water temperatures are maintained at 20 C, their oxygen consumption being only one-fourth as great at this temperature as at 30 C (Coulson and Hernandez, 1964). Since our study animals fished actively again in late afternoon before air and water cooled markedly, the observed drop in activity may represent a rest period, coupled with satiation, little related to temperature. Fishing success rates remained fairly constant until they dropped in mid-afternoon (Fig. 3).

Caiman could not hunt by sight in most pools because the water was so muddy, and they probably responded to fish movement and touch. Sight could play a role in clear water—yet success rate in muddy and clear pools were similar (Table 2)—and it was seemingly important when snapping at leaping fish.

A caiman with a fish raised its snout above water, bit several times as it shifted the prey to the desired position by moving its head [behavior termed inertial feeding by Gans (1969)], and finally gulped it down tail last. In a sample of 127 consecutively captured fish, 8% were taken onto land. Most such fish were large and required as long as 1½ hours to eat. *Plecostomus*, for example, has spiny pectoral fins which it extends laterally, preventing the caiman from swallowing it easily. A caiman with a small fish is usually ignored by others, but a large fish, especially one that splashes, may attract one or more competitors which try to appropriate it. By retreating onto land, or submerging quietly for awhile among floating water hyacinths (*Eichhornia*), caiman avoided confrontations. No caiman ever relinquished a fish, although it occasionally lost a piece to a pursuer.

There was usually little or no hunting in daytime until for unknown reasons most or all caiman in a pond sometimes started to snap and lunge at fish. For example, fishing attempts were rarely seen in Pool C during most of July, but on July 28 the 85 caiman there began to fish and continued day and night for 13 days before stopping. At other pools such fishing lasted 1–5 consecutive days. It may be conjectured that such communal activity influences hunting success in that fish constantly agitated by being pursued encounter the lurking predators more often.

### Caiman Movements in Relation to Food Supply

As illustrated by night counts at Pool D in 1979, caiman began to concentrate in ponds near the road after the rainy season when pastures and sloughs dried up: 10 March—1 caiman; 29 May—3; 27 June—25; 21 July—53; 21 Aug.—128; 12 Nov.—397±; 11 Dec.—411±. We noted that males tended to be lean when they arrived at ponds early in the dry season. Males averaged about 20% less in weight during June–July 1979 than at the end of 1978 and 1979 ($P < .05$) whereas females showed no significant differences (Table 3). During the rainy season when vast tracts are inundated, fish were

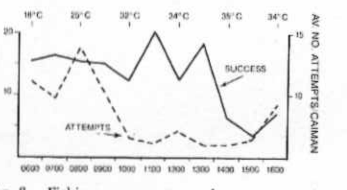


Fig. 3. Fishing success rate and average number of fish-catching attempts per caiman at hourly intervals in daytime at Pool C. Air temperatures during the period are also indicated.

Table 2. Success Rate of Fish Capture by Caiman.

| Pool | Date | No. attempts | No. successes | % success | Max. pool depth (m) | Water turbidity | Max. no. caimans in pool | No. m² per caiman |
|---|---|---|---|---|---|---|---|---|
| B | 29 VIII–2 IX 1979 | 2,724 | 468 | 17.2 | 3 | clear | 75–250± | 10–33* |
| C | 28 VII–9 VIII 1979 | 2,422 | 349 | 14.4 | 1.7 | turbid | 85 | 32 |
| D | | | | | | | | |
| in pond | 20 X 1978 | 121 | 19 | 15.7 | 1.5 | turbid | 335± | 16 |
| in riffle | 20 X 1978 | 487 | 68 | 14.0 | — | turbid | — | — |

* Caiman numbers varied with animals moving to and from an adjoining marsh.

dispersed and perhaps caiman had few opportunities to catch them. However, we do not know why marked weight loss was confined to males, especially as some females possibly fasted for weeks while guarding their nests (Crawshaw and Schaller, 1980).

Eighty-nine caiman were tagged during October–December 1978 along the road, and of these 28% were resighted along the same stretch of road during the 1979 dry season; another 54 caiman were tagged during June–August 1979, and of these 57% were resighted that year. Table 4 shows maximum distances moved by caiman between tagging and resighting. Three caiman were seen in the same pond during consecutive years. Few animals had traveled more than 4 km; the three longest distances were 7, 7.3 and 9.4 km by an adult male (snout–vent 111 cm), a subadult female (snout–vent 61 cm) and a subadult male (snout–vent 66 cm), respectively. Among the resighted caiman were 29 adult males (snout–vent > 100 cm), 16 adult females (snout–vent 80–95 cm) and 11 subadults. Of these, 16 males, 13 females and 3 subadults had traveled 0–1.9 km, and 13 males, 3 females and 8 subadults had traveled 2 km or more, indicating that subadults moved on the average longer distances than expected and females shorter distances ($P < .05$). Movement data are biased in that they fail to show caiman dispersion during seasonal flooding, but they do reveal travel distances parallel to the road between May and December.

