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NESTING ECOLOGY AND MANAGEMENT OF THE PARAGUAYAN CAIMAN (*CAIMAN YACARE*) IN THE PANTANAL OF MATO GROSSO, BRAZIL

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ABSTRACT

A total of 160 nests of the Paraguayan caiman (Caiman yacare) *were studied between 1979 and 1983 in two areas (Poconé and Miranda) in the Pantanal of Mato Grosso, Brazil.*

The reproductive season started with courtship in late August, in the early dry season, and ended in mid-April, toward the end of the wet season. Male contribution to reproduction terminated with copulation. Females selected secluded, shaded sites close to water, and built mound nests in which they deposited an average of 30 eggs. The incubation period, as estimated from embryo growth, was about 65 days, during which the embryos grew at a rate of approximately 0.37 cm per day to an average of 24 cm total length at hatching.

Poconé females were present on 12.3% of 437 visits to 82 nests, whereas in Miranda females were present on 60% of 397 visits to 49 nests. As a result, nesting success and the probability of hatching in Miranda were three-to five-fold that of Poconé (0.61-0.76 and 0.18-0.15, respectively). Egg predation, mainly by coatis and crab-eating foxes, was the main mortality factor at both sites. However, 78% of the 1980 Poconé nests were destroyed by floods. There are indications that, if well managed, caimans can be an additional source of income to ranchers in the Pantanal.

Keywords: Pantanal, Brazil; Nesting ecology; Caimans; Crocodilians; Clutch characteristics; Embryo Growth; Nest Predation; Reproductive Success; Hunting; Management.

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INTRODUCTION

One of the basic requirements to develop sound management plans is knowledge of the reproductive biology of the species in question. As stated by Magnusson (1978), three aspects of ecology important in management--habitat requirements, social interactions within the population, and life history--are most readily and profitably studied during the reproductive period.

During an ecological study conducted in the Pantanal of Mato Grosso, Brazil (Schaller *et al.*, 1984), I collected data on the reproductive biology of *Caiman yacare*. Since no field study had been conducted on the nesting ecology of this caiman, my initial objectives were to obtain basic descriptive information on the nesting characteristics of this taxon, and to analyze the variables important in determining local reproductive success (Crawshaw and Schaller, 1980). Subsequently, additional and comparative data were obtained for two more consecutive years in the same study area and for three years in a second study area, approximately 400 km away (Crawshaw, 1987, in press).

In this paper I compare and combine the data of the two areas, in an attempt to portray a broad picture of the nesting ecology of *C. yacare* in the Pantanal. In the last section, some aspects of caiman management in the Pantanal are discussed.

STUDY AREAS

The nesting ecology of caiman was studied in two different areas in the Pantanal, Poconé in the north, *circa* 100 km SW of Cuiabá, MT, and Miranda in the south, *circa* 200 km W of Campo Grande, MS. In Poconé, observations were made along the Bento Gomes river (16° 15' S, 56° 30'W) from October 1978 through March 1980. The Bento Gomes is a small river, no more than 30 m wide, bordered by a mosaic of gallery forests, thickets, pastures, and cerrado (Crawshaw and Schaller, 1980). Information on courtship behavior was collected at the Jofre ranch (17°16' S, 56° 29' W), along the Transpantanal highway, 113 km S of Poconé. Observations on caiman nesting in Miranda (19° 57' S, 56° 25' W, 400 km S of Poconé) were made in the surrounding areas of the Corcunda Lake, at one of the Miranda ranch's outposts, from July 1980 through February 1983. The lake is long (4.5 km) and narrow (50-200 m), and marks the transition from the high ground to low-lying areas subject to annual flooding. It is bordered on its east side by a continuous block of semideciduous forest, and by savannas, thickets, and gallery forest on the west side (see Prance and Schaller, 1982, for a description of the vegetation types in the Pantanal).

The Poconé caiman population was hunted intensively until 1974, while the Miranda caiman population had remained unexploited by humans (Crawshaw, 1987, 1991).

Information on caiman courtship was recorded as number of interactions, number and sex (based on estimated size) of the animals involved, context and duration of the interaction, vocalizations, response from other caiman, and general weather conditions (air and water temperature, humidity, cloud cover). Observations usually started at 0500 hrs and extended for as long as the animals remained active.

During the nesting season, caiman nests were searched for along the banks of the Bento Gomes river (in Poconé) and Corcunda lake (in Miranda) and surrounding areas. Nests were also located through the use of paid local informants. Type of data obtained at nest sites has been described elsewhere (Crawshaw, 1991).

Habitat types were roughly divided into the following categories: gallery forest, secondary forest, cerradão (a tall semideciduous forest, present only at Miranda; see Eiten, 1972, for a definition of cerrado sub-types), "caponete" (small islands of higher ground in flooded cerrado, consisting of 1-10 trees, usually associated with termite mounds; found only in Poconé) and "capão" (islands of semideciduous forest of various sizes, surrounded by flooded terrain).

At least one egg was collected from each nest to provide information on embryo development and to estimate laying and hatching dates. Eggs, embryos, and hatchlings were weighed with a Pesola spring scale (± 1 g). Linear measurements of eggs and embryos were recorded to the nearest mm with a vernier caliper. Hatchling and adult animals were measured (head length = HL; snout-vent length = SVL; tail length = TL; and total length = TOT) to the nearest cm. Adult mass was recorded to the nearest 0.1 kg on a spring balance scale.

Nest volume was calculated using the hemi-ellipsoid formula: $V = (2/3)\Pi (r_{abc})$, where a = 1/2 axial length of the nest, b = 1/2 axial width, and c = height. Egg chamber volume was calculated using the ellipsoid formula:
$V = (4/3)\Pi (r_{abc})$, where a = axial length of the chamber, b = axial width, and c = height. After the second nesting season (1980) no measurements relative to nest, chamber, or eggs were taken to avoid disturbance of females.

Temperatures were taken with a dry bulb thermometer. Chamber temperatures were measured by inserting a 50 cm length thermometer into the

egg chamber prior to the opening of the nest. Ambient temperatures were recorded 10 cm above the top of the nest.

Nesting success was expressed as the proportion of nests in which at least some eggs hatched. Hatching success was calculated as the proportion of eggs that hatched in successful nests. The probability of hatching was defined as the product of nesting and hatching success (Hall and Johnson, 1987).

A total of 26 nights was spent in a blind or in a tree near 7 different nests in an attempt to observe predators at the nests, and to record the behavior of the female and young at hatching. When a nest was found partially depredated, padded leg-hold traps (size = no. 2) were concealed on the top of the nest to obtain direct evidence on the type of predators.

Mean values are reported ± 1 SD, followed by the range. Whenever sample size permitted, parametric tests were used. Tests are specified in the text.

