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FISHING BEHAVIOR OF SPECTACLED CAIMAN IN THE VENEZUELAN LLANOS.—Although a number of studies have examined the diet of crocodilians, very little is known about foraging techniques (Gans, 1989), and many of the published descriptions concern large crocodilians taking large prey (McIlhenny, 1935; Cott, 1961; Pooley, 1982). Judging by the diverse assemblage of prey items found in their stomachs (Staton and Dixon, 1975; Seijas and Ramos, 1980; Magnusson et al., 1987), spectacled caiman (*Caiman crocodilus*) are versatile predators. Ayarzagüena (1983) described a number of foraging techniques for Venezuelan *C. crocodilus*, and Schaller and Crawshaw (1982) and Olmos and Sazima (1990) quantified some aspects of the feeding behavior of *C. crocodilus* in Brazil. In this paper, I summarize my observations of the feeding behavior of *Caiman* that were made during the course of a 4.5-year study of caiman ecology and behavior.

Methods.—Observations on caiman feeding behavior were made on Hato Masaguaral, a cattle ranch located in the central Venezuelan llanos (8°33′N, 67°37′W), between Oct. 1984 and June 1989. Most observations of surface feeding were made in a single lagoon (18 m × 71 m; 1.5–1.8 m deep) on six separate days during the annual dry season (5 Jan., 16 Feb., 23 March, and 2 May 1986; 18 Jan. 1987; and 18 Dec. 1988). Using a vehicle as a blind, caiman in the lagoon were observed continuously throughout the day from 0600–1800 h, and all feeding behaviors were recorded. During the observations, the caiman population in the lagoon ranged from

78–219 (mean = 117) and was comprised principally of caiman >60 cm SVL. The weather was similar on all days, and mean temperatures during the observation periods ranged from 29.3 C (5 Jan. 1986) to 31.4 C (23 March 1986). Additional observations were made at a large (approximately 18 ha) shallow water lagoon (<1 m deep, Guacimos Lagoon). Nocturnal observations of feeding techniques were made opportunistically during the course of other caiman-related work (Thorbjarnarson, 1991). The success rates of different fishing techniques were compared using 2 × 2 contingency tables.

Results.—Observed fishing behaviors were placed in one of three categories: surface feeding, weir fishing, and jumping. Surface-feeding caiman utilized three different fishing techniques: stationary snaps, the cross-posture (Olmos and Sazima, 1990), and trapping. Stationary snaps were rapid side swipes made while the caiman was immobile at the water's surface, usually with just the head visible above the water. The cross-posture was a similar behavior made while the caiman was slowly swimming in a semiemergent posture, typically with one or both forelimbs extended rigidly at nearly a 90° angle to the body, and with the fingertips extended upward. In this posture, the caiman slowly propelled itself forward by sculling the tail, making occasional sideswipes to capture fish. The rapid sideswipes occasionally were accompanied by a forward sweeping motion of the tail.

Prey-capture attempts made from the stationary and cross-postures were classified into two categories depending on the location of the caiman with respect to the shoreline: midwater snaps (>1 m from the shoreline) and edge snaps. The mean success rates for cross-posture and stationary snaps near the edge of the lagoon (10.3%; n = 68) and in midwater (6.6%; n = 378) were not significantly different (Mann-Whitney U-test, $P = 0.72$). The overall mean success rate for surface snaps (stationary and cross-posture) was 7.2%.

During the daylight hours, cross-posture fishing and stationary snap feeding activity was bimodal, with peaks in the midmorning and late afternoon (Fig. 1a; n = 446 observed snaps). The success rate varied considerably throughout the day but was highest in the late morning and midafternoon (Fig. 1b).

