

# THE COMMON CAIMAN

Stefan Gorzula\*

Division de Cuencas e Hidrologia,  
C. V. G. Electrificación del Caroni C. A.,  
Apartado 62418  
Caracas, Venezuela

and

Andres Eloy Seijas

Servicio Nacional de Fauna Silvestre,  
Ministerio del Ambiente y de los Recursos  
Naturales Renovables,  
Apartado 184,  
Maracay, Estado Aragua, Venezuela

## INTRODUCTION,

The common or spectacled caiman is a species complex whose taxonomy is in a confused state. Primarily for management and conservation considerations, rather than for nomenclatorial justification, we follow in this chapter the terminology of the Red Data Book (IUCN 1982), using the binomial *Caiman crocodilus* with four nominal subspecies (*C. c. apaporiensis*, *C. c. crocodilus*, *C. c. fuscus*, and *C. c. yacare* (King and Brazaitis 1971; Brazaitis 1973)). Medem (1981) discussed the validity of this usage and argued that *Caiman sclerops* should be applied to this taxon. Likewise he recognized *C. c. fuscus* as two distinct subspecies (*fuscus* and *chiapasius*), and gave full species status to *C. c. yacare* (Medem 1983). Two additional subspecies *C. c. mattogrossiensis* and *C. c. paraguayensis* have been included in another checklist (Wermuth and Mertens 1977). However, the original descriptions were based on commercial hides (Fuchs 1974) and the use of those names should be suppressed (Frair and Behler 1983).

Numerous works on *C. crocodilus* have been 'published' in Latin America as internal manuscripts of government organizations and as theses of universities. Due to the difficulty in obtaining such material we have been selective and have cited only those that we consider contain data or concepts of particular worth. Given Medem's (1981, 1983) extensive treatment of South American crocodylians and their literature, we have restricted our review in general to publications of the last two decades.

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\*The author is presently Scientific Coordinator of Sustained Management Systems, 1221 Brickell Avenue, Ninth Floor, Miami, Florida 33131.

## GEOGRAPHICAL DISTRIBUTION

The common caiman occurs from about latitude 16° 20' N in Central America to latitude 34° 00' S in South America. Off of the mainland it occurs naturally on the island of Trinidad and Tobago. Feral populations are established in the Lanier Swamp in the southwest of the Isla de Pinos (Cuba; Varona 1976), and in the State of Florida (USA) as far north as latitude 26° 40' (King and Krakauer 1966, Ellis 1980). In the accounts of subspecies we list them in order of occurrence from north to south.

*C. c. fuscus* ranges from the Pacific drainage of the states of Oaxaca and Chiapas in southern Mexico (Alvarez del Toro 1974), through Central America into northwestern South America. In Nicaragua, Costa Rica and Panama it is found in both Pacific and Caribbean lowlands (Budowski and Vaihán 1976, Dixon and Staton 1983). In northwestern South America it occurs to the west of the Andes as far south as Machala in the Gulf of Guayaquil in Ecuador (Medem 1983). The subspecies extends east through the Caribbean drainage of Colombia, in the Cauca and Magdalena basins, into the Maracaibo basin of northwestern Venezuela (Medem 1981, 1983), and along the Caribbean coast as far as the Rio Yaracuy (Medem 1983). The taxonomic relationships of the most eastern population with *C. crocodilus* along the rest of the Venezuelan Caribbean coast is not clear (Seijas 1986).

*C. c. crocodilus* is the most widespread subspecies and may well be a composite. Medem recognizes the existence of various demes in this subspecies and discusses the unpublished revision that was begun by the late K. P. Schmidt of the Chicago Natural History Museum. The subspecies occurs to the east of the Andes into northern South America in Venezuela, Guyana, Surinam, French Guiana, Colombia, Ecuador, Peru, the Amazon basin in Brazil, and the islands of Trinidad and Tobago (IUCN 1982; Medem 1983).

*C. c. apaporiensis* is known only from southeastern Colombia along a 200 km stretch of the Rio Apaporis (Medem 1981, IUCN 1982).

*C. c. yacare*, which is regarded as a full species by Medem (1983), occurs in the Llanos de Mojos region in the southeastern tributaries of the Amazon in Bolivia (rivers Beni, Mamore and Madre de Dios), in the adjacent Mato Grosso region of Brazil, and southward through the Paraguay (Parana) River basin of Paraguay and northern Argentina (IUCN 1982, Medem 1983).

## HABITAT

*C. crocodilus* is found in a wide range of aquatic habitats from sea level up to about 500 m, representing the 24° to 27° isotherm (Chiriví-Gallego 1973), and exceptionally up to 800 m (Gorzula and Paolillo 1986).

### *C. c. apaporiensis*

This subspecies is found in quiet waters and lagoons of the upper and middle Rio Apaporis. Medem (1983) notes that the water temperature of the lagoons where they occur is warmer (25 to 28° C) than that of the adjacent bodies of water (21° to 22° C) occupied by *Paleosuchus palpebrosus*.

*C. c. crocodilus*

General descriptions of the habitat of this subspecies have been given for numerous authors (Medem 1981; Ramos et al. 1981, IUCN 1982, Gorzula and Paolillo 1986). Habitat types have been described as: permanent and temporary lagoons, ponds, lakes, reservoirs, hydroelectric dams, oxbow lakes, flood plains, quiet water, bodies of water in flat lands with sandy beaches without plants, borrow pits, flooded savannas, savannas modulated with dikes, moriche and palm swamps, swamps, marshes, brackish waters in mangrove swamps, the lower areas of forest streams, flooded forest, rivers, river meanders, mudbanks at the bend of rivers, the mouth of branch creeks, shallow waters with a gradually sloping shore and many inlets, drainage ditches, canals, and sometimes in rivers near to falls and rapids.