Caiman tended to congregate in certain ponds. There were 43 ponds along the 14 km of road in November, yet about 54% of the caiman had crowded into five ponds, with Pool D containing about 410. Most other ponds of similar size and depth held fewer than 25 caiman. The same ponds had many caiman in 1978 and 1979. To test if food availability influenced pond selection, we sampled fish numbers in five ponds, all of which had only one or two caiman in them, as determined by day and night counts. Ten seine samples, each from a 5 × 10 m area, contained an average of 268 (56–600) fish weighing 3.2 (.8–8.2) kg. About 15% of these fish were of a size class (10 cm⁺) most commonly captured by larger caiman. All these ponds contained many fish, yet few caiman used them.

Eighty-five caiman fished intensively in Pool C from 28 July–9 Aug. Given the average number of fishing caiman (64.5), the average number of attempts per caiman per hour (3.5), and the average success rate (1 in 6.9 attempts) then 4,679 fish were caught between 0600 and 1700 h during the 13 days. These caiman were at least as active at night as during the day, judging by the amount of fishing activity heard. Assuming that their success rate was similar, another 5,529 fish were caught during the hours of darkness. The total calculated catch during the 13 days was 10, 208 fish, or 120 fish per caiman. At noon, on 10 Aug., all caiman were in the pond, but by 1700 h many were leaving it: 19 were seen traveling overland at that time and six more the following morning. When we sampled the pond for fish on September 1, there were only five caiman in it. Four seine samples contained an average of 575 (250–800) fish weighing 6.9 (4.9–10.2) kg, indicating that the pond had not been fished out.

Table 3. Mass (kg) of Adult Caiman at Beginning and End of Dry Season. $\bar{x} \pm$ SD (range).

| Date | Sample size | Adult male mass snout–vent length 110–125 cm | Sample size | Adult female mass snout–vent length 80–95 cm |
|---|---|---|---|---|
| Oct–Dec 1978 | 22 | 44.2 ± 7.03 (28.2–57.7) | 27 | 18.2 ± 3.72 (12.2–22.7) |
| June–July 1979 | 14 | 35.4 ± 9.11 (27.3–41.8) | 13 | 17.5 ± 2.35 (13.0–21.4) |
| Nov–Dec 1979 | 3 | 43.9 ± 4.77 (39.1–48.6) | 5 | 18.2 ± 1.16 (16.8–19.5) |



Table 4. Maximum Distances (km) Between Resightings of Tagged Caiman Along the Road in the Study Area.

| | No. animals | Kilometers 0–.9 | 1.0–1.9 | 2.0–2.9 | 3.0–3.9 | 4.0–4.9 | 5+ |
|---|---|---|---|---|---|---|---|
| Tagged Oct–Dec 1978; resighted June–Dec 1979 | 25 | 5 | 7 | 3 | 6 | 2 | 2 |
| Tagged June–Aug 1979; resighted June–Dec 1979 | 31 | 11 | 9 | 4 | 2 | 3 | 2 |

These data suggest that factors other than food availability may influence pond choice. Since most ponds were similar in size, exposure to sun, water depth and water temperature, environmental conditions have no obvious influence on the selective process. Social factors possibly determined aggregations to some extent. We estimated the snout–vent length of 637 basking caiman on 29 and 30 June 1979, and the percentage of each size class in the population was: <25 cm (young of the year) 3.6%; 25–50 cm (subadult) 14.4%; 50–75 cm (subadult) 37.8%; 75–100 cm (adult female and subadult male) 24.5%; and >100 cm (adult male) 19.7%. Adult males comprised about 20% of the population as a whole, but counts in Pools B and C, both of which held many caiman, revealed 38% and 45% males, respectively, suggesting that this age and sex class tended to concentrate. Courtship and dominance displays, as described by Garrick and Lang (1977), were first exhibited by males in late July at the height of the dry period and reached a peak in frequency during Nov. and Dec., suggesting that animals aggregated for the mating season. Nest building and egg laying extended from late Dec. to early Feb., and hatching from early March to late April (Crawshaw and Schaller, 1980), the rainy months when caiman were dispersed.

## Discussion

Paraguayan caiman are mainly fish eaters, and to capture their prey they use various strategems such as herding prey with their tails. Other crocodilians exhibit similar behavior. For example, an African crocodile (*Crocodylus niloticus*) may swim "slowly parallel to a riverbank with its tail bent toward the bank. The scales at the top of the tail riffle the water slightly, and small fish in the shallows move along ahead of the disturbance. When the crocodile turns its head around to the bank, the fish are trapped and are seized by a sideways sweep of its open jaws" (Pooley and Gans, 1976). Herding of fish has also been reported for another reptile, the matamata turtle, *Chelus fimbriatus* (Holmstrom, 1978). The African crocodile is said to use its tail to capture land mammals by sweeping them from shore into water (Guggisberg, 1972). Such behavior has also been observed in the Indian mugger (*Crocodylus palustris*) by Brander (1927) who wrote that "the mugger rushed up the beach and as he grounded he swung round his whole body and the tail swept two pigs off their feet into the water, neither of which appeared again."