Although the feeding observations were made during three separate dry seasons, seasonal trends in water level and caiman density at the study lagoon were similar (Fig. 2), and the data were combined to illustrate how feeding activity may vary throughout the course of a dry season

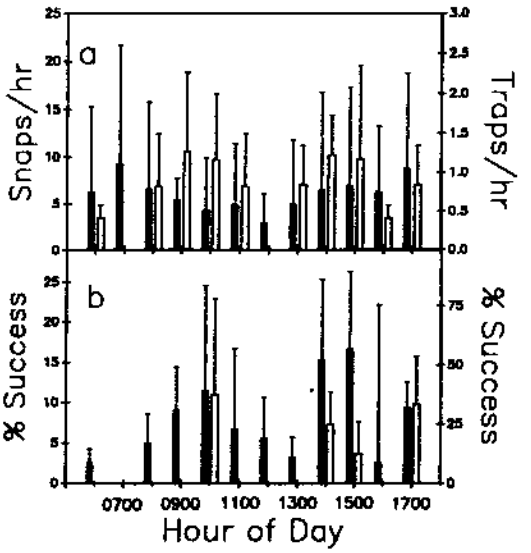

Fig. 1. Frequency distribution of (a) attempted surface feeding snaps (solid bars) and traps (open bars) and (b) percent successful snaps and traps during six days of observation (72 hours). Bars represent means plus one standard deviation.

(Dec.–May; Fig. 3). Caiman surface fishing activity was highly variable, with a strong peak in the early dry season (Jan.), and considerably less fishing was observed in the middle to late dry season. Although the population of caiman in the borrow pit varied considerably during this study, the mean number of snaps per caiman per unit time followed a similar trend (Fig. 3). Although quantitative observations were not made at night, nocturnal visits to lagoons during the dry season indicated that surface fishing activity continued at night.

Caiman also would use their body to trap fish against the shore where they could be more easily captured. Trapping behavior began with the caiman slowly swimming toward shore with its body oriented approximately perpendicular to the shoreline. As it approached the shore, the caiman slowly turned its body and oriented itself parallel to the shore and, when close enough, swept its tail and head toward the shore, effectively trapping a volume of water between itself and the shoreline. While using this fishing behavior, caiman would take advantage of irregularities along the shoreline, frequently forcing fish into small coves or indentations in the shore. Trapped fish would swim frantically and were captured by a quick sideswipe of the caiman's jaws. Trapping also followed a somewhat bimodal frequency distribution during the day (Fig. 1), and all observed successful captures

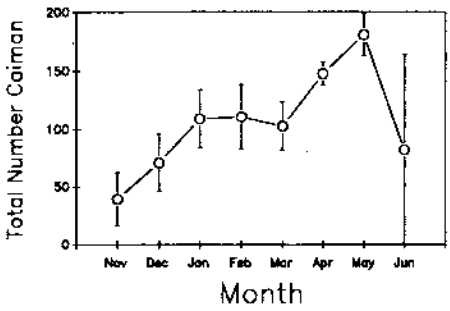

Fig. 2. Mean (±1 SD) number of nonhatchling caiman present in the study lagoon throughout the dry season; based on monthly nocturnal censuses conducted from 1985–86 to 1988–89.

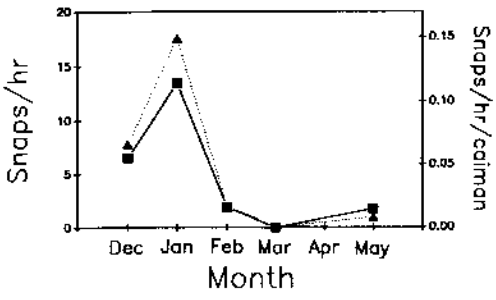

Fig. 3. Mean number of surface feeding snaps per hour (solid line) and number of snaps per caiman per hour (dotted line) throughout the dry season. Data collected during three dry seasons (see text).

were in the late morning or mid- to late afternoon. Trapping was successful in six of the 37 attempts (11.3%) observed, significantly greater than for surface snaps ($\chi^2 = 3.85$, $P < 0.05$).

In shallow, moving water, caiman were seen to use two techniques for catching prey. The first method was to orient the body parallel to the flow of water and capture prey by making rapid sideswipes. This behavior was observed several times, including once when seven caiman were oriented in two rows facing into the current (31 Dec. 1984), with their mouths slightly opened and their heads elevated in the water. Twenty-seven feeding attempts were observed, of which eight (29.6%) were successful.

