

STUDIES ON THE DRY SEASON BIOLOGY
OF *CAIMAN CROCODILUS CROCODILUS*
FROM THE VENEZUELAN LLANOS

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INTRODUCTION

The Llanos of Venezuela is a distinct biogeographical region lying circumjacent to the Orinoco River and extending north to the Andean and coastal mountain ranges of that country. The Lower Llanos consists of low-lying savannas and is characterized by pronounced seasonality in rainfall varying from 1000-1800 mm annually, most of which falls during a six month period. Temperature is relatively constant throughout the year and averages about 28°C (EWEL and MADRIZ, 1968). The flooding of 80-95% of the savannas during the wet season contrasts sharply with the dry season when only lagoons, rivers, their interlocking tributaries (*caños*), or man-made reservoirs retain water. Associated with this drastic change in humidity, vegetation is highly productive during the wet season but almost entirely dies or defoliates during the dry season (*e. g.*, see TAMAYO, 1961). The environmental factors affecting the local biota are extreme; organisms must be well adapted to meet these extremes.

Caiman crocodilus is widespread throughout northern South America and southern Central America. Although population have recently suffered greatly due to hide-hunting, this specie is common in the Venezuelan Llanos. The nesting strategy of Llanos caimans differs from that in other portions of its range (STATON and DIXON, in press), apparently an effect of the pronounced seasonal rainfall. The present paper details some ecological characteristics of this crocodilian during the intense dry season.

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STUDY SITES AND METHODS

Most observations reported herein were made at Hato Masaguaral, a cattle raising ranch and private fauna refuge located 50 km south of Calabozo, Estado de Guárico, Venezuela. This ranch has been described in detail by NEVILLE (1972) and the vegetation of the vicinity ca. 45 years ago was described by MYERS (1933). Briefly, the savannas are covered by a variety of grasses and are typified by the savanna palm, *Copernicia tectorum*. These palms, strangler figs (*Ficus* sp.), and several tree species of the Leguminosaceae constitute the bulk of woody vegetation in the area. There are a number of ponds and lagoons on the ranch, the largest being the Laguna de Los Guacimos; it occupies an area of approximately 13 hectares during the rainy season. Prior to 1962, the lagoon reduced to a small pond or entirely dried during the dry season, but since that time a pump has supplied it with subsoil water during the dry season and maintained a lagoonal surface area of about 3 hectares. During this study, however, the pump was non-functional during the latter half of the dry season, causing the lagoon to reduce to a surface area of about 1 hectare. This offered an opportunity to study the animals under conditions of diminishing water levels and crowding, as would be more natural than the relatively constant water volume normally maintained by the pump. Average annual rainfall at this site is about 1500 mm. The dry season begins with the decline of rainfall in November and extends through April or May; rainfall peaks in July/August.

Other observations were made on visits to three ranches in the state of Apure: Hato La Guanota, near San Fernando de Apure (see STATON and DIXON, in press); Hato Corozal, approximately 20 km NE Achaguas; and Hato El Porvenir, near Bruzual. Except for gallery forests near rivers and large lagoons, these areas lacked the woody vegetation characteristic of Hato Masaguaral and were predominantly grassy plains, flooded during the wet season and dry during the dry season. RAMIA (1958) described the savannas of this state. Rainfall at these sites is similar in distribution to that of Hato Masaguaral, and amounts are slightly higher.

Two hundred and forty-seven caimans were captured by noosing, grabbing, or lassoing. Soon after capture individuals were sexed according to BRAZAITIS (1968), measured and weighed. Juveniles were measured to the nearest 0.1 cm and others to the nearest 0.5 cm. Snout length was taken from the tip of the snout to the posterior edge of the cloacal opening. Specimens weighing less than 300 gm were weighed on an Ohaus triple beam

balance to the nearest 0.5 gm. Individuals up to 20 kg were weighed to the nearest 25 gm, and heavier caimans were weighed to the nearest kg.

Censuses were made at night with hand-held lights between 2000 and 2130 hrs. Due to the generally small size of the water bodies involved, the entire water surface and surrounding bank could be checked; we believe that such estimates revealed at least 90% of the individuals in a pond or lagoon. At the time of censusing, air and water temperatures varied from 23.7 to 28.6°, and 24.3 to 29.6°, respectively; relative humidity ranged from 58 to 90%; wind was rarely evident. These factors were not correlative with caiman activity. Counts were made at the Laguna de Los Guacimos on three successive nights around mid-month from January to May; from June to August, counts were made about every 4 days. Pond and lagoon surface areas were estimated geometrically. Mark-recapture methods were used on a number of hatchlings in an attempt to determine first-year normality.

Social interactions and basking behavior were studied from an arboreal blind about 100 m from the Laguna de Los Guacimos. To compliment qualitative observations, basking habits were quantified by making counts of basking individuals in a selected 200 m of the lagoon bank. Cloacal temperatures of caimans were taken with several thermometers, all of which agreed to within 1°C. Thermometers were left in caimans for 1-2 minutes; due to their massive bodies, rapid changes in cloacal temperature probably did not occur.

The stomachs of 13 hatchlings and 40 sub-adults/adults taken during the dry season were preserved in the field and later analyzed in the laboratory. The 13 juveniles were taken on a single night; others were taken throughout the dry season and can be separated into two groups according to their capture site: (1) at dry season lagoons, ponds, or *caños*, and (2) in migration from water site to water side (adults taken while traversing the savannas at night, sometimes kilometers from the nearest water; dead-on-road specimens were used). Volumetric analyses were based on ocular estimates of live body volumes. Indices of relative importance (IRI) were calculated in an attempt to balance volumetric and numerical data (PINKAS *et al.*, 1971).

RESULTS

Size, size classes, and sex ratios. *Caiman crocodilus* is a relatively small crocodylian with a maximum recorded length of 250 cm and an average

adult size of 150-200 cm (BRAZAITIS, 1973); Llanos populations conform with this generality. However, it is difficult to discuss Llanos caimans in terms of total length because numerous individuals lacked entire tails. Snout-vent length provides a better standard for size relationships and for data consideration. Snout-vent length and total length of individuals with entire tails are, however, linearly correlated (Fig. 1). In addition snout length is an indicator of both total and snout-vent length.

Weights of caimans recorded during the dry season range from 46.3 gm for a hatchling to 62.0 kg for an adult male measuring 125 cm SVL. Weight and length are related exponentially. A \log_{10} transformation of weight data yielded a curvilinear regression (Fig. 2A). However, a cubic root transformation of weight data permits a linear correlation (Fig. 2B). This seemingly results from the fact that weight is a function of volume, a 3-dimensional measurement.

The frequency of individuals in 10 cm size class intervals (SVL) is presented in Table 1. Seventy-four individuals were young-of-the-year (all in the 10-10.9 cm size class and one in the 20-29.9 cm size class). Most of these were encountered from late December through March, and young-of-the-year were seen in fewer numbers as the dry season progressed. The number of individuals in size classes representing the young of immediately preceding years was small compared to other sizes. Individuals in intermediate size classes (40-49.9 cm through 70-79.9 cm) were most abundant, comprising 50.6% of the sample. Larger animals, most of which were males, were fewer in number.

