Breeding Biology of the Spectacled Caiman, *Caiman Crocodilus Crocodilus,* in the Venezuelan Llanos

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Contents

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Abstract

The breeding biology of *Caiman crocodilus* in the Venezuelan Llanos was studied during the latter portion of the 1973 breeding season and the beginning of the 1974 season.

Courtship and copulation took place during the latter portion of the dry season and early wet season when caimans were congregated at permanent water sites. Two behavioral displays which may be involved in courtship (jumping and vertical tail display) and the courtship display of males (tail display) are described. Copulation (two observations) took place after the beginning of heavy rains in May. A drought followed these heavy rains, and the position of individuals during copulation (one observation) was altered, apparently to compensate for lower water levels.

Minimum size at reproduction for females was approximately 130 cm. Nesting occurred from mid-August through late October. Two nest types, based on construction material and sites, were encountered: nests constructed entirely of grass in open grassland, and nests of leaves, twigs, and soil in more forested situations. Nest construction, which involved formation of a vegetative mound, digging a nest chamber, egg deposition, and covering of eggs, lasted from 2 to 7 days. The nest's position relative to water was important in determining its fate. Ants were found in 56% of the nests examined.

Clutch size ranged from 17–38 eggs ($\bar{x}$ = 28.6 ± 0.91 SE). Length, width, and weight measurements of over 240 eggs averaged 63.8 mm, 40.7 mm, and 59.9 g, respectively; clutch averages of these parameters were linearly related. The average egg weight (per clutch) was greater during the beginning of the nesting season. Eggs changed little in length or width during artificial incubation; weight changes were dependent on humidity of the nests. Egg weight loss was an important factor in hatching success.

Nest care included repair of the nest after predation, remaining by the nest for long periods of time, and in a few instances, challenging the investigators. For one nest visited 34 times at night, the adult female was in the area (usually within 3 m) of the nest on 29 (85%) occasions. Prenatal mortality (nest predation) was established at 84.2%; the major predator was the lizard *Tupinambis tequixin.*

Internal nest temperatures fluctuated during a 24-h cycle and hourly temperature averages varied from 28–32 C. Grass nests were slightly warmer than nests of leaves, twigs, and dirt. Internal nest relative humidity was nearly identical for nests of different construction material, showed little variation, and ranged from 85–95%.

Linear regression analysis of total lengths of embryos sampled at different intervals before hatching yielded an estimate of 73 days as the incubation period.

Natural hatching occurred from late October through December and was witnessed once. The adult female, stimulated by vocalizations of the young, helped them escape the nest. Hatchlings from eggs incubated artificially averaged 21.49 cm total length, 11.29 cm in snout-vent length, 0.73 cm in snouth length, and 41.5 g in weight. Linear regression analyses of clutch averages of these parameters, with the exception of snout length vs. weight, were significant. Postnatal care of the young of the adult female varied and appeared to be related to the availability of water during the dry season (which followed hatching).

Introduction

The few remaining crocodilians are the last of a relatively homogenous group of reptiles which has remained little changed since the mid-Triassic (Sill 1968). Because of their affinities with the archosaurian ancestors of birds, studies of the living members may offer insight into the paleoecology of Mesozoic times and into the evolution of amniotic vertebrates in general. Despite these items of interest to the evolutionary biologist, the majority of these animals possess another character of greater value to man—their skins, which are used for various purposes by leathergood industries. Hide-hunting in areas accessible to man has contributed to the depletion of natural populations in both size and numbers of animals. Habitat destruction has amplified the effects, and almost all species are now endangered (Bustard 1971a; Cott 1971a).

Brazaitis (1968) referred to some of the evergrowing literature emphasizing the need of conservation measures for crocodilians. To coordinate such measures, the International Union for the Conservation of Nature, the New York Zoological Society, and the Natal Parks (Game and Fish Preservations Board) have sponsored recent meetings of crocodilian specialists. Artificial hatching and rearing of crocodilians (for at least part of their lives) has emerged as an answer to both the commercial demand for the animals and the need of individuals for restocking programs (Chabreck 1971; Honnegger 1971; Yangprapakorn et al. 1971; Joanen and McNease 1974). Adequate information of the life history and ecology of a species is prerequisite to efficient restocking or commercial rearing programs. With this goal in mind, Tomas Blohm and Pedro Trebau, Venezuelan conservation leaders, contacted the authors to study Llanos populations of *Caiman c. crocodilus*. Information obtained on their breeding ecology is reported herein.