RESULTS

Between 1979 and 1983, 160 C. yacare nests were found, 92 in Poconé and 68 in Miranda. Of these, 5 had been totally depredated when found and 6 had no eggs. The remaining 149 active (with eggs) nests provided information on nest, egg, embryos, and clutch sizes, ecological requirements, predation and survival rates for the two areas. Certain aspects of the analysis relied more heavily on data from the 1979-80 nesting seasons in Poconé, which were studied more intensively.

Size of Caiman at Reproduction

I have no physiological information as to age of sexual maturity of C. yacare in the Pantanal. However, measurements of 135 caiman captured for movement studies (Schaller and Crawshaw, 1982) in the Jofre ranch provided some evidence on this matter (Fig. 1, Table 1). There was a 10 cm difference in SVL and a 5 kg difference in mass between the largest female considered to be a subadult (SVL = 67 cm, mass = 9.1 kg) to the smallest female classified as an adult (SVL = 77 cm, mass = 14.1 kg). Likewise, these differences were 12 cm and 13.4 kg between the largest subadult (SVL = 78 cm, mass = 13.6 kg) and the smallest adult (SVL = 90.0 cm, mass = 27 kg) males in the sample.

This absence of large subadult males has also been noted in the Nile crocodile (Cott, 1961) and the saltwater crocodile (Messel *et al.*, 1981, Messel and Vorlicek, 1986). Habitat segregation forced by intraspecific aggression from adult animals was suggested to explain this phenomenon (Messel and Vorlicek, 1986).
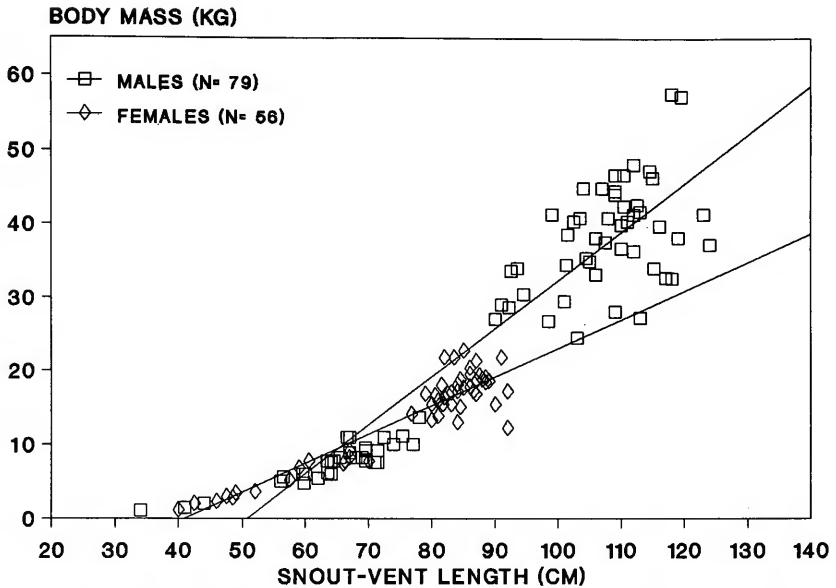
BODY MASS (KG)

Figure 1. Measurements (SVL and body mass) of 135 *C. yacare* captured in the Jofre ranch, Pantanal.

Table 1. Descriptive statistics on measurements of adult *Caiman crocodilus yacare* in northern Pantanal, Brazil. Linear measurements in cm; mass in kg

	n	*Mean*	*SD*	*Range*
Males				
Head Length	29	28.0	1.8	23.4- 31.1
Total Length	48	204.0	19.5	155.5-240.0
Snout-vent Length	48	108.0	8.3	90.0-124.0
Tail*	48	96.4	15.3	52.0-122.0
Mass	54	39.0	7.5	24.5- 57.6
Females				
Head Length	23	21.5	0.7	20.0-22.5
Total Length	41	158.0	12.2	130.0-176.5
Snout-vent Length	41	85.0	3.6	76.8- 92.0
Tail*	41	72.7	10.8	47.0- 88.0
Mass	42	17.5	2.5	12.2- 22.7

* Some animals had part of their tails missing.
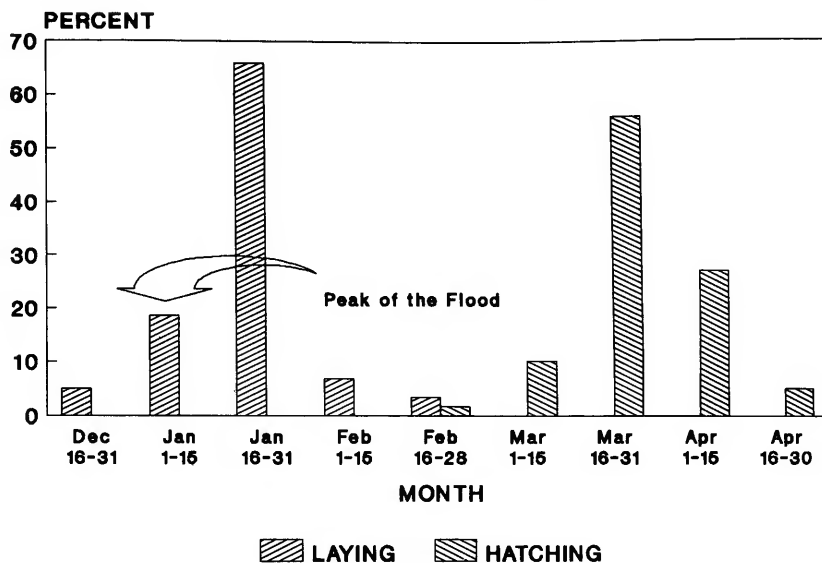
PERCENT

Figure 2. Laying and hatching periods of *C. yacare* in the Pantanal.

Breeding Season

Courtship, as evidenced by vocalizations and number of mountings in the Jofre study area, started in August and reached its peak in late November. Egg laying, as estimated on the basis of embryo development, started in late December in Poconé, with a peak from mid- to late January (Fig. 2). Thus, there was an interval of approximately 70 days between copulation and oviposition. Hatching started in late February, reached a peak in mid- to late March, and ended in late April (Fig. 2). There was a period of 58 days between the first and the last nest in which eggs were deposited, and 123 days between the first estimated oviposition and the last hatching (1979 and 1980 nests combined, N = 59). Temporal distribution of nesting events was similar between years.

Nest Characteristics

Type of habitat and distance from water. Of the 92 nests found in Poconé, 37 (40.2%) were located in secondary forest, 29 (31.5%) in gallery forest, and 26 (28.2%) in caponete. In Miranda, 38 of the 68 nests (55.9%) were found in capões, 26 (38.2%) in cerradão, and 3 (4.4%) in gallery forest.

In Poconé, 43 (54%) of 79 nests and 42 (76.3%) of 55 nests in Miranda were found at <5 m from the nearest standing water. A contingency table analysis yielded no significant differences between the two samples in relation to distance from water ($x^2 = 8.22$, df = 4, p > 0.05). The mean distance of all nests to standing water was 8.3 m ± 12.2 (0-50). Sixty-three percent of the 134 nests were built less than 5 m from water, 14.2% between 5-10 m, 8.9% between 11-20 m, 7.4% between 21-30 m, and 6.0% at distances greater than 30 m.