Climatic data have been reported for some areas (Ramos et al. 1981, Ouboter and Nanhoe 1984) and indicate that the habitat of *C. c. crocodilus* in Venezuela is characterized by a marked dry season for the first few months of the year. Ramos et al. (1981) provide limnological data for one site in the Venezuelan Llanos showing water temperatures from 26 to 30° C, pH from 5.7 to 7.5, and low concentration of minerals and nutrients, especially calcium, magnesium, carbonates, phosphorus and nitrogen. Limnological data for 15 *C. c. crocodilus* localities and 7 *Paleosuchus trigonatus* localities indicated that *Caiman* inhabits waters that are less oligotrophic than those where *P. trigonatus* occurs (Gorzula et al. 1989). The mean temperature (°C), conductivities (MHOS) and total cations (eq/l) were 26.1/22.4, 48.5/29.1, and 125.6/32.4 respectively. The range of values for conductivity, sodium, potassium and total cations fell into two distinct groupings. The ranges of values for temperature, pH, calcium and magnesium overlapped only slightly.

*C. c. crocodilus* is occasionally sympatric with other species of crocodylians, but this may be a seasonal phenomenon (Vanzolini and Gomes 1979, Medem 1981, 1983; Magnusson 1982, 1985; Gorzula and Paolillo 1986). Its present day distribution may be in part due to its expansion to places where larger crocodylian species are extinct or severely depleted due to commercial hunting (Dixon and Sioni 1977, Medem 1983). Human intervention, through the creation of reservoirs, dams and canals has favored the expansion of this subspecies by the creation of new habitats (Dixon and Sioni 1977, Magnusson 1985, Gorzula and Paolillo 1986).

*C. c. fuscus*

Compared to the previous subspecies *C. c. fuscus* is more coastal, extending only up some large rivers in Colombia and Ecuador into the low lying alluvial plains. Its habitat has been described as: quiet waters, swamps, lagoons, dams, meanders of large rivers, small streams and creeks, stormtide inner beaches, lowlands, brackish water mangrove swamps, saltwater, and ponds on offshore islands (Chirivi-Gallego 1971, 1973; Alvarez del Toro 1974, Medem 1981, 1983; IUCN 1982, Seijas 1986). Chiviri-Gallego (1971) notes that the specimens collected in saltwater habitats show flaking of the dorsal scutes. Where sympatric with *Crocodylus acutus*, this subspecies occurs in low numbers (Seijas 1986). In areas where *C. acutus* has been hunted out *C. c. fuscus* has invaded the former's niche (Medem 1981, 1983; Seijas 1986).

*C. c. yacare*

This subspecies has been described as inhabiting open waters, marshy savanna, lakes, lagoons, roadside borrow pits, and rivers (IUCN 1982, Schaller and Crawshaw 1982, Medem 1983). It avoids salt or brackish waters (IUCN 1982). Although the general habitat is similar to that of the Venezuelan Llanos with a distinct dry season in the latter half of the year, there is also a marked cool period from June to September during which the air temperature may fall to 0° C (Schaller and Crawshaw 1982).

Although this subspecies occurs in two separate river basins, the watershed is low (about 400 m above sea level). Medem's (1983) geographical generalities indicated that the flooded relatively open plains of the Llanos de Mojos, the Mato Grosso and the Pantanal form a continuum of habitat that is occupied by this subspecies. This habitat is distinct from the lowland forest habitat of *C. c. crocodilus* in the adjacent Amazon region. *C. c. yacare* is the largest subspecies attaining lengths of between 2.5 to 3.0 m. It is interesting to note that the deme of *C. c. crocodilus* which inhabits the llanos of Venezuela and Colombia, and which the late K. P. Schmidt had intended to describe as a distinct subspecies, *C. c. humboldtii* (Medem 1983), also attains large sizes (up to 2.5 m), whereas *C. c. crocodilus* in southern Venezuela are significantly smaller (Gorzula 1987).

## POPULATION DENSITIES

Problems related to the censusing of caimans have been discussed by Magnusson (1982, 1984) and others (Gorzula 1984, 1987; Gorzula and Paolillo 1986). These authors have proposed techniques for estimating size during such surveys (Magnusson 1983, Gorzula 1984). In most surveys, with the exception of the Venezuelan Llanos where caimans concentrate into well defined bodies of water during the dry season, it is not known whether the populations are partially or totally migratory. The planning of surveys with regards to factors such as tide, weather and phases of the moon is based on the individual experience of the researcher. It is not known what proportion of the true population has been counted. The surveys are frequently not repeated and densities are expressed as number per unit area of general habitat, but do not take into account within habitat preferences of the caiman. Additionally, few workers report the age- or size-structure of the population. In spite of these problems, the surveys conducted over the past ten years or so indicate that *C. crocodilus* is still a common species in many areas.

The majority of surveys have been of *C. c. crocodilus*. In riverine habitats observed densities in different countries are surprisingly uniform. In Peru, densities of 6.6 caiman/km of shore have been reported for the Rio Mairia (Morley and Sanchez 1982) and 9.02 caiman/km of shore for the Pacaya-Samiria National Reserve (Verdi et al. 1980). In the Coesewijne River in Surinam Glastra (1983) observed densities from 0.7 to 19.0 caiman/km of river, the densities being higher near the mouths of large side creeks and on sections of the river bordered by large open swamps. Mean observed densities were 3.3 caiman/km of river during the wet season and 6.41 caiman/km of river during the dry season. In the same area the overall density has been estimated at 5.3 caiman/ha of habitat (Ouboter and Nanhoe 1984). In the Venezuelan Guayana for riverine habitat and lake shore a mean density of 2.52 caiman/km has been reported (Gorzula and Paolillo 1986). In the Venezuelan Llanos Staton and Dixon (1975) calculated densities of 130 caiman/ha of lagoon during the dry season, Ayarzagüena (1983) reported 80 to 150 caiman/ha of lagoon for similar conditions and Marcellini (1979) observed a mean value of 63.5 caiman/ha of lagoon. Caimans in this area disperse over the flooded savannas during the wet season and population densities for gross habitat (including dry land) have been reported as 0.17 caiman/ha for a 78,000 ha ranch