The sex ratio of all individuals 30 cm or greater in SVL did not deviate appreciably from a 1 : 1 ratio (Table 1). However, sex ratios of size classes 70-79.9 cm and 90-99.9 through 120-129.9 cm departed from the 1: 1 ratio significantly. Females comprised 73.1% of the 70-79.9 cm size class and all individuals exceeding 90 cm in SVL were males. This is undoubtedly related to the sexual dimorphism of greater size in adult males. Apparently, the 70-79.9 cm class contained the bulk of the adult female population, while larger size classes contained the adult male population.

Movements. Caimans concentrated in lagoons, ponds and *caños* as the dry season proceeded and the surrounding savannas dried. As the smaller of these dried, they too were abandoned. Ultimately, all remaining water sites contained some concentrations of caimans, although, as will be discussed later, not all caimans were at water sites.

Figure 3 portrays the movements of caimans to and from the Laguna de Los Guacimos during the first eight months of 1974. Concentrations in

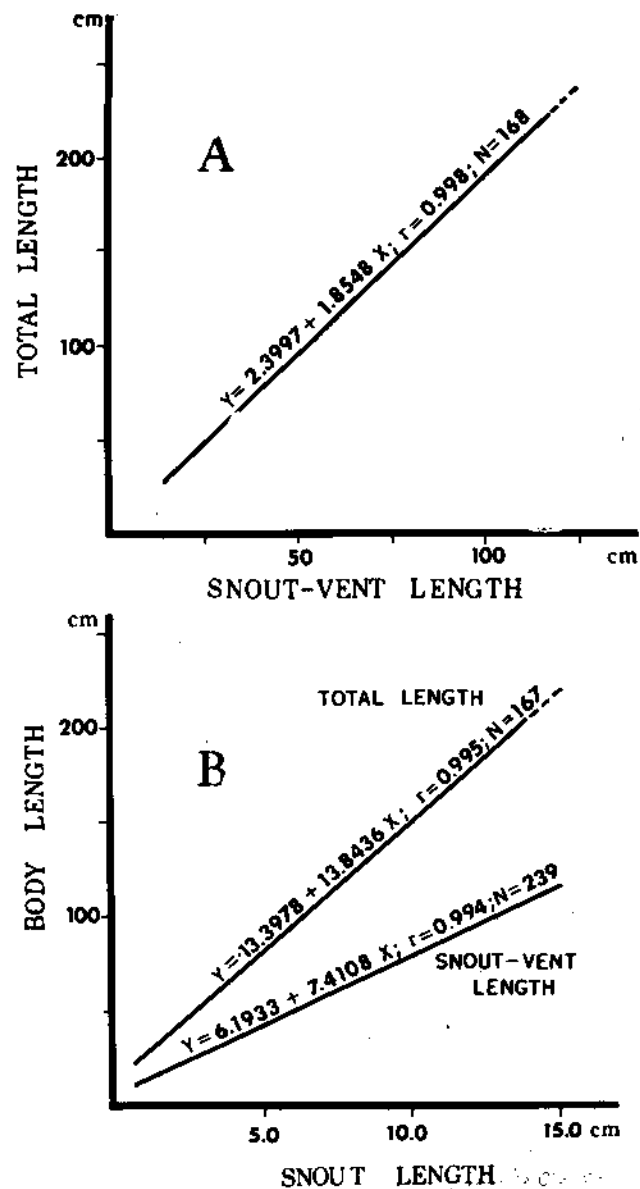


FIGURE 1

Relationships between total length, snout-vent length, and snout length for a sample of *Caiman crocodilus* from the Venezuelan Llanos during the dry season of 1974.

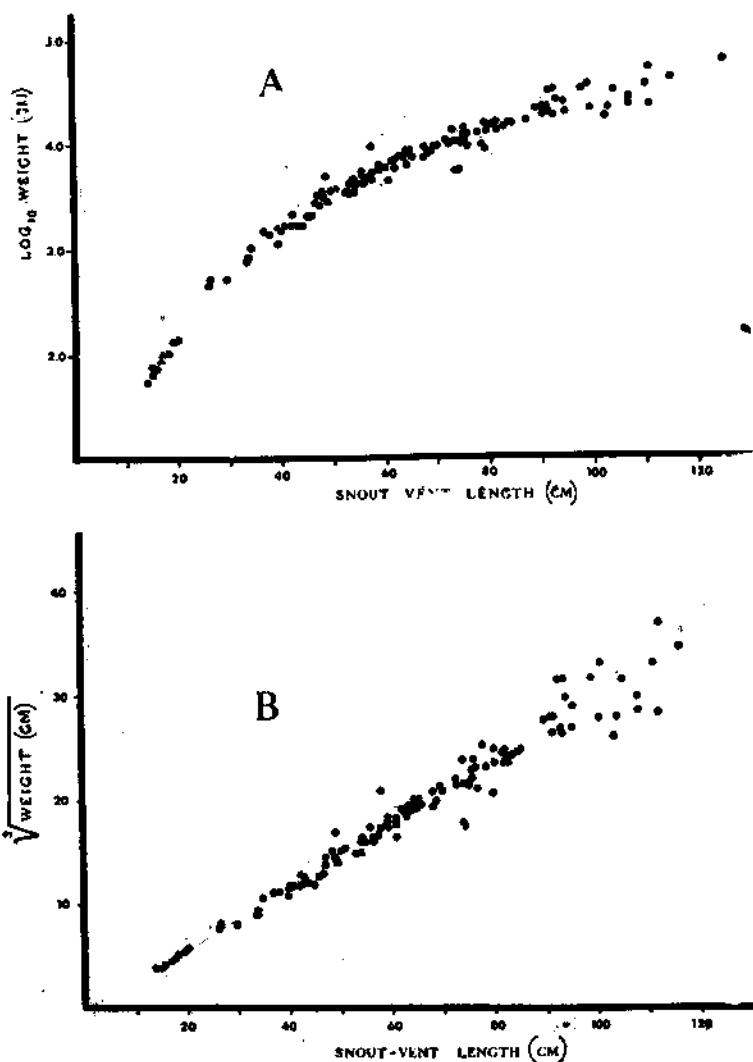


FIGURE 2

Relationship between weight and snout-vent length for a 1974 dry season sample of *Caiman crocodilus* from the Venezuelan Llanos according to logarithmic (A) and cubic root (B) transformations of weight data. Data were plotted so that there were a maximum of 20 observations per 10 cm increment in snout-vent length. Circle, 1 observation; square, 3 observations; triangle, 5 observations.

the lagoon peaked during March after which time *C. crocodilus* apparently began to abandon the lagoon as it continued to dry. Numbers continued to decrease until June when they began to rise again after a prolonged drought following early rains in May. This increase continued until July when caimans abandoned the lagoon in mass.