Nest Construction. Data on nest construction were obtained mainly during the 1982 season in Miranda. The mean construction period for 10 nests was 5.4 days ± 1.8, ranging from 3-8 days. However, since nests could only be located when the structure was already partly constructed, this average is probably a slight underestimation.

The earliest nest in construction was found on 6 January, and the last one on 11 January. One nest under construction on 9 January was abandoned by the female for at least seven days, but had eggs when revisited on 9 February. Three nests (two in Poconé, one in Miranda) were flooded before oviposition and were abandoned. Since active nests (with eggs) were found near (<30 m) two of these false or "dummy" nests (Klause, 1983), it is possible that those females had selected new, safer sites for nest construction. In Miranda, two other nests with no eggs were found at 8 m and 40 m from active nests; there was no apparent reason for the abandonment.

Nest Material. Female *C. yacare* was non-selective with nest-building material, using whatever was available at the site (Crawshaw and Schaller, 1980). From a sample of 68 nests (56 in Poconé, 12 in Miranda), 31 (45.6%) consisted of dead leaves, twigs and soil. Grass blades were used in 12 (17.6%) nests, spiny bromeliad leaves in 11 (16.2%), palm fronds in 10 (14.7%), and bamboo in four (6%).

Fifty-one out of 65 nests (78.4%) in Poconé were built against or between some kind of support. From 36 nests for which the information was recorded, 11 (30.5%) were built against one tree, nine (25.0%) against two or more trees, six (16.7%) against or over a fallen log, another six against termite mounds (mainly *Nasutitermes*), three (8.3%) against bushes, and one (2.8%) against bamboo. No significant difference was found between nest volumes of nests built with or without some kind of support (T-test = 1.29, P > 0.1).

Nest Dimensions. No difference was found in any dimension between 43 nests from which measurements were taken in 1979 (Crawshaw and Schaller, 1980)

and the 17 measured in 1980 in Poconé (T-test, $P > 0.1$). Thus, data were pooled for both seasons ($N = 60$) to provide overall means: axial length = 135.1 cm ± 19.3 (71-168); axial width = 120.6 cm ± 22 (65-160); height = 41.5 cm ± 6.4 (30-60). Average nest volume for 60 nests in Poconé was 0.362 m^3 ± 0.12 (0.093-0.667). Only two nests were measured in Miranda and their dimensions fell within the ranges of Poconé nests.

In constructing the nest, the female gathers material within a 3.5 m radius, as measured from the center of the nest (Crawshaw and Schaller, 1980). Therefore, nest volume is, most likely, mainly a function of material available at the site. However, assuming that females are more vulnerable to predators (natural and human) during the time they are on land searching for a site and/or building the nest, one could expect that other variables, such as type of habitat and distance from water, would also affect nest size. A one-way ANOVA indicated no significant differences in nest volume between habitats ($F_{2,59}$ = 2.30, $P > 0.1$). Only 6% of the observed variation (r_1, or coefficient of intraclass variation, Sokal and Rohlf, 1981) occurred among habitats, the remaining 94% resulting from within habitats variation. No correlation was found between nest volume and distance from water ($N = 60$). These results suggest that nest volume is determined, as hypothesized, by the amount of material available at the site and physiological constraints on the individual females.

Site use and re-use. —The smallest distance between two active nests in a given season was 6 m. For a sample of 14 nests in Poconé, the average distance from a nest to the closest, known, active nest was 30 m ± 13.5 (15-60). For six nests in Miranda for which the nearest neighbor distance was recorded, the mean distance was 9.3 m ± 3.72 (6-16).

Two nests in Poconé and two in Miranda were built on top of nests used in previous seasons. The Poconé nests were used in 1979 and 1981; this represented a 4.8% nest reuse, but in alternate years. A third nest found in 1981 was built 12 m from the remains of a nest monitored in 1979, indicating a 7.3% site reuse. I do not know if these sites were re-used by the same females. If so, one could infer that at least some females tend to reproduce every other year.

Five nests (3 in Poconé, 2 in Miranda) were built less than 10 m from previously used nests. Two other nests in Miranda and 1 in Poconé were built between 10-20 m from nests that had been used in the previous year.

Clutch and Egg Characteristics

Information on clutch size was collected from 80 nests, 63 in Poconé and 17 in Miranda. Five nests (three from Poconé and two from Miranda)

were excluded from calculations because I suspected they had been partially depredated before discovery. Mean clutch size did not differ between the two areas (T-test, df = 73, P > 0.05), with a combined mean of 30.7 eggs ± 4.63 (20-41, N = 75). Clutch size was positively correlated (r^2 = 0.56, df = 33, P < 0.001) with clutch mass (X = 2,266 g ± 0.424; range = 1,314-3,043 g; N = 35), and clutch mass showed an identical correlation with average egg mass (72.4 g ± 8.9; 26.4-90.5; N = 1,088). Average egg chamber (N = 50) dimensions were: axial length = 28.4 cm ± 4.8 (23-45); axial width = 23.6 cm ± 3.7 (15-37); height = 10.2 cm ± 2.9 (4-19.5). As would be expected, mean chamber volume (7,365 cm^3 ± 3,403 [2,827-21,659]) was positively correlated with number of eggs (R^2 = 0.22, df = 48, P < 0.001). There was an inverse correlation between the number of days in the laying period (53 days) and the total clutch weight (R^2 = 0.14, df = 31, P < 0.05). Likewise, the number of days in the laying period was inversely correlated with mean egg mass for 33 clutches in 1979 (R^2 = 0.18, df = 31, P < 0.05).

The mean ratio for clutch mass relative to female body mass (as a relative measure of female investment in reproduction) for 3 females captured at their nests was 0.13 (0.12-0.17). The highest value (0.17) was from an 80 cm SVL female that weighed 13.6 kg, with a corresponding clutch mass for 28 eggs of 2,244 g. However, her overall appearance suggested a poor physical condition when compared to the average mass of 17 kg ± 2.1 (15.4-21.8) for eight females with SVL between 80 and 82 cm. On the other hand, since the heaviest (21.8 kg) female in this size class was captured in mid-December, it is likely that her mass was augmented by the mass of her developing eggs. These results suggest some caution as to the period in which this type of information is collected: i.e., pre- or post-oviposition, or out of the reproductive cycle of the female.