Caiman were more frequently observed using a variation of this feeding technique that I refer to as weir fishing. Weir-fishing caiman would orient their bodies almost perpendicular to the flow of water, with the head angled slightly downstream. By positioning its body across the current, the caiman would divert much of the stream flow, forcing it to pass by its head. In this posture, the caiman would sit with its mouth partially open and snap at passing fish. In one case, a large caiman (approximately 2.7 m) was observed weir fishing in a stream on another ranch. This caiman had selected a natural dam formed by a rock ledge in a location where the stream (averaging approximately 3–4 m across) narrowed to a width of about 2 m. Weir fishing in this location allowed the caiman to divert all the fish moving up or down the stream past his jaws. Of nine observed attempts by weir-fishing caiman to capture prey, four (44.4%) were successful. The overall success rate of these two flowing water fishing techniques (33.3%) was significantly greater than for either surface snaps ($\chi^2 = 27.48$, $P < 0.0001$) or trapping ($\chi^2 = 4.18$, $P < 0.05$).

Jumping behavior was commonly seen in shallow water during the dry season, particularly in the early dry season. Caiman would jump with the use of the hind limbs, propelling themselves upward and forward with the forelimbs folded against the body. Jumping caiman would only partially emerge from the water, and only rarely was more than two-thirds of the body visible. When reentering the water the caiman would lean off to one side, avoiding a midventral ("bellyflop") entry. Jumps were frequently followed by a sharp turn of the body, up to 180°, and a sideways sweeping of the head. Caiman would typically initiate a jump while submerged or less frequently from a floating posture. Jumps were either single or repeated. On occasion, caiman were seen jumping into schools of small caracoids, many of which would leap out of the water as the caiman splashed down into their midst. As a fishing technique, jumping had a very low success rate. Of 414 jumps observed at the Guacimos lagoon only four (1%) resulted in the observed capture of a fish. In the lagoon pit where 12-hour activity observations were conducted, 71 jumps were made without one observed capture. The overall jumping success rate (0.8%) was by far the lowest of all observed fishing techniques and was significantly lower than the success rate for any other fishing technique ($\chi^2 \geq 23.05$, $P < 0.0001$). Jumping was observed among all caiman size classes, including hatchlings who jumped in attempts to capture aquatic insects in shallow water. However, jumping was most commonly noted among adult caiman during the dry season.

Observations on underwater feeding behavior were not possible because of the turbid water. However, on a number of occasions, caiman were observed searching underwater for prey in shallow water. Caiman placed their heads underwater and made tight circling movements of up to 360°. This circling behavior was not unlike

the movements made following jumps, and both presumably are attempts to locate and capture prey very close to the caiman's body. Twice, caiman followed this circling behavior by extending their bodies parallel to the shore and moving sideways in a trapping behavior.

Discussion.—Peak caiman fishing activity on Masaguaral was observed during the early dry season (Jan.), coinciding with a period of reduced water availability and increased fish biomass (Taphorn and Lilyestrom, 1984; Lowe-McConnell, 1975) and an increased incidence of fish in the diet of llanos caiman (Fitzgerald, 1988; Thorbjarnarson, 1993). During the late dry season on Masaguaral, fishing activity and the consumption of fish decline (Thorbjarnarson, 1993), presumably because of reduced fish availability caused by severe dry season conditions, including adverse physiochemical factors (high temperature, low oxygen availability), reduced food availability, and predation by ichthyophagous fish (Taphorn and Lilyestrom, 1984). The effect of caiman predation on dry season fish communities is unknown.

Although the diet of adult caiman largely consists of fish (Seijas and Ramos, 1980; Magnusson et al., 1987; Fitzgerald, 1988), caiman lack the morphological specializations (long, slender snout such as in the gharial *Gavialis gangeticus*) that is commonly associated with piscivory (Bellairs, 1970; Thorbjarnarson, 1990). Caiman appear to rely instead on a number of behaviors that increase the likelihood of successful prey capture. These techniques concentrate fish into small areas where they are more easily captured (trapping, cross-posture, weir fishing) or capitalize on surprise (jumping). Three of the prey-capture techniques described here (surface snaps, trapping, and weir fishing) are similar to those reported by Schaller and Crawshaw (1982) for *C. crocodilus yacare* in the Pantanal of Brazil. However, the trapping tactic used by the Pantanal caiman appears to be subtly different in that the caiman would orient itself perpendicular to the shoreline and move sideways before arcing its body toward land (Schaller and Crawshaw, 1982). Trapping behavior may be widespread among the Crocodylia; Pooley and Gans (1976) reported a somewhat similar behavior in *Crocodylus niloticus*, and I have observed captive *Crocodylus palustris* using trapping behavior to catch fish.