(Ayarzagüena 1983), 0.21 for the same ranch (D'Andria 1980), 0.19 for a series of ranches covering a total area of 233,800 ha (Seijas 1986), and 1.11/ha for a 75,000 ha ranch (Woodward and David 1985). In modulated savannas in the same area dry season densities were 3.1 caiman/ha of water surface, dropping to 1.6 caiman/ha in the wet season (Ramos et al. 1981). For the Venezuelan Guayana one study (Gorzula 1978) estimated densities of 100 caiman/ha of lagoon during the dry season and 10 caiman/ha of lagoon during the wet season. Subsequent results for this region (Gorzula and Paolillo 1986) estimate an overall density of 6.64 caiman/ha of lagoon or 23.4 caiman/km of lagoon shoreline.

Populations of *C. c. fuscus* along the northern coast of Venezuela have been surveyed by Seijas (1986). In lacustrine habitats a mean density of 5.8 caiman/km of shoreline was reported for 144 km of lake shore where *C. c. fuscus* occurs alone, but only 2.5 caiman/km (in 45.3 km of lake shore) where they were sympatric with *Crocodylus acutus*. Likewise, in riverine habitat densities were higher (7.1 caiman/km along 143 km of river) in habitats where *C. acutus* was absent than where they were sympatric (1.5 caiman/km along 86.9 km of river).

In the pantanal area of Brazil Schaller and Crawshaw (1982) counted a total of 2,368 *C. c. yacare* in borrow pits along a 14 km stretch of the Transpantanal Highway. They estimated that this figure represented 75% of the total population.

## POPULATION STRUCTURE

The studies that have been made to date of the population structure of the spectacled caiman have been of size structure, rather than age structure, of populations of this species. Results of ten such studies are shown in Figure 1. Since certain authors did not include hatchlings in their analysis, we have eliminated data for hatchlings from those reports that did so. It should also be noted that, due to the high mortality that may occur in hatchlings, these percentages may vary greatly within a given population in a short period of time. Likewise, authors varied in which parameter was used to express size, using either the snout-vent length or the total length of the animals. In order to facilitate a direct comparison between the use of both parameters two scales have been given, one for the snout-vent length in mm and the other for the total length in m. Staton and Dixon's (1975) regression of  $Y = 2.3997 + 1.8548X$  was applied in order to calibrate the two scales.

As a broad generality, yearlings of this species reach a snout-vent length of approximately 200 mm (Chirivi-Gallegos 1971, Blohm 1973, Rivero-Blanco 1974, Staton and Dixon 1975, 1977; Gorzula 1978, Verdi et al. 1980, Medem 1981, Ayarzagüena 1983). Females reach sexual maturity as, or slightly before, they attain a snout-vent length of 600 mm. With the exception of certain cases reported by Medem (1981) for *C. c. apaporienis*, females do not grow larger than a snout-vent length of 900 mm. Males possible reach maturity at a larger size than females do, but attain substantially greater maximum sizes. Thus for the size frequency histograms of the Venezuelan Llanos population (Fig 1: A, B, C, D and E) the first size class shown (class II individuals) represent the non-hatchling immature portion of the population, the second size class shown (class III) represent all of the sexually mature females of the population and the smaller mature males, and the third size class (class IV) represents adult males. All of these populations have suffered no significant hunting pressure for at least ten years. In spite of different methodologies being employed they show reasonably similar size structures, especially with respect to the class IV portion. The Brazilian Pantanal population of *C. c. yacare* studied by Schaller and Crawshaw (1982; Fig. 1: F) is shown with four size classes. The first two represent non-hatchling subadults (class II), the third represent adult females and subadults males (class III), and the fourth are the