Social interactions. The result of the large congregations of caimans during the dry season is that they must co-exist in close quarters. This gregarious habit is associated with a social hierarchy based on size and in which territorial and courtship behavior are intertwined (STATON and DIXON, in press. Large caimans, presumably males, display by means of a tail display. Individuals nearby have several behavioral options open to them: (1) receptive females may approach him and courtship and copulation may follow; (2) caimans may leave the area or submerge without any action taken by the displayer; (3) the caimans may remain surfaced in the area, causing the displayer to approach the "intruder". The results of the latter (3) varied: (a) usually the intruder leaves the area, often chased by the displayer; (b) sometimes the two, usually when of equal size, tail display near each other, their bodies parallel; the smaller of the two leaves the area; or (c) if they display as in (b) and still remain stalemated, they briefly thrash out at each other, the smaller individuals then leaving. Following such interaction between displaying and intruding caimans, copulation was rarely seen and options (2) and (3) were far more common events. When there was a great disparity in sizes between individuals, they behaved as in (2); equal-sized individuals more often behaved as in (3).

Thrashing out amongst individuals at a standstill was a rare event, but intruding individuals were frequently chased. These occasions might result in the loss of a part of the intruder's tail or even cannibalism. As mentioned priorly, caimans often have a stub tail, and Fig. 4 delineates the occurrence of stub tails according to size class and sex. The incidence of stub tails increased with size, and females more commonly possessed stub tails when size classes are compared.

Thermoregulation. Thirty-five cloacal temperatures of caimans ranging from about 50 to 100 cm in SVL and taken under a variety of conditions during the dry season ranged from 25.3 to 33.0°C ($\bar{x} = 30.0^\circ\text{C}$). Table 2 segregates these temperatures according to conditions and time of day. Afternoon cloacal temperatures were higher than those taken in the early morning or night. In addition, cloacal temperatures were related to the activity of the caiman at the time of capture. Of special interest are the caimans hiding in the shade of thick vegetation during the various times of the day. The former

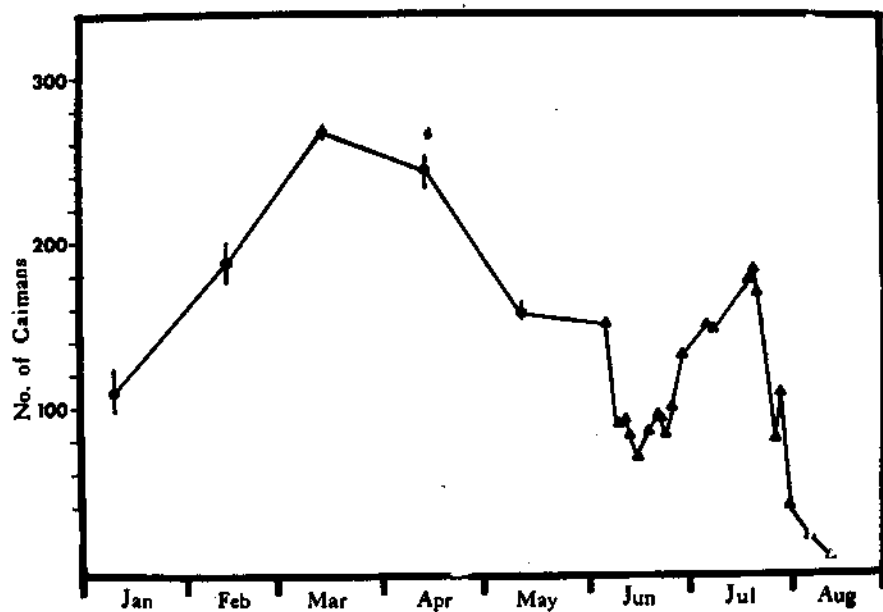


FIGURE 3

Results of *Caiman crocodilus* censuses at the Laguna de Los Guacimos, Hato Masagual, Guárico, during the 1974 dry season. Circles represent the mean of censuses on 3 consecutive nights (ranges indicated by vertical line). Triangles represent one-night counts.

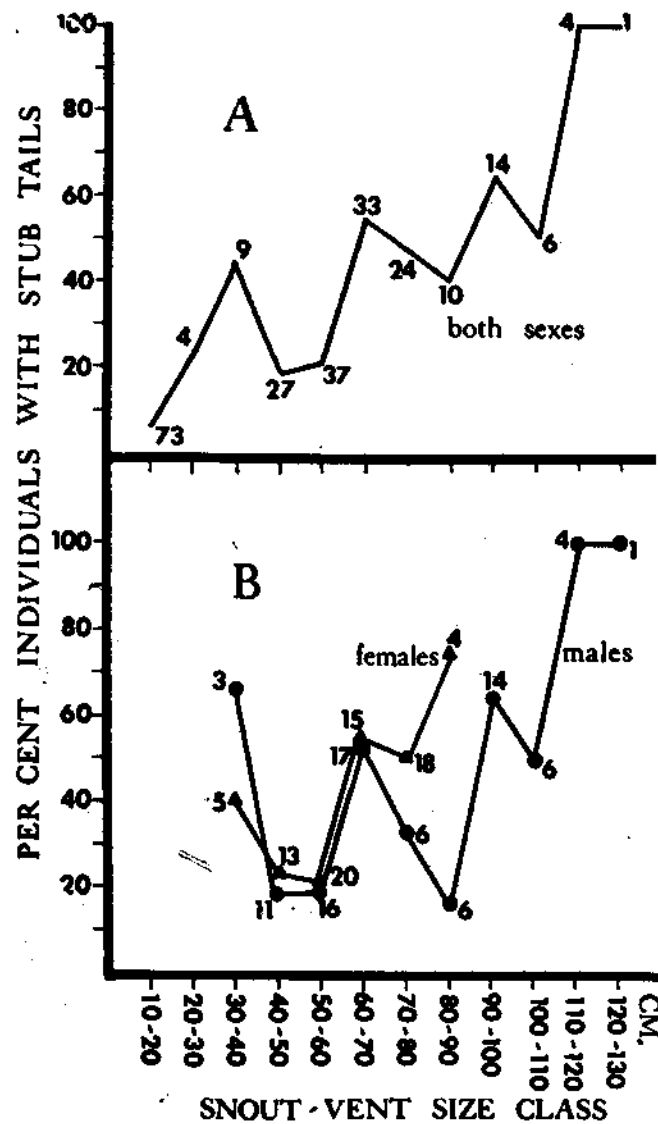


FIGURE 4

The occurrence of incomplete (stub) tails in a 1974 dry season sample of 247 *Caiman crocodilus* from the Venezuelan Llanos. Sexes are considered jointly (A) and separately (B).

were all found together near a drying *caño* containing shallow water. Shaded air temperature was 35.5°C, but the average cloacal temperature of the caimans, some buried in moist litter and debris, was 31.5°C. Caimans at sites of receding water also dug themselves into the remaining mud, often mixed with grass, for recorded periods of up to 24 hrs. In the case of two such individuals found close together at the same time, body temperatures were 30.8 and 31.3°C while nearby water was 36.9°C. The mud surface was heated to 35.0°C, but only 10 cm below, temperature was 31.5°C. Burrowing apparently kept the caimans relatively cool.