Pooley and Gans (1976) noted that subadult African crocodiles "often form a semicircle where a channel enters a pan, facing the inrushing water and snapping up the fish that emerge from the river." The authors considered this an example of cooperative hunting.

We observed similar behavior when caiman gathered at road culverts, and when two or more caiman formed a weir at a riffle. Such behavior is a form of proto-cooperation (Allee, 1958) rather than cooperation in the sense of a joint action in the performance of a defined task; any help fishing crocodilians gave each other seemed inadvertent.

Caiman appeared to have little difficulty in catching the concentrated fish during the dry season, yet a third of their stomachs were empty, indicating that the animals had not eaten during the previous 3 days or so (Pooley and Gans, 1976). With their low metabolic requirements, caiman can fast for weeks (Coulson and Hernandez, 1964), and this probably enables many of them to crowd into one pool for long periods without exhausting the food supply. However, the reasons remain obscure why most caiman aggregate in certain ponds almost to the exclusion of other suitable ones nearby. Recent observations on maternal behavior (Staton and Dixon, 1977; Deitz and Hines, 1980) and communication (Garrick and Lang, 1977) have revealed some of the intricacies in social responses of crocodilians, and this study presents suggestive evidence that feeding behavior and movement patterns are also influenced by social factors.

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# Changes in the Food Niche during Postmetamorphic Ontogeny of the Frog *Pseudacris triseriata*

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**The food niche and foraging strategies of the chorus frog *Pseudacris triseriata* were investigated by examining the prey/predator size relationship as it relates to prey availability, and they were found to be dynamic from metamorphosis to adulthood. Snout to vent length of the frogs proved to be a good predictor of the mean size of prey taken.**

**Relative availability of the different sized prey items in the environment was estimated from samples of potential prey obtained by suction sampling. This availability information was used in addition to the data on stomach contents to describe the foraging strategies of the different size classes of frogs. It was found that small frogs (≤17.0 mm) ate prey as they were encountered in the environment, and that large frogs (≥23.1 mm) selected larger prey which were rarer in the community. Intermediate sized frogs (between 17.1 and 23.0 mm) were characterized by an intermediate pattern. Intermediate frogs consumed large numbers of prey per unit time, and the possibility that this facilitated rapid growth is discussed.**

**The mean maximum prey size increased with increasing frog size, but leveled off for the largest size classes, whereas mean minimum prey size continued to increase with increasing frog size. The large frogs were selective in their diet as they apparently chose the more optimal (in terms of benefits and costs of pursuit, capture and consumption) sized prey while they discriminated against the smaller prey. This ontogenetic pattern of foraging strategies is somewhat unique among predators for which there exists information in the literature, and it is suggested that the small body size (<30 mm) of *P. triseriata* relative to the size of their prey (terrestrial arthropods) allows this pattern.**

THE availability of prey is an important factor to be considered in models of optimal foraging strategies (Schoener, 1971), but it is often a difficult parameter to measure. Nevertheless, empirical data for prey abundance have been examined in studies of feeding strategies, and it has been found that various insectivorous birds and anoline lizards select the larger and rarer of the available prey (Root, 1967; Gibb and Betts, 1963; Hespenheide, 1971; Bryant, 1973; Sexton et al., 1972; Schoener and Gorman, 1968). Wong and Ward (1972) reported that very small yellow perch fry also select the less common prey sizes.

Early attempts to quantify prey availability in relation to prey selected were made by Hess and Swartz (1940) and Allen (1941). They compared the relative abundance of each type of food in the stomachs to the relative abundance of the same prey in the community of potential prey in the neighboring environment. This ratio of relative abundances was termed the "forage ratio," and it has been used widely (as well as Ivlev's 1961 modification of it: the electivity index). More recent attempts to consider the availability of prey in the investigation of a predator's diet have been made by Schoener (1974a) and Chesson (1978).

Intraspecific differences in feeding by different size classes due to age have been reported for some lizards (Schoener, 1967, 1968a; Schoener and Gorman, 1968; Sexton et al., 1972; and Simon, 1976), sunfish (Werner, 1974), yellow perch (Griffiths, 1975) and plaice larvae (Shelbourne, 1962). This study makes comparisons of the intraspecific food niche of the chorus frog *Pseudacris triseriata* at different stages of the post-metamorphic life in order to describe and to attempt to explain changes in the food niche from metamorphosis to adulthood. In addition to describing the changes in the relationships between predator and prey sizes during the growth of the frog, emphasis also has been placed on determining the rela-