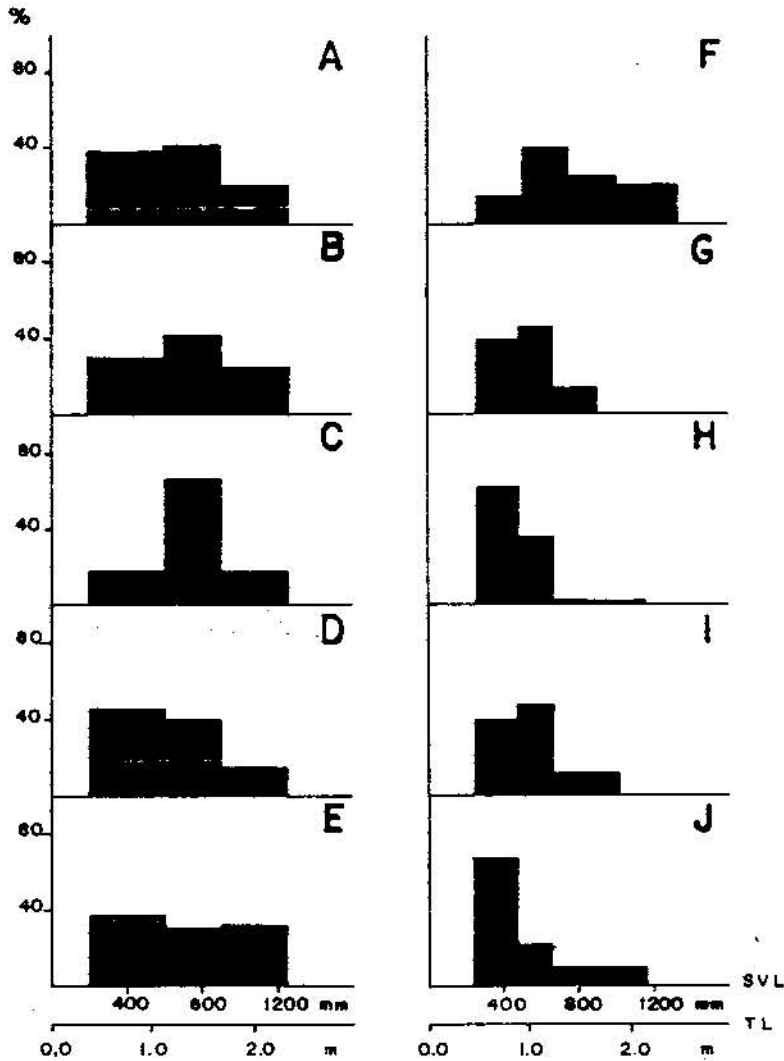


Figure 1. The size structure of nine populations of *Caiman crocodilus* - A: Venezuelan Llanos, captures, N = 219 (Ayarzagüena 1980); B: Venezuelan Llanos, visual size estimates, N = 296 (Ayarzagüena 1980); C: Venezuelan Llanos, visual size estimates, N = 13,185 (Seijas 1984); D: Venezuelan Llanos, captures, N = 174 (Staton and Dixon 1975) E: Venezuelan Llanos, visual size estimates, N = 4,570 (Woodward and David 1985); F = Brazilian Pantanal, visual size estimates, N = 637 (Schaller and Crawshaw 1982); G = Venezuelan Guayana, captures, N = 119 (Gorzula 1978); H = Brazilian Amazonas, visual size estimates, N = 112 (Magnusson 1982); I = Surinam, visual size estimates, N = 213 (Glastra 1983); J = Surinam, captures, N = 337 (Ouboter and Nanhoe 1984). SVL = snout-vent length in mm. TL = total length in m.

adults males (class IV). It has been already pointed out that *C. c. yacare* shares certain characteristics of its general ecology with the Venezuelan Llanos deme of *C. c. crocodilus*. It is thus an additional curiosity that the yacare caiman population studied, which was probably under moderate if not intense hunting pressure, should show a population size structure with a marked similarity to those of the Venezuelan Llanos populations.

The populations of *C. c. crocodilus* studied in the Venezuelan Guayana, Brazil and Surinam (Fig. 1: G, H, I, J) are markedly different in size frequency distribution from those of the Llanos or Pantanal, but again fairly similar between themselves. In these cases the three size classes shown were arbitrarily chosen to illustrate the general trend of the population structure, and do not correspond to the classes II, III and VI. All four populations were reported to be, or have been recently, under slight to heavy commercial hunting pressure. However, Gorzula's unpublished follow-up of the El Manteco population for some fourteen years after a total hunting ban was enforced suggest that this size structure is normal of *C. c. crocodilus*, at least in the Venezuelan Guayana.

## REPRODUCTION

Authors have generally concluded that the sex ratio of *C. crocodilus* populations is 1:1, although in some data it seems that this might not necessarily be so (Gorzula 1978, Ouboter and Nanhoe 1984). The fact that males attain larger sizes results in marked differences in sex ratio within certain size classes (Staton and Dixon 1975, Schaller and Crawshaw 1982, Ayarzagüena 1983). External sexual dimorphism has been examined by Ayarzagüena (1983) who showed that female *C. crocodilus* have proportionally larger and more rounded eyes. In general females start breeding when they have reached a total length of 1.14 m. However, Chiviri-Gallego (1971) reported a breeding female *C. c. fuscus* of 1.08 m. The basic breeding strategy of this species is that of a mound builder that nests during the mid wet season, producing young at the beginning of the dry season.

**Courtship and mating** - In the Llanos and Pantanal at the end of the respective dry seasons caimans are concentrated in small permanent bodies of water. Although these aggregations are of a passive nature due to environmental factors, there is evidence that *C. crocodilus* does make active breeding aggregations (Schaller and Crawshaw 1982, Ouboter and Nanhoe 1984). Breeding behavior has been observed in the llanos from March to August (Staton and Dixon 1977) and in the Pantanal from July to December (Schaller and Crawshaw 1982). Courtship involves jumping, a horizontal tail display, a vertical tail display, head slapping and tail slapping (Alvarez del Toro 1974, Staton and Dixon 1977, Ayarzagüena 1983). Vocalizations play little or no part in the courtship of Llanos caiman (Staton and Dixon 1977). Nibbling by the female of the male's lower mandible and mutual neck rubbing have been observed during pre-coitus (Alvarez del Toro 1974, Staton and Dixon 1977). Copulatory position may vary according to the depth of water where it is carried out. The male is usually on top of the female but one case was observed where the female was on top of the male (Staton and Dixon 1977). Copulation lasts from four minutes to half an hour (Alvarez del Toro 1974, Staton and Dixon 1977).

**Nesting** - Nesting in *C. crocodilus* has been reported from August to October in the Llanos (Staton and Dixon 1977) and in the mouth of the Amazon during May and June (Best 1984). *C. c. fuscus* breeds all year round in Colombia, but with a peak of nesting activity from January to March (Medem 1981, IUCN 1982). *C. c. yacare* nests between December and April (Crawshaw and Schaller 1980). Caimans used the material closest to the nest site for construction (Alvarez del Toro 1974). In the Llanos nests constructed in open savanna were of *Paspalum fasciculatum*, and those in