Mean egg linear measurements (N = 1088) were as follows: axial length = 68.0 mm ± 3.9 (50.4-79.3); axial width = 42.9 mm ± 2.0 (30.0-48.4). Mean egg mass (N = 110) was 74.5 g ± 6.4 (39.6-85.8). Egg mass showed the greatest variation, with a corrected coefficient of variation (V^*, Sokal and Rohlf, 1981) of 12.4%, followed by length with 5.7%, and width with 4.4%. Egg mass was positively correlated with egg length and width, following the equation: y = -124.4 + length (1.018) + width (2.97), (F = 395, R^2 = 0.88, df = 109). Egg measurements varied considerably among clutches. A one-way analysis of variance indicated significant differences in egg masses between 10 clutches from the 1979 season (F = 92.9, df = 296, P < 0.001). The proportion of variation in egg masses among nests (r_I = coefficient of intraclass correlation, Sokal and Rohlf, 1981) was 0.76.

Temperature. Mean egg chamber temperatures ($29.7°C \pm 1.85$ [26.0-32.0]) differed significantly from the mean external temperatures ($26.9°C \pm 2.54$ [21.0-35.2]) for a set of 146 readings taken from 55 nests in Poconé, during the 1979 and 1980 nesting seasons ($t = 12.37$, $P < 0.001$, paired T-test).

Two nests, the first in normal shade conditions in gallery forest, and the second in a more exposed situation in caponete, were monitored continuously for a 24 hours period in the 1980 season. Internal and external temperatures were significantly different for both nests (paired T-test, $P < 0.0001$). The difference between internal and external means for the exposed nest ($5.8°C$, $t = 7.4$, $df = 23$) was greater than that of the nest with more vegetative cover ($1.58°C$, $t = 6.52$, $df = 23$).

Embryo development and incubation period. A total of 133 eggs was collected from 84 nests in Poconé and Miranda to provide information on embryo development and incubation period.

Length differences of embryos measured in 30 nests were positively correlated with the interval of days ($R^2 = 0.86$, $df = 41$, $P < 0.001$). The resulting regression line ($y = -0.19 + 0.39x$) indicates almost isometric growth of embryonic *C. yacare* (Fig. 3).

Average daily increment in length throughout the incubation period was 0.37 cm/day ± 0.12 (0.2-0.8, $N = 43$). Thus, approximately 65 days were required for an embryo to reach the average total length at hatching (24 cm). It should be noted, however, that the incubation period may be extended somewhat due to within clutch variation in embryo development. Therefore, hatching may be delayed several days after development of some embryos has been completed (Crawshaw and Schaller, 1980). Hatching dates, estimated on the basis of embryo measurements, were compared to actual hatching dates for six nests, as a check for the accuracy of this method (Table 2). The mean error of my estimates for the six nests was 2.3 ± 4.1 days. My results confirm the utility of embryo growth curves for predicting hatching dates, as reported by Hall (1985) for *Crocodylus novaeguineae*.

Hatchlings and Growth

Twenty hatchlings from two nests (17 from one nest) showed the following mean linear measurements: total length = 24.0 cm ± 0.5 (23.1-25.2); SVL = 11.7 cm ± 0.3 (11-12.2); and tail = 12.3 cm ± 0.4 (11.8-13.1). Average mass was 50.5 g ± 3.7 (46-62). Mass was correlated with SVL ($P < 0.05$) and with total length ($P < 0.01$) (Table 3). On the other hand, the correlation was much higher ($P < 0.0001$) between measurements of 31 juveniles, presumably from a single clutch, that were captured in an isolated pond, in September 1979 (Table 3).

Table 2. Field test results of estimated clutch ages of *Caiman yacare* in Poconé (1979), using embryo total length (cm) as a predictor

Nest No.	Total Length when found	Estimated hatching	Actual hatching	Error (days)
25	3.5	5 April	1 April	+4
6	5.7	22 March	18 March	+4
23	6.4	28 March	19 March	+9
39	13.5	23 March	24 March	-1
12	14.6	2 March	3 March	-1
36	15.2	16 March	17 March	-1
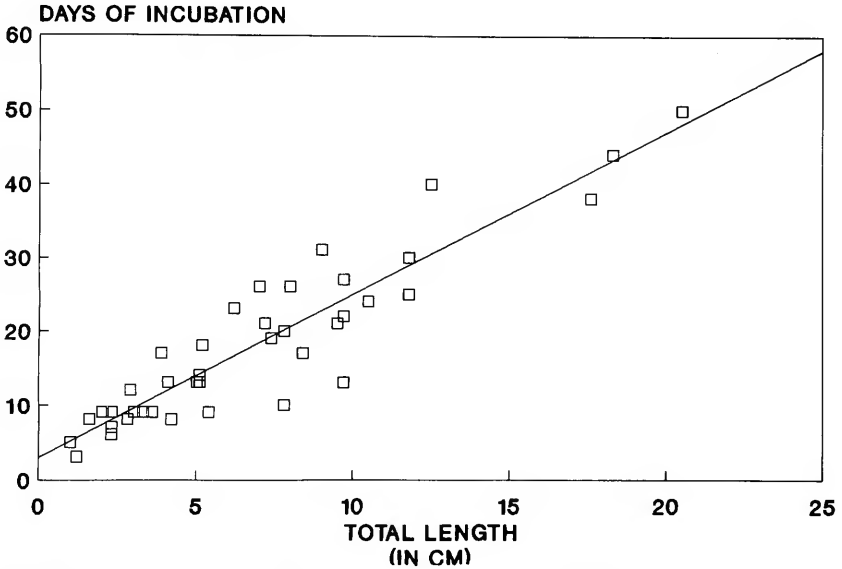
Figure 3. Embryonic growth of *C. yacare* in the Pantanal, based on measurements taken from 43 embryos from 21 nests.

Assuming that these juveniles hatched sometime in March 1979, their growth rate during this 6 month period, as compared to the 17 hatchlings, was roughly 0.55 mm/day, with a weight gain of 0.43 g/day. Measurements of hatchlings and juveniles are given in Table 4, showing the estimated percent increment during the 6 month period. Of the 31 juveniles, 21 (68%) were

females. Females were significantly larger (t = -3.06, df = 29, P < 0.005) and heavier (t = 2.68, df = 29, P < 0.01) than males (Fig. 4). A faster growth rate in females than in males during the first year of life has also been reported in alligators (Ferguson and Joanen, 1983).

Note: Brazaitis (1969) stated that cloacal determination of sex of individuals <75 cm in some species of crocodilians is potentially inaccurate, due to similarities in the genital apparatus. However, I found differences in the cliteropenis of juvenile male and female *C. yacare* to be sufficient for distinguishing sex by visual inspection. Webb *et al.* (1984) reported that "sexes assigned by visual inspection of the cliteropenis [of hatchling *Crocodylus johnstoni* and *C. porosus* 10-14 cm SVL] where the same as those assigned by examination of gonad histology".