That caimans attempted to avoid overheating during the dry season is also reflected in their patterns of basking behavior. Figure 5 quantifies periodical observations of basking caimans at different times in the dry season. In April, when water depths still approached 1-1.5 m in portions of the lagoon near the basking sites, many caimans emerged to bask in the morning and late afternoon. Few individuals were out of the water during the midafternoon heat. As the dry season progressed and water levels decreased, fewer and fewer individuals emerged to bask, even during the early morning and late afternoon hours. By May, individuals emerged only during the late afternoon, and by early June, individuals remained in the water for long periods of time and surfaced irregularly. A few large displaying males were surfaced throughout the day, but most caimans were submerged. Other caimans left the lagoon as water levels decreased and hid in the shade of a forest about 200 m away; one remained in the same place for 2 weeks.

Stomach contents and feeding habits. Table 3 outlines the stomach contents of 13 hatchlings ranging in size from 13.6 to 20.0 cm SVL collected in grassy ponds ranging from 100-1000 m² in surface area. Over 90% of the identifiable food items were aquatic. Adult Hydrophilidae accounted for over 2/3 of the prey items, and insects of this family were obviously the preferred food choice amongst a wide variety of possibilities. Considering volume and number of individuals represented, the Hydrophilidae, Dytiscidae, Scarabidae, Belastomatidae, Carabidae, Naucoridae, and larval Odonata are the most abundant items. Indices of relative importance (IRI) based on these groups only (Table 3) again point to the Hydrophilidae as the predominant food item. Odonata larvae accounted for less than 2% of the IRI; other less abundant groups disregarded in the IRI computations would not appreciably affect the results.

Stomach contents of hatchlings were usually well masticated. This agrees with observations on captive hatchlings which masticated their food well before swallowing.

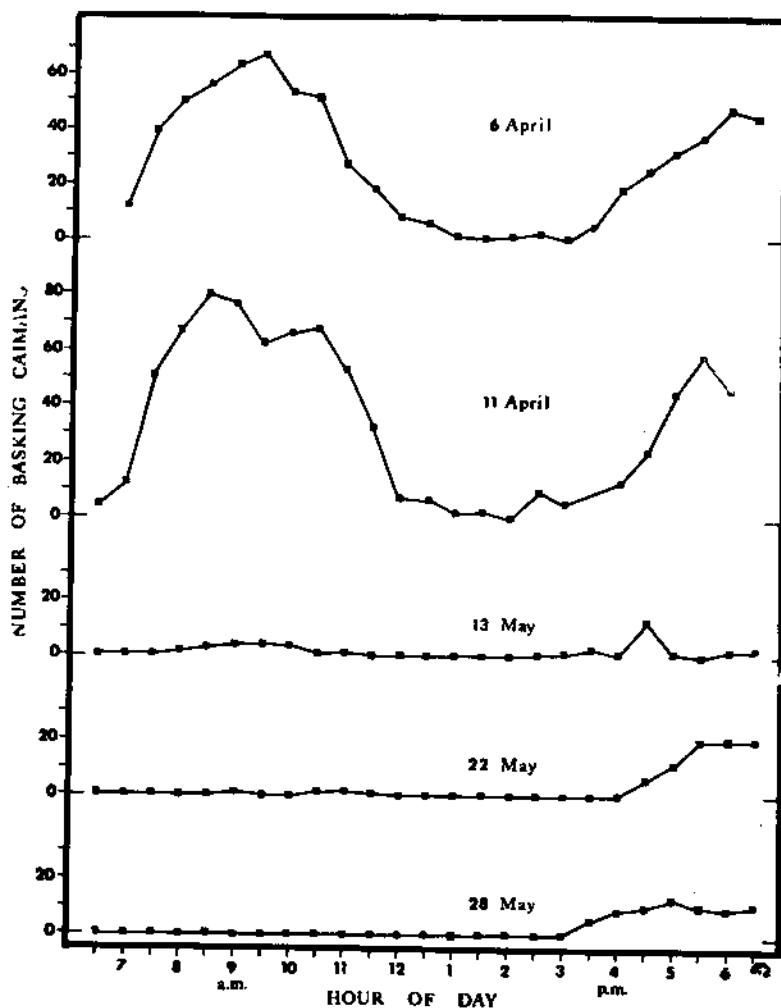


FIGURE 5

Numbers of *Caiman crocodilus* basking along a 200 m stretch of lagoon bank during the daylight hours at different times during the 1974 dry season at the Laguna de Los Guacimos, Hato Masaguaral, Guárico.

Five of 40 subadult/adult caimans ranging in size from 23.5 to 99.5 cm SVL lacked food in their stomachs. The stomach contents of the remaining 35 are given in Table 4. The armored catfish, *Hoplosternum* sp., was the dominant food item in the stomachs. However, this food item was ingested only by caiman at lagoons, *caños*, or ponds, as opposed to caimans who were in migration and contained a somewhat different prey selection. For example, in addition to the case of *Hoplosternum*, the occurrence of *Ciclasoma* sp., unidentified fish (3 species), Pomaceae snails, and dytiscid and belastomatid water beetles were also unimodal with respect to one of the groups. In addition, although there were an almost equal number of food items for each of the 2 groups, the migrating caimans ($n = 15$) contained representatives of 17 of the categories in Table 4 while lagoon-, caño-, or pond-dwelling caimans ($n = 20$) contained only 12.

Food items in the stomachs of subadult and adult caimans were not well masticated. *Hoplosternum* sp. specimens were usually bit into 2 or 3 pieces, but entire specimens of this and other fish were present; the head was usually severed. Entire elytra of water beetles were often found.

Not all food items are believed to have been taken as prey. *Caiman crocodilus* ate a dead Capybara (*Hydrochoerus hydrochoeris*) (Fig. 6) as well as a dead Red Howler Monkey (*Alouatta ursina*) introduced into the area of the caimans. The remains of armadillos (*Dasybus* sp.) reported in Table 1 are probably carrion food items as in both cases only the caudal and sacral vertebrae and hind leg bones were found. The single pectoral spine of the large catfish *Pseudoplatystoma* sp. in a stomach without any other remains also suggests carrion feeding.

Non-food items in caiman stomachs included bits of vegetation apparently accidentally ingested, parasitic nematodes, and gastroliths. The great majority of gastroliths were found in migrating caimans. This may be explained by the fact that dead-on-road specimens, herein often considered migrational, have a greater probability of ingesting stones near gravel-surfaced highways. Some gastroliths, however, appeared to be seeds. Gastroliths from adults/subadults weighed up to 3.9 g ($\bar{x} = 0.6$ g, $n = 41$, 32.5% frequency of occurrence); some were negligible in mass. Lengths or diameters of gastroliths ranged from 1.3 to 20.0 mm ($\bar{x} = 9.3$ mm). A maximum of 12 gastroliths occurred in a single stomach. There appeared to be no correlation between caiman size and the occurrence of gastroliths. The incidence of a single small gastrolith (0.7 mm diameter; negligible mass) in a hatchling 3 months old (Table 3) indicates that they are not limited to larger *C. crocodilus*.