or near to gallery forest were made of leaves, twigs and soil (Staton and Dixon 1977). Nest sizes of *C. c. crocodilus* in the Llanos have been reported as a mean diameter of between 80 and 110 cm with a height of 40 to 50 cm (Rivero-Blanco 1974), and as a mean length of 117 cm, a mean width of 104.5 cm and with a mean height of 44.5 cm (Staton and Dixon 1977). Nests of *C. c. yacare* average 134 x 117 cm and 40.5 cm height (Crawshaw and Schaller 1980). A single nest of *C. c. apaporiensis* with ten eggs has been found (Medem 1981). Clutch sizes in *C. c. crocodilus* vary from 14 to 40 eggs with a mean about 29 (Rivero-Blanco 1974, Staton and Dixon 1977). In *C. c. fuscus* smaller clutch size from 12 to 32 eggs have been reported (Alvarez del Toro 1974, Medem 1981, IUCN 1982). *C. c. yacare* produces larger clutch sizes of 21 to 38 in Brazil (Crawshaw and Schaller 1980, Schaller and Crawshaw 1982) and 23 to 41 in Bolivia (mean 33.6; IUCN 1982). Clutch size may depend in part on the size of the female. Eggs are elliptical to round, white, hard shelled and rugose. Eggs of *C. c. apaporiensis* measured 66 x 63 mm (Medem 1981). Those of *C. c. crocodilus* in the Llanos averaged 64 x 41 mm and weighed 60 g (Rivero-Blanco 1974; Staton and Dixon 1977). Eggs of this subspecies in Surinam are more elongate (Ouboter and Nanhoe 1984). *C. c. fuscus* eggs have been reported as being from 63 to 70 mm long, 38 to 41 mm wide and weighing 40 to 45 g (Medem 1981). Nest temperatures has been measured from 25 to 32 C with a mean temperature in the order of 29 to 30° C (Blohm 1973, Staton and Dixon 1977, Crawshaw and Schaller 1980, Medem 1981). Incubation periods are from 70 to 90 days in *C. c. crocodilus* (Staton and Dixon 1977) and 75 to 80 days in *C. c. fuscus* (Alvarez del Toro 1974). Several authors have observed that the female regularly attends and guards the nest site during the incubation period (Blohm 1973, Crawshaw and Schaller 1980, Ayarzagüena 1983) and Alvarez del Toro (1974) also observed nest attendance by the male. Hatching is accompanied by vocalization of the young (Staton and Dixon 1977, Gorzula 1978). The female, sometimes with the help of the male, opens the nest and escorts the young to the water (Alvarez del Toro 1974; Staton and Dixon 1977; Crawshaw and Schaller 1980). The female may carry the young in her mouth (Alvarez del Toro 1974), and there is evidence that she may also assist hatching by cracking eggs open in her mouth (Crawshaw and Schaller 1980). Hatching in the Venezuelan Llanos occurs from October to December with a peak in November (Staton and Dixon 1977). Peak hatching in the Brazilian Pantanal takes place in March (Crawshaw and Schaller 1980).

**Postnesting period** - After hatching the young stay together in discrete pods (Alvarez del Toro 1974, Staton and Dixon 1977, Gorzula 1978, Medem 1981, Ayarzagüena 1983, Romero 1983, Ouboter and Nanhoe 1984, Gorzula 1986). Single sex pods have been reported (Ouboter and Nanhoe 1984), and pods of mixed ages have also been observed (Gorzula 1985). Adult caimans defend pods in response to distress calls (Staton and Dixon 1977, Gorzula 1978, Staton 1978, Romero 1983, Ayarzagüena 1983, Ouboter and Nanhoe 1984, Gorzula 1986). Defensive behavior by the adults ranges from displaying to outright attack. The defending adult is not necessarily a parent (Gorzula 1978; Gorzula and Paolillo 1986). Although the pods generally stay near the nest site, pods with a female in attendance have been observed undergoing migration (Ayarzagüena 1983, Ouboter and Nanhoe 1984). Pods may stay together for a year and a half before dispersing, resulting in the female breeding during alternate years (Gorzula 1978, Ouboter and Nanhoe 1984).

## GROWTH

The few studies on growth rate in wild populations have been of *C. c. crocodilus* (Fig. 2). Gorzula (1978) used mark-recapture data to produce a growth curve for a population of spectacled caimans inhabiting the savanna lagoons in the Venezuelan Guayana. It was estimated that caimans reach a total length of slightly less than one meter in six years. It was also shown that caimans less than two years old grew steadily during the whole year, but thereafter the growth rate slowed during the dry seasons. In an exceptionally dry year there was no growth registered in five caimans with total lengths of between 0.90 and 1.20 m, whereas during a wet year two caimans within this