Table 3. Regression equations for predicting dimensions of *Caiman yacare* hatchlings (N = 17) and juveniles (N = 31) from two clutches in Poconé, 1979. M = mass (g); TOT = total length (cm); S = snout-vent length (cm); H = head length (cm); SEE = standard error of the estimate

To predict:	From:		Equation	SEE	r2
Hatchlings					
M	TOT	M =	21.6 + 1.1T	1.2	0.21
	S	M =	20.7 + 2.4S	1.2	0.27
Juveniles					
M	TOT	M =	-256.5 + 11.3T	12.4	0.77
	S	M =	-352.9 + 27.8S	13.5	0.73
	H	M =	-283.3 + 85 H	11.6	0.80
TOT	S	TOT =	-5.8 + 2.3S	0.8	0.83

Fate of the Nests

Nests in which the eggs had hatched usually had about one third of the nest top excavated, with the egg chamber exposed. Eggshells were typically concentrated in the chamber and immediately around it. Eggs that hatched with no female assistance had their shells almost intact, with an opening on one of the extremities of the egg. On the other hand, shattered shells, but whole membranes suggested female assistance at hatching. On nests that had been raided by predators, the irregularly broken eggshells were usually scattered around the nest, to distances of up to 30 m. In some cases, the predator could

be identified by tracks around and on the nest. Flooded nests usually still retained the rotten eggs in the chamber, having been abandoned by the female.

Nest fates in Poconé and Miranda are depicted in Fig. 5a, b. Figure 6 compares nest fates between areas and the results for the two areas combined.

Nesting and Hatching Success. Overall, nesting success (nests in which at least some eggs hatched) was three times greater ($z = 5.9$, $P < 0.001$) in Miranda than in Poconé (Table 5; Crawshaw, 1987, 1991). Accordingly, the probability of hatching (nesting success x hatching success) was also three times higher in Miranda, since there was no significant difference between hatching success rates between the two areas (Table 5; $z = 2$, $P > 0.05$).

Table 4. Measurements of 17 hatchlings from the same nest, and of 31 juveniles, presumably also from a single clutch (see text), with the estimated percent increment (from the means) during a 6-month period. TOT = total length (cm); SVL = snout-vent length (cm); TL = tail (cm); M = mass (g)

		Hatchlings			Juveniles		
	n	Mean	SD	n	Mean	SD	% Change
TOT	17	24.1	0.5	31	34.1	2.0	+141.5
SVL	17	11.8	0.3	31	17.3	0.8	+146.6
TL	17	12.3	3.8	31	16.7	1.3	+135.8
M	17	49.2	1.3	31	129.0	19.8	+262.2

There was no difference in nesting success between the different habitats in Poconé, all years combined ($x^2 = 0.8$, df = 2, $P > 0.1$). However, there was a significant association between habitat type and whether a failed nest was flooded or depredated ($x^2 = 29.6$, df= 2, $P < 0.005$); $N = 70$). Nests located in gallery forest ($N = 23$) were more susceptible to flooding ($x^2 = 13.9$, $P < 0.001$), than they were to predation ($x^2 = 4.8$, $P < 0.05$). On the other hand, nests located in secondary forest ($N = 29$) showed the reverse pattern ($x^2 = 7.45$, $P < 0.01$). There was no such relationship for 18 nests located in caponete ($P > 0.1$). In Miranda, no significant association between habitat type and nest fate was found ($x^2 = 6.8$, df = 4, $P > 0.1$; $N = 63$).

The fate of 74 nests in Poconé was related to their horizontal distance from water ($x^2 = 35.7$, df = 6, $P < 0.005$). Predation rates were significantly higher than expected for nests built up to 20 m away from water, but not for those built at greater distances. Likewise, nests located close to water (less than 5 m) were significantly more prone to flooding than those at larger distances ($x^2 = 7.1$, df = 1, $P < 0.005$). No such relationships were found for
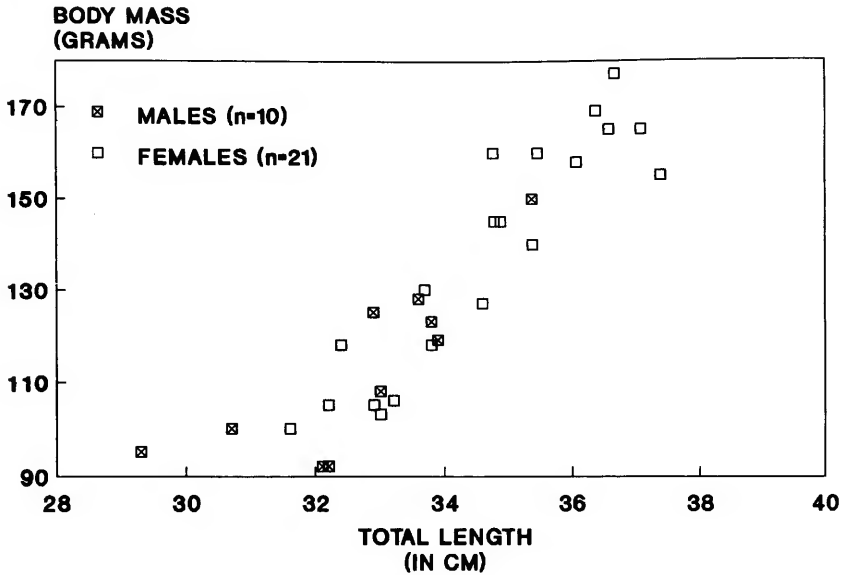
**BODY MASS
(GRAMS)**

Figure 4. Measurements (total length and body mass) of male and female juvenile caiman (N = 31), presumably from a single clutch, Poconé, Pantanal.

51 nests in Miranda (x^2 = 3.07, df = 6, P > 0.05).

Nest failure. Predation: Natural predation was the most important factor affecting egg survivorship in the two areas (Crawshaw,1987, 1991). In 32 nests from the 1979 season, first predation occurred only after 10 days post-oviposition for each individual nest reaching a peak between days 20 and 25. Considering the entire nesting season (the period between the earliest laying date and the latest hatching date): 113 days in 1979, predators seemed to have a delayed response to the seasonal resource (Fig. 7). Nest predation only started after day 40 of the season, and reached a peak around day 60. No nests were found depredated after day 75 of the 1979 nesting season. The cumulative probability of predation for 39 nests of the 1979 season in Poconé increased from 0 in day 30 to 0.82 at day 75 (Fig. 7).