FIGURE 6

A *Caiman crocodilus* feeding on a dead capybara (*Hydrochoerus hydrochoeris*) at night during the 1974 dry season at Ito Masaguaral, Guárico. Photo by Ralph Dessau.

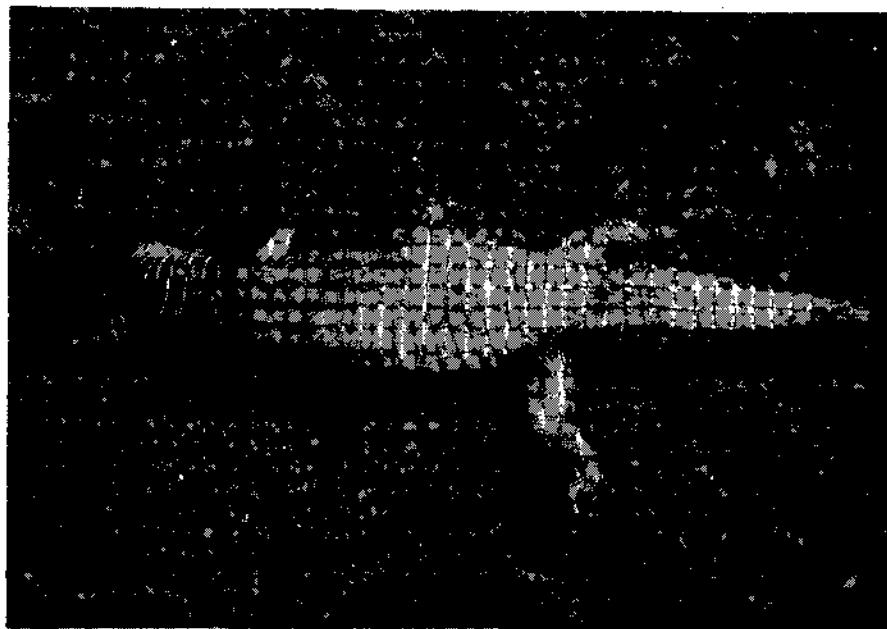


FIGURE 7

A cannibalized *Caiman crocodilus* taken from an adult male *C. crocodilus* during the dry season of 1974 at Ito Masaguaral, Guárico.

As the dry season progressed, food resources apparently diminished. During the latter half of the season, it was not uncommon to see caimans attempt to steal food from others. In one case, a large caiman, having caught a large fish, was chased for 20-30 m by several other large caimans; he eventually found escape on the bank 5 m from water where he fed.

Cannibalism may also be mentioned as a feeding habit of caimans as on two occasions (Fig. 7) it was witnessed on individuals 40-50 cm SVL. Frequent attempts at cannibalism are undoubtedly made in association with social interactions between large adults and subadults. Cannibalism is suspected as a main cause of the death of 35 marked-and-released hatchlings in a small crowded pond (see *Mortality*). Cannibalism appeared to be related to population density.

Mortality. At dry season aggregations, caimans are faced with drying, crowding, and a diminishing food supply. Their combined effects impinges on *C. crocodilus*, mainly on old weak individuals and on juveniles. Several old, emaciated adults who had apparently lost their hierarchical positions to younger males were in evidence in the Laguna de Los Guacimos. In addition, the carcass of an old male and the skull of another were found, and these deaths are probably attributable to starvation. Disease may have contributed to their deaths, but this was not the case for a 30 cm SVL subadult found dead and immediately dissected; it was emaciated and died of lack nutrition. Such caimans have been dying anyway, but the stress of the dry season probably hastened their deaths.

More drastically affected by the conditions brought on by the dry season are the young caimans, particularly hatchlings-of-the-year. Reduction of standing water sites placed young caimans, which remained at this water, in contact with actively-feeding large wading birds such as White Necked Herons, *Ardea cocoi*; Jabiru Storks, *Jabiru mycteria*; Wood Storks, *Mycteria americana*; Maguari Storks, *Euxenura galeata*; Common Egrets, *Casmerodius albus*; and Anhingas, *Anhinga anhinga*. Other potential predators such as various snakes, raccoons, and foxes were present at such water sites. An anaconda, *Eunectes murinus*, was found eating a subadult caiman ca. 40 cm SVL on one occasion. In addition, adult caimans may feed on hatchlings if they are not protected by the mother, which is the case when water recedes so much as to make it uninhabitable to the adult. Of 35 hatchlings captured, marked, and released in a windmill-supplied pond (Molino Quince, Table 5) during early February 1974, none were found during April. The pond was small enough so that the presence of at least a few young, if present, would have been detected, and caimans were present in unusually high numbers. Hatchlings were probably not dug into the mud as indicated by

the activity of caimans at this pond and of hatchlings at other similar ponds. A total of 78 hatchlings were seen in various ponds in February, but only 13 were seen in April. The likelihood of the hatchlings leaving the ponds is very small; they probably could not have survived the intense heat of the dry savannas surrounding the ponds for miles, and the adults had not left either. Mortality of these 78 hatchlings is estimated at 83.3%, using the total, or 100% using the marked-and-recaptured specimens. They were not being protected by their mothers as was found in other cases (STATON and DIXON, in press) and it seems highly probable that much the predation in this crowded pond was due to cannibalism.

Carrying Capacity. Although *C. crocodilus* is known to aestivate (MEDEM, 1958), and as mentioned previously herein, they may seek temporary refuge from the aridity and heat in the shade of gallery forests, the great majority of the population will be present at suitable water sites as long as they are available. The population in the Laguna de Los Guacimos peaked in March/April of 1974 (Fig. 3), even though water levels had diminished until that time (despite the water being supplied artificially). At that time, approximately 1/2 to 2/3 of the way through the dry season, caiman density presumably became great enough so as to force some from the lagoon in search of shade or other water. By mid-June, when the lagoon's water surface area was approximately 1/4 to 1/3 that of March levels, censuses of caimans had also been reduced to about 1/4 that of March numbers.

Thus, because of the predictability of climatic conditions, seasonal variation in standing water levels, and the correlated behavior of caimans, the location of the majority of the population of *C. crocodilus* at given times of the year can be predicted. In effect, most caimans are expected to be located at relatively permanent water bodies 1/2 to 2/3 of the way through the dry season. Prior to this, savannas still contained drying water where caimans might have remained before migrating to more permanent sites. After this time, caimans may have begun to aestivate or seek the shade of forests. Combined censuses of lagoons, ponds and all caiman-inhabited waters at this time then provide a reliable estimate of the average population density of *C. crocodilus*. Combined with estimates of standing water levels in the Llanos, the total population or carrying capacity of the Llanos environment for this species could be estimated.

Counts made of caimans, excluding hatchlings, in ponds, portions of caños, or lagoons ranging from 940 to 66,375 m² surface area during the month of April 1974 are shown in Tables 5. Densities ranged from 0.01 to 0.90 caimans/m² and averaged 0.013 caimans/m². The abnormality of the Molino Quince census is explained by the fact this pond is located near a

caño which contains caimans during the early dry season until it dries; those caimans migrate to Molino Quince as it is the only other water body nearby. Water depth may be an important factor influencing densities, but was not considered in this preliminary study.