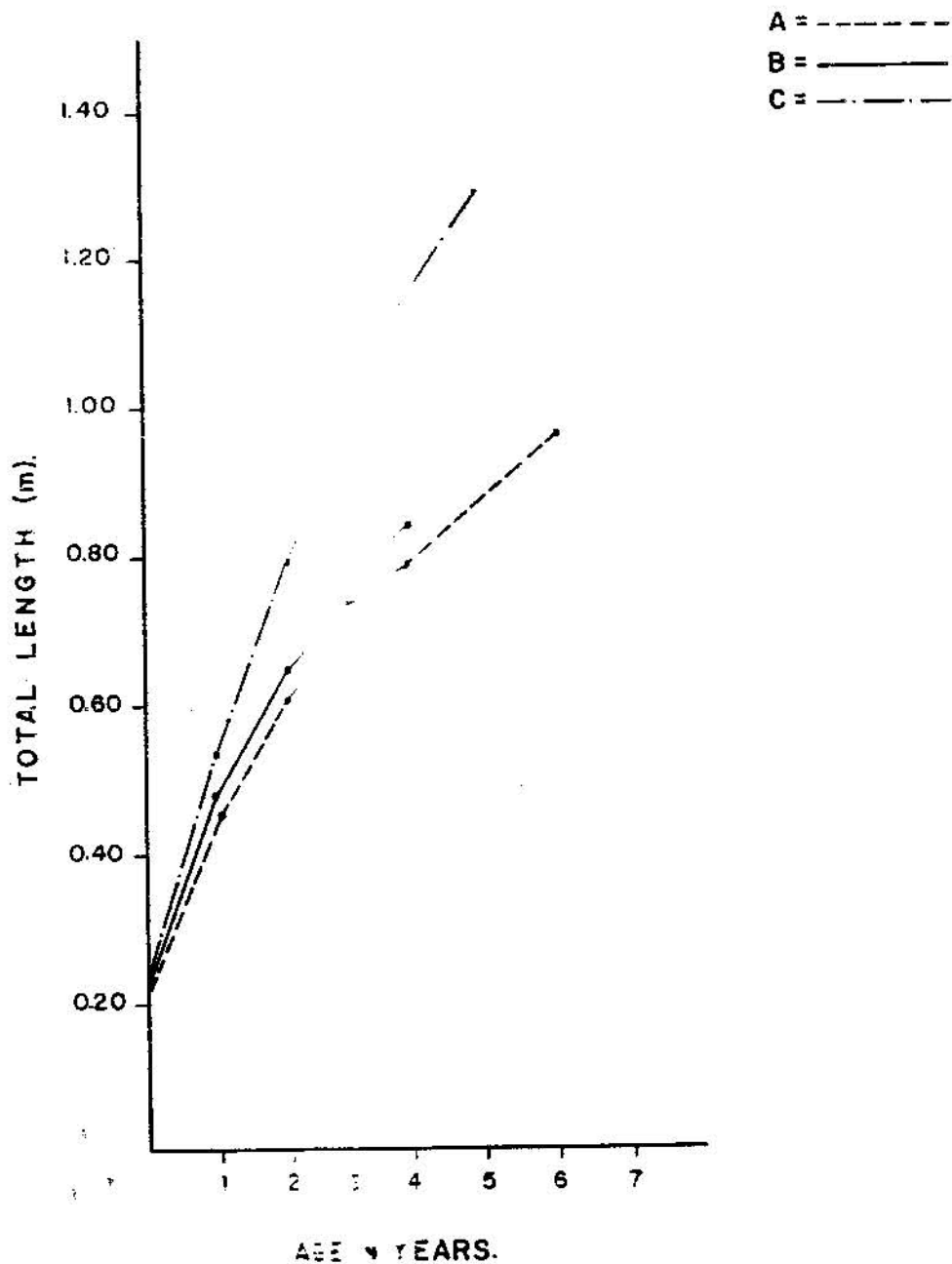


Figure 2. Growth rates of *Caiman crocodilus* in three populations - A: the Venezuelan Guayana (Gorzula 1978); B: the Venezuelan Llanos (Ayarzagüena 1980); Surinam (Ouboter and Nanhoe 1984).

size range grew some ten centimeters each. Ayarzagüena (1983) using size frequency histogram analyses produced a similar growth curve for caimans in the Venezuelan Llanos. Ouboter and Nanhoe (1984) using mark-recapture data for a population of spectacled caimans in Surinam, demonstrated significantly faster growth rates. Caimans were estimated to reach a total length of nearly 1.30 m in five years. They suggest that the differences in growth rate, compared to that of caimans in the Venezuelan Guayana, were due to food availability.

The three studies of growth rate in wild populations show growth rates of between 2.0 and 2.6 cm/month during the first year of life. These results are similar to the growth rates of hatchlings kept under captive conditions (Rivero-Blanco 1974, Rodriguez-Arvelo and Robinson 1986). However, Rivero-Blanco (1974) reported some exceptional growth rates for hatchlings that reached lengths of between 55 and 60 cm in ten months.

### FOOD AND FEEDING

Although over much of the range of *C. crocodilus* there have been no detailed studies of diet and feeding strategies, it may be said that this species diet, as in other crocodylians, is very varied and depend upon the size of the individuals, the season of the year and the specific characteristics of the habitat where they live. Hatchlings and juveniles feed mainly on invertebrates, insects (principally Coleoptera) being the major food items. Juveniles and adults also feed on snails, shrimps and crabs (Donoso-Barros 1965, Chirivi-Gallegos 1971, 1973; Alvarez del Toro 1974, Staton and Dixon 1975, Castroviejo et al. 1976, Gorzula 1978, Vanzolini and Gomes 1979, Seijas and Ramos 1980, Verdi et al. 1980, Medem 1981, Ouboter and Nanhoe 1984). In subadults and adults vertebrates progressively acquire more importance, including not only fishes and other aquatic vertebrates, but also terrestrial species (Medem 1981; Alvarez del Toro 1974). Cannibalism has also been reported (Staton and Dixon 1975; Schaller and Crawshaw 1982) and feeding on carrion (Staton and Dixon 1975).

The variations in diet that have been demonstrated by different studies, including those carried out in localities that are relatively near to each other (Castroviejo et al. 1976, Seijas and Ramos 1980, Ayarzagüena 1983), may be interpreted as being due to differences in faunal composition between localities, rather than due to the food preferences of specific populations of caimans. The importance of each food item, therefore, depends principally upon the relative abundance with which it occurs in the locality. For example, the commonest fish found in the stomach contents of caiman in a Venezuelan Llanos locality (Seijas and Ramos 1980), correspond precisely to the most abundant species that inhabit those waters (Ramos et al. 1981). Gorzula (1978) indicated the importance of anurans in the diet of caimans in the Venezuelan Guayana during the rainy season, when these anurans are abundant. Snails and crabs are important in caiman diets in areas where these invertebrates are very common (Alvarez del Toro 1974, Medem 1981, Ayarzagüena 1983).

Feeding strategies and feeding behavior have received little attention in the literature. Our observations and the literature suggest, as a broad generality, that the common caiman exploits shallow waters and the narrow littoral fringes of extensive bodies of water. Some types of feeding behavior have been described in the literature. Ayarzagüena (Ayarzagüena 1983) distinguished the following feeding strategies: lying in ambush for terrestrial prey, localization of prey by the sounds that the prey species produce; lying in wait for prey, principally fishes, that arrive by chance at the site where the caiman is. Schaller and Crawshaw (Schaller and Crawshaw 1982) describe additional strategies, among which there is one where the caimans "drive", using their body and tail, fish towards the shore or into shallow waters where capture is easier. Ambushing and actively

hunting of prey on dry land has also been observed (Medem 1981; Alvarez del Toro 1974; Ayarzagüena 1983).