Predation rates were significantly higher in Poconé than in Miranda, all years combined (z = 3.8, P < 0.001). Coatis (*Nasua nasua*) were the main predators in Poconé, and perhaps also in Miranda. They were usually seen in groups of 2-7 animals (one group with 22 individuals was seen elsewhere in the Pantanal). In nests raided by this species, the eggshells were scattered in several directions, at distances up to 15 m, indicating more than one individu-
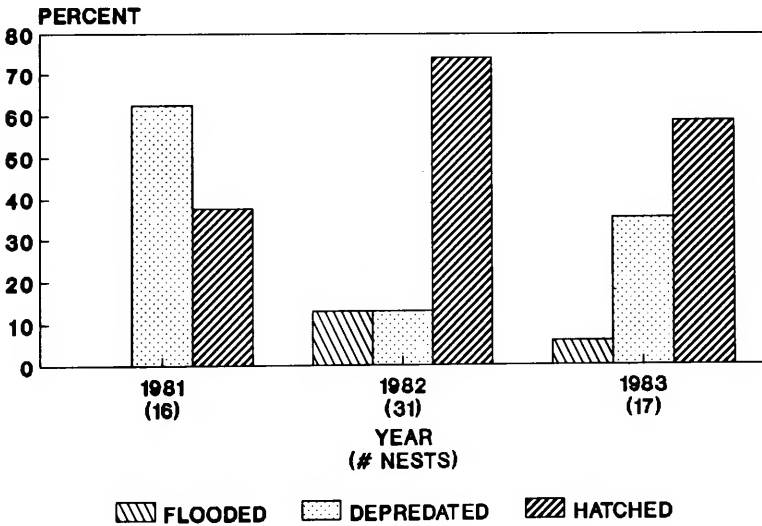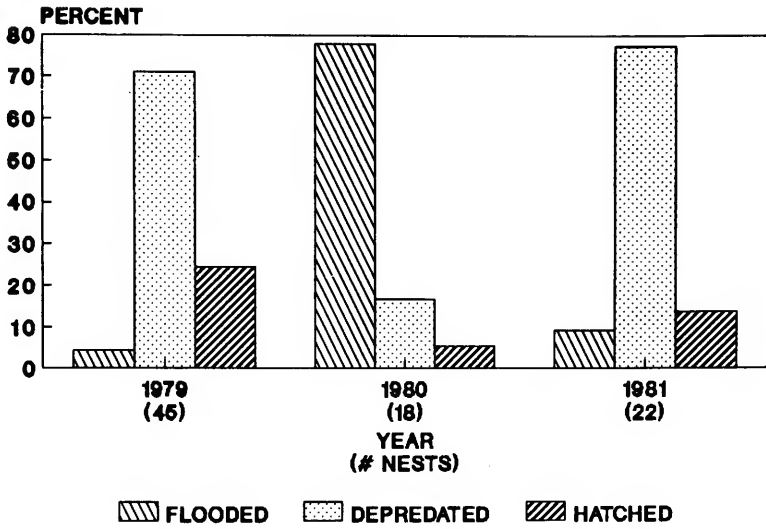
Figure 5. Fate of caiman nests in Poconé (Fig. 5a; 1979-1981) and Miranda (Fig. 5b; 1981-1983), Pantanal (from Crawshaw, 1991).

Table 5. Reproductive success of *Caiman yacare* in Poconé and Miranda, Pantanal. N = number of nests; (A) = nesting success; (B) = hatching success; (A x B) = probability of hatching; (C) = recruitment [N x 30 x (A x B) ÷ N]. (*Note: 30 = mean number of eggs per nest)

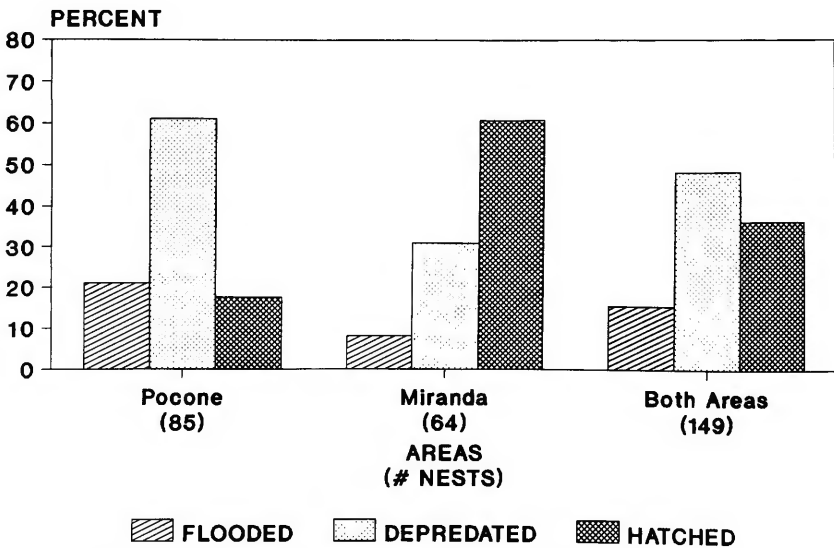| Area and Year	N	(A)	(B)	(A x B)	(C)
Poconé:					
1979	45	0.24	0.80	0.19	5.7
1980	18	0.06	0.73	0.04	1.2
1981	22	0.14	0.90	0.13	3.9
1979-1981	85	0.18	0.82	0.15	4.5
Miranda:					
1981	16	0.38	0.79	0.30	9.0
1982	31	0.74	0.82	0.61	18.3
1983	17	0.59	0.65	0.38	11.4
1981-1983	64	0.61	0.76	0.76	13.8
Both areas:	149	0.36	0.79	0.28	8.4

Figure 6. Comparison of caiman nest fates between Poconé and Miranda, 1979-1983, and the combined results for the two areas (from Crawshaw, 1991).

al predator.

I obtained direct evidence of predation by coatis at four nests. Three animals were trapped at two nests that had been partially depredated. I saw coatis preying on two other nests. Evidence at nest sites indicated coati predation on a total of 25 nests, or 46.3% of all nest predation at Poconé. Coatis were also present in Miranda, but not as common as in the Poconé area. Although predation pattern suggested coati predation in four instances in Miranda (13.3%), no direct evidence of nest predation by coatis was found. The second most important predator was the crab-eating fox (*Dusicyon* [=*Cerdocyon*] *thous*). In Poconé, it was trapped at one nest, observed preying on eggs and hatchlings at another nest, and suspected of being responsible for the destruction of another five nests. In Miranda, circumstantial evidence suggested fox predation on four of 20 nests (20%).

One opossum (*Didelphis albiventris*) was trapped at one nest in Poconé in 1980. However, given the scarcity of the species in the area (only two records were obtained in 18 months), predation on caiman nests by this species in Poconé is probably negligible. One nest in Poconé was completely destroyed by domestic pigs (*Sus scrofa*).

In Miranda, one tegu lizard (*Tupinambis teguixin*) was captured in a trap set on a partially preyed nest, and two other tegus were seen close to active nests. The predation pattern of *Tupinambis* on caiman nests in the Pantanal was apparently the same as described by Staton and Dixon (1977) in the Venezuelan llanos.

Several nests were repeatedly depredated in Poconé and Miranda, with 1-10 eggs being taken at a time (see also Crawshaw and Schaller, 1980). In some cases, it is possible that partial nest predation by one species facilitates predation by other species (or individuals with overlapping home ranges), by releasing odors normally confined to the egg chamber. Evidence from 6 nests from the 1979 season suggested that predation by tegu lizards was followed by predation by coatis, after intervals that ranged from 1 to 16 days (X = 7.8 ± 6.5).