DISCUSSION

The most extreme annual change in the Llanos environment is the transition from flooded to arid conditions. Caimans respond by dispersing over the flooded savannas during the wet season and migrating to permanent water bodies as the dry season progresses. Similarly, adult *Caiman crocodilus* from the savannas of San Juan de Arama, Colombia, are known to migrate to rivers with the progression of the dry season (MEDEM, 1958). It is unknown, however, whether these migrations to and from permanent water bodies are random or whether the home range of an individual includes particular areas for both the wet and dry season.

Correlated with seasonal migration of caimans is a change in diet. For example, of the 8 food items in Table 4, of which greater than 10 were found in a sample, only one (Hydrophilidae) is fairly evenly distributed in the stomachs of migrational and lagoon or *caño*-dwelling caimans. This difference seemingly results from different feeding opportunities for *C. crocodilus* according to their activity, and the greater variety of items in the diet of migrating caimans apparently results from a wider variety of opportunities encountered during migration. Whether caimans are cannibalistic or eat carrion during the wet season is unknown, but the opportunity and/or need for such feeding appears to be less during the wet season.

At the dry season lagoons, a size-regulated social hierarchy which systematizes their gregarious habits, possibly regulating population density, and which is intertwined with breeding behavior is established. Within this system, all individuals are treated equally by displaying males and the response of other individuals determines the interaction, if any, to follow. Other than greater size in males, sexual dimorphism is not developed and smaller males and females are treated equally by displaying males as demonstrated by the similar incidence of stub tails in both sexes; hence, behavior is the key to sex recognition. Observations herein agree with those of COLLIAS (1944): "The same display is used by males in threat and in courtship, as a rule, only in species... in which the sexes appear alike; in such cases one function of the display is to serve as a method of sex diagnosis, since a male will depart or respond similarly and a fight may ensue, while

a female will either depart or respond with a behavior which may eventually lead to mating." CECELIA BLOHM (pers. comm.) has observed captive unsexed juvenile caimans nibble on the chin of an adult believed to be a male, and we subsequently have made similar observations. Such nibbling appeared to have taken place preceding copulation under natural conditions (STATON and DIXON, in press); whether subordinate males may also nibble to avoid harm (as seen in captivity, perhaps) is not known. The role, if any, of two other behavioral displays, "jumping" and a "vertical tail display" (STATON and DIXON, in press) in this social system is not understood. MEDEM (1962) has stated that in the rainforests of Choco, Colombia, territoriality exists in *C. crocodilus* in that larger individuals were repeatedly seen in the same location and fought to defend their "territories." Whether a social hierarchy existed was not discussed by MEDEM. The need for a social hierarchy seemingly diminishes in a habitat of relatively stable water table, greater dispersal of individuals, and fewer opportunities for interactions. In the Llanos, however, the hierarchy may serve to regulate population density in crowded situations during the stressful dry season and help to insure the survival of the fittest individuals.

The age class structure of the population shows that the annual recruitment into the population is small, resulting from the high mortality of young caimans. This pattern may be characteristic of high density populations of most, if not all, crocodilian species.

The extent to which *C. crocodilus* burrows to avoid heat and drought is unclear. In this study, they were only observed to burrow in shallow water/soft mud situations and it is not known how long they remain in this condition. Discrete burrows were not found. MEDEM (1958) states that while adult caimans from the savannas of San Juan de Arama migrate to more permanent water bodies, young aestivated, but he does not indicate the period of duration. Communal above-water-level burrows serve as retreat from cold for young *Crocodilus niloticus*, and adults of this species also burrow under drought conditions, deepening drying ponds in the process (POOLEY, 1969). POOLEY suggests that the latter helps to maintain community diversity as has been described for *Alligator mississippiensis* in Florida (CRAIGHEAD, 1968; KUSHLAN, 1974). *Caiman crocodilus* probably benefits the Llanos very little in this manner as the intense six month dry season reduces water levels rapidly. As opposed to those observations on *Crocodylus niloticus* and *Alligator mississippiensis*, food was not in abundance for Llanos caimans, especially late in the drought.

Daily thermoregulation is achieved by periodic basking in the sun and cooling in the water. *Crocodylus niloticus* shows similar bimodal trends in

basking (COTT, 1961; MODHA, 1968) and CLOUDSLEY-THOMPSON (1964) has demonstrated a diurnal rhythm for this species which is correlative with the basking peaks and which is affected by environmental temperature. Under laboratory conditions, *Caiman crocodilus* enters water to cool after basking and reaching its "maximum voluntary tolerance" (DIEFENBACH, 1975). The shift from a bimodal basking cycle in April to no basking in June by Llanos *C. crocodilus* seemingly results from a diminishing water level and resulting lesser thermoregulatory options and/or needs rather than being an immediate temperature effect. Cloacal temperatures of *C. crocodilus* reported herein are lower than those reported by DIEFENBACH (1975) for laboratory specimens of this species.

NEILL (1971) has argued that insects do not constitute a major part of the diet of young crocodilians and that many insects found in the stomachs of crocodilians are a result of secondary ingestion. JACKSON *et al.* (1974) have demonstrated a faster digestion of would-be insectivorous vertebrates eaten by crocodilians, as opposed to the slower digesting insects, and hence supplied a basis for NEILL's belief. However, this argument is valid only to a certain degree. One would expect to find some fresh or entire portions of the vertebrates supposedly introducing the insects into the crocodilian stomachs secondarily. However, of 520 food items found in the stomachs of young *C. crocodilus*, only 4 were vertebrates. In contrast, hydrophilid water beetles were the most abundant food item, even when numerical frequency and volume are considered together (IRI, Table 3). Even if secondary ingestion is considered, it would only account for the presence of the terrestrial insects, if Neill's argument is followed. However, secondary ingestion need not only be the only method by which terrestrial insects may be consumed by caimans. During the dry season, conditions are extremely arid and terrestrial insects might be found at the margins of ponds and lagoons where young caimans might feed on them. Captive young *C. crocodilus* have been observed to feed freely on insects attracted to their outside enclosures by an overhanging lightbulb. The bulk of the diet of young *C. crocodilus*, at least in the Llanos is aquatic insects.

Caiman crocodilus, and perhaps all crocodilians to varying degrees, meet the criteria outlined by PIANKA (1970) characteristic of K-selected species. The coincidence with criteria concerning population size and climate - "Fairly constant in time, equilibrium; at or near carrying capacity of the environment..." and "...predictable...", respectively, have allowed an evaluation of the carrying capacity of this species in the Llanos. The figures, although variable, may be combined with standing water estimates to give an average estimate of population size and, combined with size and weight

estimates (Fig. 1), may be useful in determining standing crop of *Caiman crocodilus*; this species, at least in Amazonian aquatic communities (along with three other crocodilian species), is an important link in the nutrient chain. (FITTKAU, 1970).