## PREDATION

Numerous animals have been indicated as natural enemies of *C. crocodilus* (Table 1). The stages of life in which the spectacled caiman is most susceptible to predation are the eggs and the hatchlings. The golden tegu lizard, *Tupinambis nigropunctatus*, is implicated as the most serious predator of eggs in the Venezuelan Llanos (Rivero-Blanco 1974, Ayarzagüena 1983). Here and in other localities other real or potential predators of eggs include the crested caracara (*Polyborus plancus*), the crab-eating fox (*Cerdocyon thous*), and the raccoon (*Procyon* sp.; Leitao de Carvahlo 1951, Alvarez del Toro 1974, Rivero-Blanco 1974, Gorzula 1978, Ayarzagüena 1983).

Among the predators of hatchlings and juveniles are some species of fish (Alvarez del Toro 1974) and aquatic birds such as the maguary stork (*Euxenura maguari*), the American wood stork (*Mycteria americana*), the jabiru stork (*Jabiru mycteria*) and the white necked heron (*Ardea cocoi*). Captive animals have been observed to eat hatchling *C. crocodilus* (Gorzula 1978, Medem 1981), which suggests that many animals would be predators of hatchling caimans if given the opportunity.

Predators of adult caiman such as the Orinoco crocodile (*Crocodylus intermedius*), the American crocodile (*C. acutus*), the black caiman (*Melanosuchus niger*), and the jaguar (*Panthera onca*), have been exterminated over much of their former ranges. Perhaps the most important predator of large spectacled caiman (apart from man) in the present day is the anaconda (*Eunectes murinus*; Staton and Dixon 1975, Medem 1981, 1983; Ayarzagüena 1983, Lopez-Corcuera 1984). Medem (1981) cites the case of a 2.05 m long spectacled caiman found in the stomach content of an anaconda, and Lopez-Corcuera (1984) published an old photograph of a similar case.

## ACTIVITY AND BEHAVIOR

**Annual activity cycles** - In the Venezuelan Llanos (Staton and Dixon 1975, Ayarzagüena 1983), the Venezuelan Guayana (Gorzula 1978), Surinam (Ouboter and Nanhoe 1984), and the Brazilian Pantanal (Schaller and Crawshaw 1982) the population ethology of *C. crocodilus* is characterized by dry season concentrations and dispersal in the rainy season. It has been described above how reproduction is linked to this cycle. In some areas or in exceptionally dry years caiman may aestivate by burrowing into the mud of drying lagoons (Staton and Dixon 1975, Dixon and Sioni 1977, Medem 1981). In other areas the dry season concentrations of fish are a significant food resource that is exploited by the caimans, and the dry season is thus a period of activity and growth (Schaller and Crawshaw 1982, Ouboter and Nanhoe 1984). Staton and Dixon (1975) observed that in the Venezuelan Llanos dry season concentration commenced in January and ended in July, with peak concentrations in March. Caimans frequently returned to the same dry season refuge lagoon in consecutive years in the Brazilian Pantanal (Schaller and Crawshaw 1982), but in some instances males move to lagoons up to 9.4 km away. In general, females moved less than expected and subadults moved more than expected. In Surinam (Ouboter and Nanhoe 1984) dry season home ranges from 11 to 35 ha were observed in telemetry studies. Caimans in Surinam displaced up to 3 km in the rainy season. In the Venezuelan Guayana (Gorzula 1978) caimans migrate to temporary lagoons during the rainy season. These lagoons were used by the same caimans on successive years. Single night foraging migrations to small pools for frogs were also observed during the rainy

Table 1: Predators of the common caiman, *Caiman crocodilus*.

Scientific name	Common name	Life stage	Source
<b>PISCES</b>			
<i>Hoplias macrophthalmus</i> <i>Serrasalmus</i> sp.	Catfish Piranha	Hatchlings Hatchlings	Medem 1983. Ayarzagüena 1980; Blohm 1973.
<i>Lepidosteus tropius</i>		Hatchlings	Alvarez del Toro 1974.
<b>REPTILIA</b>			
<i>Tupinambis nigropunctatus</i>	Golden tegu	Eggs	Ayarzagüena 1980; Rivero-Blanco 1974; Staton and Dixon 1977.
<i>Drymarchon corais</i> <i>Eunectes murinus</i>	Indigo snake Anaconda	Hatchlings Adults	Alvarez del Toro 1974. Medem 1983; Ayarzagüena 1980; Staton and Dixon 1975; Lopez-Corcuera 1984.
<i>Chelus fimbriatus</i> <i>Phrynops geoffroanus</i> <i>Melanosuchus niger</i> <i>Crocodylus acutus</i> <i>Crocodylus intermedius</i>	Matamata Side-neck turtle Black caiman Caribbean crocodile Orinoco crocodile	Hatchlings Hatchlings Adults Adults Adults	Medem 1981. Medem 1981. Medem 1981. Medem 1981. Medem 1981.
<b>AVES</b>			
<i>Ardea cocoi</i> <i>Heterocnus mexicanus</i> <i>Nycticorax nycticorax</i>	White-necked heron Tiger-bittern Black-crowned night heron	Juveniles Hatchlings Hatchlings	Gorzula 1978. Alvarez del Toro 1974. Ayarzagüena 1980.
<i>Mycteria americana</i> <i>Euxenura maguari</i> <i>Jabiru mycteria</i>	American wood stork Maguari stork Jabiru stork	Juveniles Juveniles Juveniles	Gorzula 1978. Staton and Dixon 1977. Gorzula 1978; Romero 1983.
<i>Buteogallus unubitinga</i> <i>Polyborus plancus</i>	Great black hawk Crested caracara	Hatchlings Eggs	Ayarzagüena 1980. Ayarzagüena 1980; Rivero-Blanco 1974.
<b>MAMMALIA</b>			
<i>Cerdocyon thous</i>	Crab-eating fox	Hatchlings	Ayarzagüena 1980; Gorzula 1978;
<i>Procyon</i> spp.	Raccoon	Eggs	Leitao de Carvahlo 1951. Medem 1983; Alvarez del Toro 1974.
<i>Nasua nasua</i>	Coatimundi	Eggs	Crawshaw and Schaller: 1980. Leitao de Carvahlo 1951.
<i>Felis pardalis</i> <i>Panthera onca</i> <i>Sus scrofa</i> <i>Cebus</i> sp.	Ocelot Jaguar Domestic pig Capuchin monkey	Juveniles Adults Hatchlings Eggs	Alvarez del Toro 1974 Medem 1983. Gorzula 1978. Crawshaw and Schaller: 1980