In two instances, tayras (*Eira barbara*) were seen close to recently depredated nests in Miranda. This species was relatively common in the area and regularly preys on bird nests. Thus, it seemed likely that they would also prey on caiman nests. The pattern of predation on some nests in Miranda did not fit that of *Nasua* or *Dusicyon*, and it is tempting to suggest that tayras were the responsible predator in these instances. Fitch and Nadeau (1980) reported tayras to be one of the major egg predators of caimans at Iguazú, in northern Argentina.

Ants (two unidentified species) killed and ate a total of 10 live hatchlings in two nests in Poconé. In addition, ants also ate several embryos from eggs
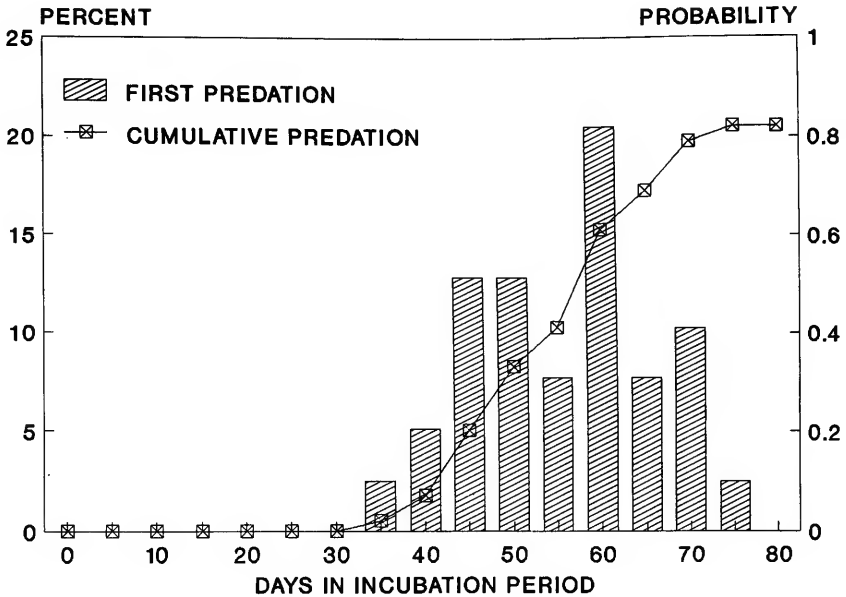
Figure 7. Timing of first predation, in relation to the incubation period, and the cumulative probability of predation for 39 nests in the 1979 nesting season, Poconé.

cracked by predators or accidentally broken by the female in another 3 nests. Overall, ants (3⁺ species) were found in 12 nests. It is possible that this association is partly caused by the ants using the nests as a refuge during the floods. Cintra (1985) mentioned *Solenopsis invicta* as preying on caiman hatchlings incubated in semi-natural conditions.

Flooding: In Poconé, 2 of 45 active nests (4.4%) in 1979, and 2 of 22 nests (9.1%) in 1981 were flooded (6% for the two years combined). However, flooding destroyed 78% of 18 nests in 1980, increasing the combined total flood loss for 1979-81 in Poconé to 19.5%. The high mortality due to flooding in 1980 was apparently a result of a 2 month delay in the flood peak, as compared to 1979 and 1981. In those years, flooding peaked during the first 10 days of January, whereas in 1980 the peak was in early March, after most of the females had layed their eggs.

Only four of 31 active nests (12.9%) at Miranda were flooded in 1982, while none were found flooded in 1981 and 1983 (Fig. 5b). The total percentage of nest destruction due to flooding in Miranda was 5.9%, while the overall figure for the two areas, all years combined (154 nests), was 13.7% (Fig. 6).

Effect of research activities on the fate of the nests: It is difficult to assess the

effect of research activities on egg mortality. Some females tended to decrease nest attendance after disturbed by humans, while others completely abandoned the nest during daytime hours. For instance, there was a decrease from 21% to 3.6% in female presence from the first to the fourth visit to nests in 1979 (Table 6). Therefore, predation rates may have been affected somewhat in that even the passive presence of a female at the nest may decrease chances of predation (Deitz and Hines, 1980). However, this apparently was not always the case: six nests in Miranda at which the females had been passively present during my visits were partially preyed upon. Given the difference in behavior displayed by individual females toward humans (Crawshaw, 1991), I surmised that aggressive females were more likely to drive away natural predators.

Table 6. Percentage of females present at nests in the first three visits to *Caiman yacare* nests (N = 134) in the Pantanal.

		Visits (%)			
Area and Year	n	1st	2nd	3rd	% Change
Poconé					
1979	43	21.0	8.1	6.4	-69.5
1980	18	28.0	23.5	11.7	-58.2
1981*	18	28.0	-	-	
Miranda					
1981	11	91.0	91.0	62.5	-31.3
1982	28	60.7	60.7	69.2	+14.0
1983	16	56.2	33.0	42.8	-23.8

* Nests were visited only twice, once in mid-season, and once at the end of the season.

DISCUSSION

The additional data on nesting characteristics of *Caiman yacare* are consistent with the results presented by Crawshaw and Schaller (1980), and show many similarities to nesting of other crocodilians. No significant differences were found on nest, clutch, or egg measurements between years or

between the two areas. As noted earlier, nesting of *C. yacare* in the Pantanal closely resembles that of *C. crocodilus* in the Venezuelan llanos, as described by Staton and Dixon (1977) and Ayarzaguena (1983).

For both species, most of the nesting seems to occur during the early wet season. For *C. yacare*, courtship started early in the dry season, reaching a peak in late November, when most caiman were concentrated in the few remaining ponds. Egg laying and incubation coincided with the height of the rainy season (Fig. 1). Although not quantified in Miranda, the timing of the reproductive events was apparently the same in both study areas.

The timing of nesting events for both *C. crocodilus* (Staton and Dixon, 1977) and *C. yacare* (Crawshaw and Schaller, 1980; this study), seem to be more related to seasonal rainfall and flooding patterns than to temperatures, as found for alligators in the Everglades National Park (Jacobsen and Kushlan, 1986).

The size at which *C. yacare* attain sexual maturity in the wild is not known. The smallest female considered to be an adult (as judging by her weight) in this study had a total length of 144.5 cm (76.5 cm SVL), but I do not know if she was reproductively active. This is slightly larger than the 60-67.7 cm SVL (Ayarzaguena, 1983; Staton and Dixon, 1977) and 125 cm total length reported for *C. crocodilus* (Blohm, 1973; Chirivi-Gallego, 1973; Rivero Blanco, 1974). This is not surprising, however, since *C. yacare* in the Pantanal seems to be slightly larger than *C. crocodilus*, as indicated by mean adult sizes given by Dixon and Staton (1983).