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SUMMARY

In reaction to cyclic flooding and drying of savannas, *C. crocodilus* periodically disperses over flooded savannas and migrates to more permanent water bodies during the dry season. During the course of the migration, diet is slightly altered, probably as a result of different opportunities for feeding. The main food item for adult and subadult *C. crocodilus* at dry season lagoons is the armored catfish, *Hoplosternon* sp.; carrion is also eaten and cannibalism was observed. Hatchlings feed primarily on hydrophilid water beetles. At the lagoons, a social hierarchy based on size is established. The social hierarchy may help to regulate density and is intertwined with breeding

behavior. Age class structure data indicate that annual recruitment into the population is low. Adult males are larger than females and correlations between weight, total length, snout-vent length, and snout length are demonstrated. Thermoregulation during the dry season appears to be directed toward avoidance of overheating; this is achieved by remaining in water for seasonally varying periods of time throughout the day, burrowing into mud, and hiding in the shade of gallery forest floors. Recorded body (cloacal) temperatures vary between 25.3° and 33.0°C. The predictability of the environment and of *C. crocodilus*'s response to it has allowed a method for determining average population density for this species in the Llanos; this data may be used to determine the carrying capacity of the Llanos environment for this species.

RESUMEN

Estudios previos indicaron que la estrategia de nidificación de *C. crocodilus* en los Llanos de Venezuela es diferente de la reportada para otros lugares donde este animal existe. Esta diferencia es, aparentemente, resultado de las pronunciadas lluvias estacionales de los Llanos. El presente estudio detalla algunas características ecológicas de la baba durante el intenso período seco. Se presentan datos sobre tamaño (longitud de la cloaca al hocico, longitud total, longitud del hocico y peso) del *C. crocodilus* y se muestran correlaciones entre éstos. La estructura poblacional en relación al tamaño indica que la mayoría de los individuos (50,6%) miden entre 40 y 80 centímetros de longitud (cloaca al hocico). La proporción de machos y hembras en la población entera es aproximadamente 1 : 1, aún cuando las hembras constituyeron el 73,1% de la clase de 70-79.9 centímetros (longitud cloaca al hocico) y todos los individuos mayores de 90 centímetros (longitud de cloaca al hocico) eran machos. Esto se debe al dimorfismo sexual de tamaño adulto en esta especie. Los datos indicaron que el reclutamiento anual dentro de la población subadulta es mínimo, aparentemente como resultado de la alta mortalidad en individuos pequeños.

La drástica variación anual de precipitación y de los niveles de agua resultan en migraciones estacionales entre las sabanas inundadas durante el período lluvioso y aguas más permanentes durante el período de sequía.

En las aguas permanentes se encuentran agrupaciones de babas y se establece una jerarquía social basada en el tamaño del animal. Esta jerarquía social se entrelaza con el comportamiento sexual y sistematiza los hábitos gregarios de la baba, aparentemente regulando la densidad. Son presentados datos sobre ocho agrupaciones (durante sequía) y se demuestra que son

relativamente constantes. Se sugiere combinar estos datos con los de estructura poblacional en relación al tamaño y peso para hacer una estimación de la capacidad de carga.

Las temperaturas cloacales variaron entre 25,3 y 33,0°C. El comportamiento de asolearse es cuantificado y demuestra que cuando el agua es relativamente abundante las babas se asolean frecuentemente durante la mañana y las últimas horas de la tarde. Pero, cuando los niveles de agua bajan, lo que sucede cuando una laguna o caño se seca, las babas se asolean menos y, cuando hay sol pueden hasta permanecer en el agua durante todo el día. Algunas babas abandonan las lagunas para esconderse a la sombra del bosque mientras que otras se entierran en el barro.

La dieta de *C. crocodilus* pequeño la constituyen principalmente insectos acuáticos, especialmente hydrophilidos. Subadulto y adulto come una dieta de pescados (*Hoplosternum* sp.), aves, ratones, ranas e insectos (principalmente hydrophilidos). La dieta de las babas en migración es más variada que la de las que están en aguas más permanentes.

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TABLE 1

Size class diversity and sex ratios of 247 *Caiman crocodilus* captured during the dry season of 1973-74 in the Venezuelan Llanos.

| Size Class (cm) (SVL) | No. of Individuals | Sex | | |
|--------------------------|-----------------------|--------|------|---------|
| | | female | male | unsexed |
| 10-19.9 | 73 | 0 | 0 | 73* |
| 20-29.9 | 4 | 0 | 0 | 4* |
| 30-39.9 | 9 | 5 | 3 | 1** |
| 40-49.9 | 27 | 13 | 11 | 3** |
| 50-59.9 | 38 | 21 | 16 | 1** |
| 60-69.9 | 34 | 16 | 17 | 1** |
| 70-79.9 | 26 | 19 | 7 | 0 |
| 80-89.9 | 10 | 4 | 6 | 0 |
| 90-99.9 | 15 | 0 | 15 | 0 |
| 100-109.9 | 6 | 0 | 6 | 0 |
| 110-119.9 | 4 | 0 | 4 | 0 |
| 120-129.9 | 1 | 0 | 1 | 0 |
| Total | 247 | 78 | 86 | 83 |

* Sex not determinable.
** Data omitted.

TABLE 2

Mean environmental temperatures and average cloacal temperatures of 35 *Caiman crocodilus* taken under a variety of conditions during the dry season in the Venezuelan. Temperatures are in degrees Centigrade. (clo = cloacal; wat = water; sub = substrate).

| Hour of day | in shallow water | | | in shade | | | walking or on bank | | | dug in mud or grass | | | |
|-------------|------------------|------|------|-------------|------|-----|--------------------|------|------|---------------------|-------------------|-------------------|---------------------------|
| | clo | air | wat | clo | air | wat | clo | air | wat | clo | air | wat | sub ¹ |
| 0600-1200 | — | — | — | — | — | — | — | — | — | 27.0 | ? | — | 27.0 |
| 1200-1800 | 28.5 (2) | 25.0 | 27.5 | 31.5 (6) | 35.0 | ? | — | — | — | 30.7 (3) | 32.9 ² | 36.9 ² | 35.0 ² 31.5 |
| 1800-2400 | 28.2 (15) | 34.9 | 26.5 | — | — | — | 28.7 (4) | 25.7 | 26.4 | 27.1 (4) | 25.6 | 25.3 | — |

1. upper temperature = surface temperature; lower = 10 cm below surface.

2. based on two observations.