The cross-posture and surface snap fishing behaviors reported here are relatively low success foraging techniques used for the capture of small fish at or near the surface of the water. Many of the fish captured with this technique may be characins (suborder Characoidei), which are reported to school close to the surface of the water where they feed on organic debris blown in from surrounding terrestrial areas (D. Taphorn, pers. comm.). The cross-posture technique appears to herd these fish into the region around the caiman's head, where they can be captured with a rapid side swipe of the jaws. The cross-posture fishing technique was first described by Olmos and Sazima (1990) for caiman in the Pantanal of Brazil, which had a similar success rate of fish captures (5.7%). The somewhat higher fishing success rate (15.9%) reported by Schaller and Crawshaw (1982) included several different fishing tactics. Olmos and Sazima (1990) suggested that small characins may be attracted to feed on caiman epidermal material. The suggestion by Olmos and Sazima (1990) that caiman fishing in the cross-posture are capturing air-gulping fish rising from the bottom of the lagoon was not confirmed by my observations.

Weir fishing is a low-energy foraging strategy (Fitzgerald, 1988; Ayarzagüena, 1983) that capitalizes on the upstream (rheotaxis) movements of many fishes that inhabit tropical seasonal savannas (Lowe-McConnell, 1975). In this regard, the weir-fishing tactic appears to be particularly important in the capture of the erythrinid *Hoplias malabaricus*, which exhibits a strong tendency for rheotaxis and comprises a significant portion of the diet of llanos caiman (Staton and Dixon, 1975; Seijas and Ramos, 1980; Ayarzagüena, 1983). However, the frequency with which this technique is used, and therefore its relative importance as a food-procuring behavior, is unknown. Most of my observations of caiman using this fishing technique involve running water from human-made sources (e.g., the breaking of a water-retaining dike). However, the use of the weir-fishing technique has also been reported under natural conditions in *Caiman* (Schaller and Crawshaw, 1982), and *Paleosuchus trigonatus* (Magnusson, 1989).

The high energy, low-success jumping fishing tactic is somewhat more difficult to understand as a foraging strategy. Staton and Dixon (USFWS, 1977, unpubl.) suggested that caiman jumping behavior was a courtship display of unknown function but also indicated that it could be a low efficiency foraging tactic (approximately five fish captures in 150–200 jumps). Fitzgerald (1988) classified jumping as a foraging technique, noting that it was the only energetically expensive foraging behavior observed. W. E. Magnusson (pers. comm.) suggested that it may serve to disorient fish or mix deoxygenated bottom water so that fish be-

come more vulnerable to other fishing techniques. However, under conditions of very high fish density, jumping may be an effective foraging tactic, as was noted by Ayarzagüena (1983).

Observations on underwater foraging tactics are virtually impossible in the turbid water where caiman are typically encountered. Nevertheless, the results of dietary studies at the study site suggest that most of a caiman's food is not captured at the water's surface. On Masaguaral, bottom-dwelling fish (e.g., *Hoplosternum littorale*), crabs, and snails are the prey most frequently consumed (Thorbjarnarson, 1991, 1993). Caiman do not have good underwater vision (Fleishman et al., 1988) and do not need visual cues for underwater prey capture (Fleishman and Rand, 1989). This is obvious in most caiman habitats where turbid waters result in zero underwater visibility. It seems probable that prey capture underwater is accomplished principally by touch (Schaller and Crawshaw, 1982; Platt and Brantley, 1991). The heads of crocodilians (P. Brazaitis and L. Garrick, unpubl. data) are covered with small pitlike integumentary sense organs, whose ultrastructure is similar to mechanoreceptors seen in other reptiles (von Düring 1973a, 1973b) and may be very sensitive to the contact of underwater objects. The sweeping underwater movements of the head made by caiman and other crocodilians (Platt and Brantley, 1991; Thorbjarnarson, 1991) probably serve to contact prey. The touching of prey underwater has been observed to produce undirected snapping behavior under captive conditions (Davenport et al., 1990). Once grabbed, gustation may be important in distinguishing prey from nonprey items (Scott and Weldon, 1990).

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JOHN B. THORBJARNARSON, *NYZS Wildlife Conservation Society, Bronx, New York 10460.* Submitted 23 March 1992. Accepted 17 Nov. 1992. Section editors: D. Cundall and F. Irish.