Chirivi-Gallego (1973) adequately summarized the literature on reproduction in the various subspecies of *C. crocodilus* and exemplified the anecdotal nature of much of the available information. Alvarez del Toro (1974) has recently compiled years of observations on *Caiman crocodilus chiapasius* and other Mexican crocodilians. Rivero Blanco (1974) performed introductory studies on the life history of a Llanos population of this species, especially those aspects pertaining to egg production. The results of Rivero Blanco's study were generally unavailable to the authors during the field period of the present study, and the results of his and our studies represent quantitative information on the breeding biology of Llanos populations of the species.

Materials and Methods

Breeding behavior was observed with binoculars from a tree-borne blind about 100 m from the lagoon in which caimans were breeding. Larger animals were assumed to be males and measurements on numerous adults substantiate this assumption.

Nests were visited as often as possible at prescribed times. On the first visit to a nest, an attempt was made to record the following information: size of nest (length, width, height), location of the nest relative to water and vegetation, presence of ants in the nest, composition of nest material, and clutch size. On the first and subsequent visits, the following additional information was noted: presence of the adult (female) at the nest, air temperature 1 cm above the nest, nest temperatures 1-2 cm beneath the surface and at a depth of approximately 15 cm within the nest, and evidence of predation. Temperatures were recorded with several thermometers whose total variation did not exceed 1 C. Relative humidity was recorded with a Dial Hygrometer probe.

Varying numbers of eggs, usually 10 or more, were removed from the nests and returned to headquarters where they were measured with vernier callipers (length and width) and weighed with a triple beam balance. Additional data on length and width of the eggs were occasionally taken at the nest. Eggs were marked and incubated in a variety of artificial nests. Temperatures within these nests were checked regularly and humidities recorded occasionally. Snout-vent length, total length, and snout length (spectacle to nasal opening) of hatchlings were measured to the nearest 0.5 mm; they were weighed to the nearest 0.1 g. Captured adults were measured to the nearest 0.5 cm.

The Venezuelan Llanos

This tropical savanna region consists of flat lowlands extending from just west of the Amacuro Delta of the Rio Orinoco and south of the coastal and Venezuelan Andes Sierras. The entire area has a 6-month rainy season/dry season, with rainfall varying between 1.0 and 1.8 m annually; year-round average daily temperatures range between 26-30 C (Ewel and Madriz 1968). Fifty-year (1921-1971) monthly rainfall averages for San Fernando de Apure and 19-year (1952-1971) monthly rainfall averages for Corozo Pando, representative of the sites that we studied, are presented in Fig. 1. In most areas, 80-85% of the savannas flood during the rainy season (Fig. 2 A, B), which extends roughly from May to November in our study areas. In contrast, only large lagoons, rivers, *caños*, and man-made reservoirs
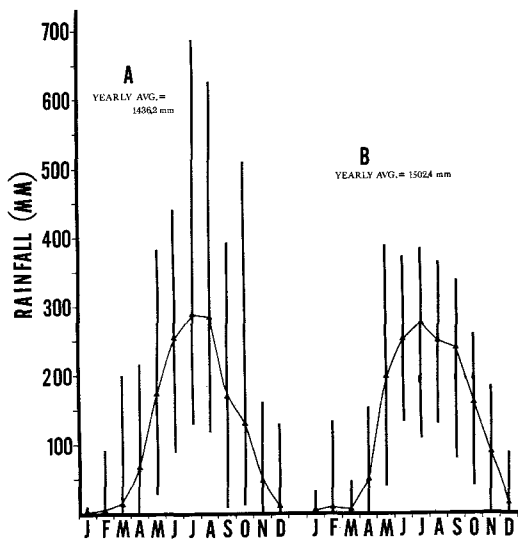
Fig. 1. Rainfall in the study area of the Venezuelan Llanos as indicated by 51 year (1921–71) monthly averages for San Fernando de Apure (A) and 20 year (1952–71) monthly averages for Corozo Pando (B). Data courtesy of the Ministerio de Operaciones Publicas, Direccion General de Recursos Hidraulicos, Direccion de Informacion Basica, Division de Hidrologia, Venezuela.