TABLE 3

Stomach contents of 13 hatchling *Caiman crocodilus* captured on 9 March 1974 at Hato La Guanota, near San Fernando de Apure in grassy ponds ranging from 100 to 1000m² in surface area.

| Item | Total No. Items | % Total No. Items | % Frequency of Occurrence | IRI |
|---------------------------------|-----------------|-------------------|---------------------------|--------|
| Gastroliths | — | — | 7.6 | — |
| Vegetation | — | — | 46.2 | — |
| Nematodes | — | — | 46.2 | — |
| Unidentified Animal Matter | — | — | 30.7 | — |
| <i>Identifiable Food Items:</i> | | | | |
| Arthropoda: Insecta | | | | |
| Unidentified | 2 | 0.4 | 15.4 | — |
| Odonata | | | | |
| Caenagrionidae adults | 1 | 0.2 | 7.6 | — |
| Caenagrionidae larvae | 1 | 0.2 | 7.6 | — |
| Libellulidae larvae | 10 | 1.9 | 38.5 | 207.9 |
| Orthoptera | | | | |
| Gryllidae adults | 2 | 0.4 | 15.4 | — |
| Gryllidae larvae | 1 | 0.2 | 7.6 | — |
| Hemiptera | | | | |
| Veliidae | 7 | 1.3 | 23.1 | — |
| Belastomatidae | 17 | 3.3 | 61.5 | 1143.9 |
| Gerridae | 1 | 0.2 | 7.6 | — |
| Naucoridae | 16 | 3.1 | 69.2 | 276.8 |
| Corixidae | 4 | 0.8 | 30.8 | — |

TABLE 3 CON'D

| Item | Total No. Items | % Total No. Items | % Frequency of Occurrence | IRI |
|-----------------------------|-----------------|-------------------|---------------------------|---------|
| Coleoptera | | | | |
| Unidentified | 1 | 0.2 | 7.6 | — |
| Scarabaeidae | 24 | 4.6 | 69.2 | 1439.4 |
| Carabidae | 15 | 2.8 | 53.8 | 451.9 |
| Bostrichidae | 1 | 0.2 | 7.6 | — |
| Dytiscidae | 33 | 6.4 | 84.6 | 2512.6 |
| Gyrinidae | 1 | 0.2 | 7.6 | — |
| Hydrophilidae adults | 362 | 69.6 | 100.0 | 11310.0 |
| Hydrophilidae larvae | 3 | 0.6 | 23.1 | — |
| Diptera | | | | |
| Nematocera | 1 | 0.2 | 7.6 | — |
| Cyclorrhapha: | 1 | 0.2 | 7.6 | — |
| Lepidoptera | 1 | 0.2 | 7.6 | — |
| Platyhelminthes | | | | |
| Turbellaria | 1 | 0.2 | 7.6 | — |
| Annelidae | | | | |
| Hirudinea | 1 | 0.2 | 7.6 | — |
| Mollusca | | | | |
| Gastropoda | 9 | 1.7 | 38.5 | — |
| Chordata: Vertebrata | | | | |
| Pisces | 3 | 0.6 | 15.4 | — |
| Amphibia | | | | |
| Hylidae | 1 | 0.2 | 7.6 | — |
| Total: | 520 | | | |

TABLE 4

Stomach contents of 40 subadult and adult *Caiman crocodilus* collected throughout the dry season in the Venezuelan Llanos.

| Item | No. of Items* | | | % Total No. items | % Frequency of Occurrence | IRI |
|--|---------------|----|-------|-------------------|---------------------------|--------|
| | M | L | total | | | |
| Gastroliths | 42 | 10 | 52 | — | 32.5 | — |
| Vegetation | — | — | — | — | 12.5 | — |
| Nematodes | — | — | — | — | 20.0 | — |
| <i>Empty stomachs lacking food items</i> | 3 | 2 | 5 | — | 12.5 | — |
| <i>Food items in 35 stomachs:</i> | | | | | | |
| Pisces | | | | | | |
| Cypriniformes | | | | | | |
| <i>Hoplosternum</i> sp. | 0 | 30 | 30 | 14.9 | 30.0 | 1783.6 |
| <i>Pseudoplatystoma</i> sp. | 1 | 0 | 1 | 0.5 | 2.5 | 12.2 |
| <i>Hoplias</i> sp. | 0 | 1 | 1 | 0.5 | 2.5 | 28.1 |
| Unidentified | 0 | 2 | 2 | 1.0 | 7.5 | 5.8 |
| Perciformes | | | | | | |
| <i>Cichlasoma</i> sp. | 26 | 0 | 26 | 12.9 | 2.5 | 55.4 |
| Synbranchiformes | | | | | | |
| <i>Synbranchus</i> sp. | 1 | 3 | 4 | 2.0 | 5.3 | 43.2 |
| Unidentified | 11 | 2 | 13 | 6.5 | 7.5 | 104.9 |
| Amphibia | | | | | | |
| Anura | | | | | | |
| <i>Leptodactylus</i> sp. | 2 | 0 | 2 | 1.0 | 2.5 | 10.2 |

TABLE 4 CON'D.

| Item | No. of Items* | | | % Total No. items | % Occurrence % Frequency | IRI |
|-----------------------------|---------------|-----|-------|----------------------|-----------------------------|--------|
| | M | L | total | | | |
| Aves | | | | | | |
| Tyrannidae | | | | | | |
| <i>Todirostrum</i> sp. | 1 | 0 | 1 | 0.5 | 2.5 | 3.5 |
| Unidentified | 1 | 1 | 2 | 1.0 | 5.0 | 14.3 |
| Mammalia | | | | | | |
| Edentata | | | | | | |
| <i>Dasypus</i> sp. | 2 | 0 | 2 | 1.0 | 5.0 | 17.7 |
| Rodentia | | | | | | |
| Heteromyidae | 1 | 1 | 2 | 1.0 | 5.0 | 30.2 |
| Mollusca | | | | | | |
| Gastropoda | | | | | | |
| Pilidae (<i>Pomacea</i> ?) | 22 | 0 | 22 | 10.9 | 17.5 | 280.0 |
| Arthropoda | | | | | | |
| Arachnida | 1 | 0 | 1 | 0.5 | 2.5 | 1.7 |
| Crustacea | | | | | | |
| Decapoda | 3 | 1 | 4 | 2.0 | 10.0 | 47.9 |
| Insecta | | | | | | |
| Hydrophilidae | 22 | 18 | 40 | 19.9 | 37.5 | 1171.2 |
| Dytiscidae | 1 | 12 | 13 | 6.5 | 10.0 | 92.3 |
| Belastomatidae | 2 | 27 | 29 | 14.4 | 20.0 | 460.3 |
| Unidentified | 2 | 3 | 5 | 2.5 | 2.5 | 9.3 |
| Unidentified | 1 | 0 | 1 | 0.5 | 2.5 | 1.7 |
| Total: | 100 | 101 | 201 | | | |

* Sample divided into caimans at dry season lagoons, *caños*, or ponds (L) and those in migration (M).

TABLE 5

April 1974 densities of *Caiman crocodilus* in water bodies of different sizes in the Venezuelan Llanos. Censuses included all individuals except hatchlings-of-the-year.

| Locality | No. of Caimans | Area (m ²) | Caimans/m ² |
|------------------------|-------------------|------------------------|------------------------|
| Hato Masaguaral | | | |
| Laguna de Los Guacimos | 253 | 32,000 | 0.008 |
| "Pond A" | 38 | 3,690 | 0.010 |
| Caño Caracol | 52 | 3,460 | 0.015 |
| Hato El Porvenir | | | |
| Mineguitas | 22 | 940 | 0.023 |
| Molino Quince | 110 | 1,230 | 0.089 |
| Caño Agua Verde | 45 | 6,480 | 0.007 |
| "Pond Z" | 18 | 1,034 | 0.017 |
| Laguna La Salera | 1239 | 66,375 | 0.018 |