Assuming a growth rate similar to that of captive *C. yacare* (33.3 cm/year in the first four years of life; Brazaitis, 1986), females would attain adult size at approximately 4.5 years of age, and males at 5.5 years. Identical growth rates have been reported for captive *C. crocodilus* (Blohm, 1973; Chirivi-Gallego, 1973; Rivero Blanco, 1974). However, growth rates of captive individuals, under relatively constant conditions, may not be applicable to wild populations. Based on mark and recapture studies, Gorzula (1978) estimated that *C. crocodilus* in the Venezuelan Guyana required 6 years to reach a total length of 97 cm.

Minimum age at reproduction, and site-specific growth rates, are critical aspects in management considerations. This is clearly illustrated by the American alligator (*Alligator mississippiensis*). Males and females become sexually mature when they reach 182 cm total length, in both North Carolina and Louisiana populations (Klause, 1983). Yet, Louisiana alligators reach this length at 6 to 8 years (Chabreck and Joanen, 1979), while in North Carolina males and females require approximately 15 and 19 years to attain that size (Fuller, 1981).

Magnusson *et al.* (1985) suggested that *Paleosuchus trigonatus* nests

in tropical rainforest used the heat produced by termite mounds and insulation by the nest material to maintain the eggs at about 30°C. I do not know if *C. yacare* nests gained any heat advantage from close proximity to termite mounds. However, the relatively low percentage of those built against termite mounds (16.7%) and the probably much lighter vegetation cover over nests in the Pantanal, as compared to undisturbed tropical rainforest, suggest that this alternative heat source is not as important to *C. yacare* as it may be to *Paleosuchus*.

Although based on a small sample (N = 3), the same ratio between clutch mass and female body mass (0.13) was also obtained by dividing the average clutch weight (2.266 kg, N = 35) by the mean weight of female *C. yacare* (17.4 kg, N = 42). The ratio obtained for *C. crocodilus*, derived from data from Staton and Dixon (1977), is approximately 0.11 (mean clutch weight = 1.713 kg; estimated adult female mass = 15 kg). These figures are much greater than those found for *Crocodylus johnstoni* (*circa* 0.05; Webb *et al.*, 1983), and those derived for *Alligator mississippiensis* (0.07; mean clutch mass = 2.946 kg [Deitz and Hines, 1980]; mean adult female mass = 39.7 kg [Fuller, 1981]), and *C. niloticus* (approximately 0.06; mean clutch mass = about 6 kg [Modha, 1967]; mean female mass = 98 kg [Cott, 1961]). More information on this important aspect of crocodilian reproductive ecology is necessary to understand the possible reasons for this higher reproductive investment in females of the two mentioned subspecies of caiman. One obvious reason for the lower ratio for the two latter species is the greater female body mass, in relation to clutch mass. However, the question remains why caimans, given their smaller size, did not reduce clutch (such as *Crocodylus johnstoni*, with a mean of 13.2 eggs, Webb *et al.*, 1983) or egg size, in order to reduce clutch mass? On the other hand, if the higher ratio found for *Caiman* is not excessive, why don't the larger species have larger clutches?

Based on earlier work on crocodilian courtship (Modha, 1967; Garrick and Lang, 1977, Garrick *et al.*, 1978), one could expect that larger (more dominant) females would breed earlier in the season, and would lay larger clutches with heavier eggs. This pattern has been found in some lizards and snakes (Fitch, 1970). The inverse correlation found in *C. yacare* between timing of oviposition and clutch mass, as well as with mean egg mass, has important implications regarding individual reproductive success, and is possibly related to social factors. Assuming that larger eggs (and therefore larger hatchlings) represent an advantage during the first year of life of young caimans, a mechanism for the natural selection of fittest individuals seems evident (Dixon and Staton, 1983). This has also been suggested for the lizard *Uta stansburiana* (Medica and Turner, 1976). However, it is possible that the number (and may be mass) of eggs is subject to seasonal and/or annual variations, at least in species inhabiting variable

environments (Turner, 1977), as well as to female age.

The observed delay in nest predation (Fig. 7) is probably related to the opportunistic character of the predators, which were presumably not searching specifically for nests, but stumbled upon them during the time of highest nest density. Raccoons (*Procyon lotor*) were reported to show a similar delayed response to predation on alligator eggs (Joanen, 1969).

Although predation was responsible for most egg mortality, in some years flooding may take a heavier toll, as occurred in Poconé in 1980 (Fig. 5a). This potential hazard to nests had already been noted by Crawshaw and Schaller (1980), who stated that by laying their eggs after the peak of the flood, caimans avoided nest inundation. Interestingly, the laying peak in 1981 shifted to mid-February, in contrast to the 1979-80 pattern; this phenomenon suggests that females could be responding to environmental conditions experienced in the previous year.

Information presented herein regarding female nesting behavior in response to flood levels, and to changes in hunting pressure, appears to be facultative responses to changes in environmental conditions. This potential to adapt to prevailing ecological conditions and a relatively high reproductive rate (8.4 hatchlings per nesting female *C. yacare* per year, Table 5) allows populations to colonize new areas and, if given enough time, to spring back after intense hunting, as has happened in several areas of the Pantanal, in the last decades. Presently, hundreds of thousands (millions, according to some sources) of caiman skins are taken annually from the Pantanal into Paraguay and Bolivia, and exported to European countries. This rampant illegal scheme is detrimental not only for local caiman populations, but also to the local economy, with a loss of a potentially valuable natural resource. At the same time, cattle ranching, which has been the main economy in the Pantanal for the last 200 years, has been steadily declining in the last decade, due to unusually high floods and mismanagement. Considering the high reproductive potential of *Caiman yacare* in the Pantanal if adequately managed, the rational exploitation of caiman may provide an alternative and sustainable source of income to ranchers.

Caiman ranching and farming in Brazil has recently received much propaganda at a popular level, usually with exaggerated figures on its economic advantages (e.g. Westlehner, 1987). As a result, over 100 private ranchers throughout Brazil have requested permission to harvest caiman (F. Whidolzer pers. com.; only *C. yacare* is being considered so far). However, only 8 have been granted official registration by IBAMA (The Brazilian Institute for the Environment and Renewable Natural Resources), and only three have permits to commercially exploit the animals. The largest one, on the São Vicente ranch

in the Pantanal (estimated caiman population: 13,000), collects eggs from the wild and transfers them to artificial hatcheries. In 1987, the ranch had over 1,500 caiman in captivity, the largest ones being two years old. Recent legislation by IBAMA on the subject restrict permits to properties within the Pantanal region, and requires that 10% of the annual production be restored into the wild (A. Tunes, IBAMA, pers. com.). The Empresa Brasileira de Pesquisa Agropecuária-EMBRAPA maintains a research station in the Corumbá region, where data on several aspects of caiman biology are being collected.

One cannot overemphasize the immediate need for research if caimans are to be managed successfully in the Pantanal. As pointed out by Magnusson (1984), caiman exploitation may well prove not to be a feasible alternative anyhow. However, the emergent picture from present-day Pantanal certainly makes it worth trying.

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