Hato Masaguaral.—A ranch located 8 km N Corozo Pando (Estado de Guarico) at an elevation of 75 m. Masaguaral is considerably more wooded than La Guanota. *Capernicia tectorum* (savanna palm), *Ficus* sp. (strangler figs), and various species of the family Leguminosae are the dominant woody vegetation. Variety of grasses and herbs comprise the nonwoody vascular flora. The vegetation of this site has been described in detail by Neville (1972). Observations on breeding behavior during the initiation of the 1974 breeding season were made at Laguna de Los Guacimos. This lagoon covers approximately 13 ha during the wet season and decreases in area to approximately 3 ha during the dry season. It is maintained at the latter level by mechanical pumping of subsoil water; before installation of the pump in February 1962, it frequently became dry. The lagoon is surrounded by a sparse forest peripheral to the lagoon's wet season flood plains. Breeding behavior and nesting were studied at Hato Masaguaral from February through August 1974.
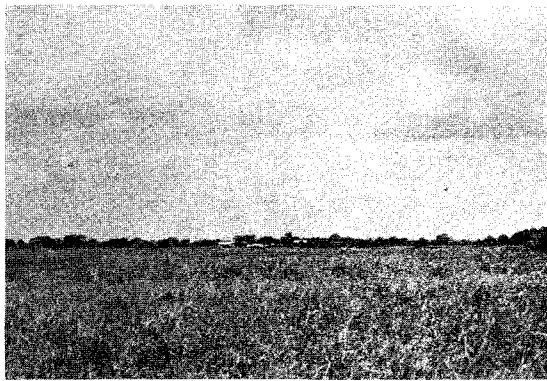
Results and Discussion

It is important to emphasize that the data were recorded during two breeding seasons (latter part of the 1973 season at Hato La Guanota and the beginning of the 1974 season at Hato Masaguaral). However, to present an overall picture of the breeding season in the natural sequence of events, the data from the 2 years are combined as much as possible and considered in their normal order of succession.

Breeding Behavior

Courtship and breeding occurred during the early wet season (May-August) when *C. crocodilus* were congregated at water sites where they had endured the dry season. Following a 34-mm rain on 14 May 1974, the pump to the Laguna de Los Guacimos was stopped; a 35-day drought followed, and the lagoon's area reduced to approximately one-third of its previous level and a maximum depth of 50 cm. Courtship was noted soon after the 14 May rain and continued through early August. The only observations of copulation were made during the drought.

Courtship displays. Three displays were observed which may represent courtship activities; but other functions may be involved.

1. Jumping. From 20 February through mid-June, caimans were frequently observed to leap partially or fully from the water (Fig. 3A) with their bodies at a 60° or more angle. The tails of smaller individuals sometimes emerged from the water, but larger individuals managed only to lift their bodies

retain any water during the peak of the dry season (December-April). In the Llanos soils vary from gravels to silts, generally, from north to south (Myers 1933); soils were sands or silts in the areas we were located. Studies of the breeding biology of *C. crocodilus* were conducted at the following sites.

Hato La Guanota.—A cattle ranch located 6 km W San Fernando de Apure (estado de Apure) on the east bank of the Rio Apure Viejo at an elevation of 68 m. The area is predominantly grassland dominated by gamelote *(Paspalum fasciculatum)* and widely interspersed by dense thickets called matos. The gallery forest, dominated by a number of species of the family Leguminosae, has been extensively cleared. Nesting ecology of caimans was investigated at Hato La Guanota from October through mid-December 1973, and the ranch was periodically revisited thereafter.