season in this area. In addition to seasonal migrations "forced migrations" by caimans from areas under heavy hunting pressure by man have been registered in Colombia (Medem 1981).

**Diel activity cycles** - In the Venezuelan Guayana and Surinam, *C. crocodilus* is essentially a nocturnal species and basking during the day has been observed only infrequently (Gorzula 1978, Ouboter and Nanhoe 1984). However, in many other areas basking is a normal part of the daily activity pattern of this species (Alvarez del Toro 1974, Staton and Dixon 1975, Maness 1976, Marcellini 1979, Schaller and Crawshaw 1982, Ayarzagüena 1983, Seijas 1986). In the Venezuelan Llanos a bimodal cycle of basking has been reported by several authors. The two modes correspond with the morning rise and the late afternoon drop in air temperature. This behavior is assumed to be thermoregulatory. Maness (1976) observed early morning basking followed by a second period between 1700 and 1800 hours. Marcellini (cited in Medem 1981) recorded peak morning basking activity at 0900 hours followed by even greater basking activity from 1600 to 1800 hours. The proportion of caimans basking at any one time did not exceed 36% of the highest number counted during night surveys. Staton and Dixon (1975) showed that the marked bimodal basking activity observed in April had virtually ceased by May. Ayarzagüena (1983), however, observed that bimodal basking activity did occur during the wet season on sunny days during periods of several days without rain, but was absent on rainy or cloudy days. The basking behavior of individual animals has not been followed.

Gorzula (1978) recorded mean cloacal temperature of 27.27° C (sd = 0.88) for caimans in savanna lagoons in the Venezuelan Guayana. Staton and Dixon (1975) found that body temperature of caimans during the dry season in the Venezuelan Llanos ranged from 25.5 to 33.0° C (mean 30° C), with the highest temperatures occurring during late afternoon. Diefenbach (1975) showed that preferred body temperatures in laboratory experiments ranged from 28.5 to 36.2° C and were size dependent. Ouboter and Nanhoe (1984) demonstrated a similar phenomenon in wild caught caimans in Surinam.

Spectacled caiman often dive in response to a predator such as man and may stay under the water up to 80 min (Gorzula 1978). Such diving is accompanied by bradycardia (Gaunt and Gans 1969, Garrick and Saiff 1974).

**Social behavior** - *C. crocodilus* is a territorial species. The incidence of stub-tailed individuals increases with size in populations in the Venezuelan Llanos, the Venezuelan Guayana, and Surinam and is presumably the result of intraspecific fighting (Staton and Dixon 1975, Gorzula 1978, Ouboter and Nanhoe 1984). However in the Brazilian Amazon region there was no correlation between incidence of damage and the size class of the individuals (Magnusson 1985). Territorial behavior has been observed in the Venezuelan Llanos (Staton and Dixon 1975). The resident caiman displays to the intruder by tail-flagging. Infrequently the intruder may reply with a similar display. Usually such interactions result in the intruder fleeing or being chased out by the resident. Territoriality has been demonstrated indirectly by Gorzula (1978) who displaced marked caimans into similar lagoons that contained caimans. In 15 of 18 such trials caimans returned to the original lagoon where they were first captured. In three instances the caiman remained in the lagoon where they had been displaced. Homing up to 2.4 km was recorded. On one occasion a caiman was recaptured while homing, and it was concluded that the caiman had waited until the first rainy night to effect its return.

*C. crocodilus* has paired throat and cloacal musk glands. Caiman often release musk upon being captured (Gorzula 1978). Musk squeezed from the throat glands of a hatchling and mixed in the water elicited a strange swimming response in the mixed pod from which it had been captured (Gorzula 1986). Musk is not always present in these glands, but no correlation between or other factors has yet been described, nor has any function for musk yet been proposed.

Ayarzagüena (1983) produced an ethogram for *C. crocodilus*. He also listed three non-vocal and eight vocal sounds as part of the repertoire of auditory signals of this species. He considered the three non-vocal sounds (palmada de cabeza, geiser nasal and chasquido) to have territorial and threat functions. Six of the vocal sounds (bramido, ronquido, pujido grave, pujido agudo, pujido atenuado and aviso de peligro) were produced exclusively by adult caimans. The two remaining sounds were the "distress" and "contact" calls of hatchlings.

Territoriality and social hierarchy in the spectacled caiman are undoubtedly maintained by a very complex series of visual, auditory and chemical signals. However, most observations of caiman behavior have to date been either limited to special situations, such as daytime observation of dry season concentration of caimans, or have involved human/caiman interaction, such as capturing hatchlings and observing the response of adults. These brief insights into the behavior of the spectacled caiman are far from providing a comprehensive understanding of the complex intraspecific communication of a caiman community.

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