A Wet season habitat photograph of Hato La Guanota

D Nest of *Caiman crocodilus* in wooded situation

B Wet season habitat photograph of Hato Masaguaral

E Nest of *C. crocodilus* raided by *Tupinambis tequixin*

C Nest of *Caiman crocodilus* in open, grassy situation

F Nest of *C. crocodilus* after a portion of the clutch hatched

Fig. 2. Natural habitat and nests of *Caiman crocodilus* during the wet season. (A) Hato La Guanota, near San Fernando de Apure; (B) Hato Masaguaral, near Corozo Pando, Guarico; (C) Nest of C. *crocodilus* in open grassy situation; (D) Nest of C. *crocodilus* in wooded situation; (E) Nest of C. *crocodilus* raided by tegu lizard, *Tupinambis tequixin*; (F) Nest of C. *crocodilus* after a portion of the inside clutch hatched.
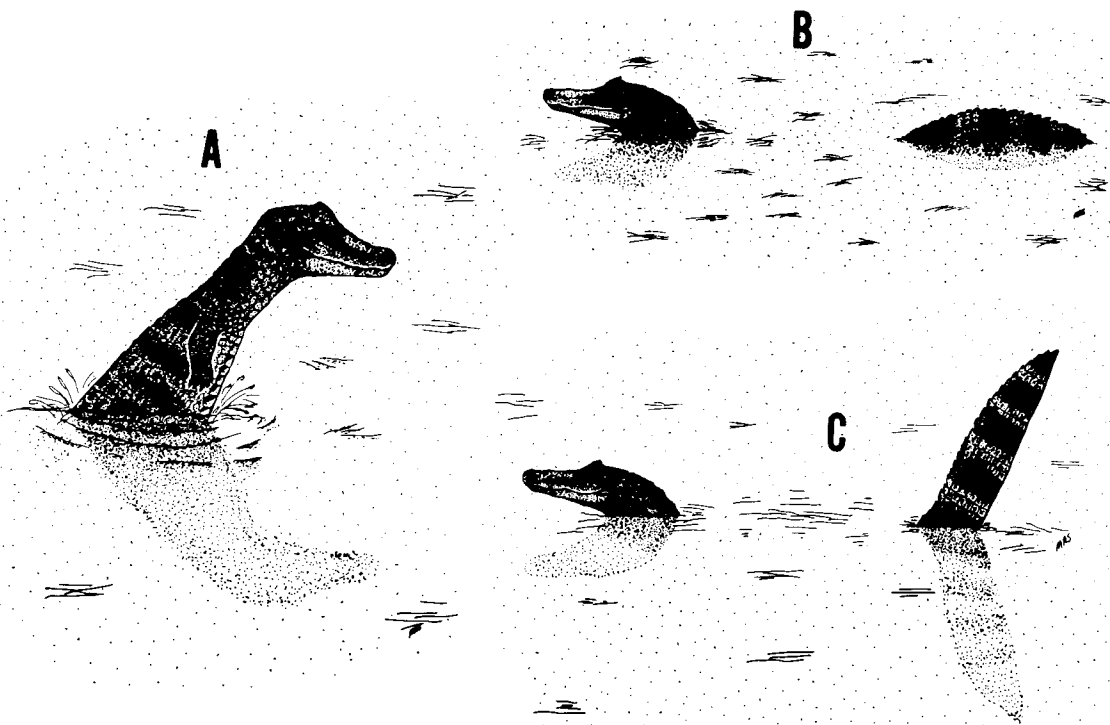
Fig. 3. Behavioral displays of *Caiman crocodilus* during precourtship and courtship periods (A) Jumping; (B) Tail display; (C) Vertical tail display.

from the water. The head returned to the water first and was sometimes slapped sideways powerfully against the water. Such activities were performed only by individuals 1.0 m or greater in total length. This behavior was most common during March and April, and could be seen at any hour of the day (sometimes heard at night). Jumping may represent a precourtship or preterritorial activity. No function can be presently assigned. On about 5 of the 150–200 occasions jumping was observed, individuals surfaced with a fish in their mouths; since caimans always surface to chew and swallow prey, it would appear that if this behavior is a feeding mechanism, it is very inefficient.

2. Tail Display. The usual courtship display of *C. crocodilus*, observed from May through early August, consisted of the male floating at the water's surface with only the head and tail exposed. The head was held so that the lower mandible was at the water's surface; the tail was at the water's surface (Fig. 3B). On occasion, the head was angled at 45-60°, and during June and July the tail was often moved laterally or vertically in conjunction with the display. Displaying was most intense from sunrise until 0900 h, but occasional displays by a few large

individuals were observed at most times of the day. The few instances in which copulation was seen were preceded by this display. The tail display was usually seen in the deepest part of the lagoon, which varied from approximately 0.5 to 1.5 m.

3. Vertical Tail Display. Another display involving the tail was first noted on 30 May 1974. In this display the caiman (always exceeding 1.0 m in total length and assumed to be a male) raised its tail from the water in a vertical position; the head was slightly angled above the water (Fig. 3C). This vertical tail display, by a large male first seen at 0724 h on 30 May (A) elicited the same behavior by nearby caimans (presumed males). These individuals, mostly 1.5 m or greater in total length, displayed and then swam to an area a few meters from caiman A. All displayed in the usual fashion (tail display), and gradually the group disbanded, smaller individuals leaving first. After about 20 min, only one individual (B) remained. Approached by caiman A, caiman B soon disappeared. The vertical tail display was not seen again until 23 June, but it was common during July. Never again was it seen to elicit a group display although isolated individuals in the lagoon performed the display at the same time. This display was

never observed in conjunction with copulation and did not elicit aggression on the part of other caimans.

Modha (1967:82) refers to the male "courtship splash display" in *Crocodylus niloticus:* "Slowly the male raises his tail upwards so that it is arched in a semi-circle with the tip touching the waters surface. He then raises his head and neck so that the lower jaw just touches the water. His neck seems to swell. Soon after this bubbles of water emerge on either side of his body between the fore- and the hind limbs. At this stage his body is almost under water. He then splashes water by lashing his tail sideways and opening and closing his jaws simultaneously. . . ." The two most basic components of this display are arching of the tail and subsequent splashing. Both may be indicative of the size of the male displaying. In *C. crocodilus*, the same is accomplished by the jumping behavior or by either of the tail displays. However, splashing of water (produced by jumping) was not associated with a tail display in caimans as in *Crocodylus niloticus*. Jumping was most intense during March and April, and the tail display was most common from May to July; seemingly, tail displaying replaced jumping. Jumping could thus be interpreted as precourtship behavior, and tail displaying as true courtship behavior.

In *Crocodylus niloticus*, the courting display was only exhibited by territorial males which established basking territories and courted and mated in the water offshore (Modha 1967). In *Caiman crocodilus*, basking territories are not established and individuals frequently bask gregariously. However, displaying males are definitely aggressive toward nearby individuals which are not receptive females. Other than the sexual dimorphism of greater male size, the sexes are nearly impossible to distinguish in *Caiman crocodilus*. Temporary territories are established during display, their most obvious function being to serve as an arena for courtship. The male approaches nearby caimans (especially displaying individuals) which are thereby in his territory. The approached individuals usually retreat by swimming away or submerging. Reaction of other caimans appeared to be based on relative size. Smaller individuals were always subordinate to larger ones in such instances. A smaller individual that did not retreat was vigorously attacked and often chased for 10-20 m. A social hierarchy was thus established in which size was the controlling factor. The size of the displaying tail or the distance from the head to the tail could indicate size to conspecifics. Although larger individuals often lunged vigorously at smaller ones, they never fought. *Caiman crocodilus* never battled as has been described for *Alligator mississippiensis* (McIlhenny 1935) and *Crocodylus niloticus* (Modha 1967). The tail display thus appears to be,

besides a courtship mechanism, a territorial or spacing mechanism which allows members of this species to coexist in relatively crowded lagoons.

Vocalizations played little or no part in the courtship of Llanos caimans. The roar of bull alligators and crocodiles was not heard at any time from *C. crocodilus*. Occasionally during the dry season and early wet season, sounds resembling a bark were emitted during the day and night by isolated individuals; only once was it heard in conjunction with a courtship display. On that occasion (23 July), the male arched its head and emitted a faint bark. If caimans vocalize in conjunction with the display, it is very weak and was not heard by the observer (usually 100 m from the animals).

Copulation. Coitus was observed on 23 and 28 May. Observations made on 13 June may also have been of copulation. Males involved were estimated to be 1.7-2.0 m total length and females from 1.2-1.5 m.

The following description of copulation combines the observations of 23 and 28 May; differences between these are noted. Preceding copulation, the male's head and tail emerged from the water at approximately 45°. The female approached the head of the male and appeared to nibble the lower mandibles of the latter (action obscured because head of male was directed away from the observer). (Juveniles have been observed to nibble at the jaws of adults in captivity [Staton and Dixon, personal observation; C. Blohm, personal communication] and may represent a mechanism to impede aggressive behavior by adult males. This nibbling may be analogous to the prenuptial display of female *Crocodylus niloticus* in which she angles her head from the water and utters gutteral sounds [Modha 1967].) The female then reversed her direction; the male swam over her back, apparently mounting her. The dorsal anterior three-fourths of the male's body and the tail tip were above the water (Fig. 4A) and the female was under water at all times. During copulation, the two swam around slowly within a small area powered by the male's tail, which was constantly paddled toward the right of his medial plane. The tail was never observed to move to the left of this plane, which may indicate the female's position. In both instances, copulation lasted 4 min, but each ended differently. On 23 May, the male suddenly lunged forward; 20 s later the female appeared about 1.5 m to his left. On 28 May, the male shifted to a floating position, only his head showing; the female appeared slightly to his left 10 s later. This overall description is similar to that of Alvarez del Toro (1974) for *C. c. chiapasius* except he states that copulation lasts 30 min, and that it is performed while the caimans have paused in the water after swimming around.
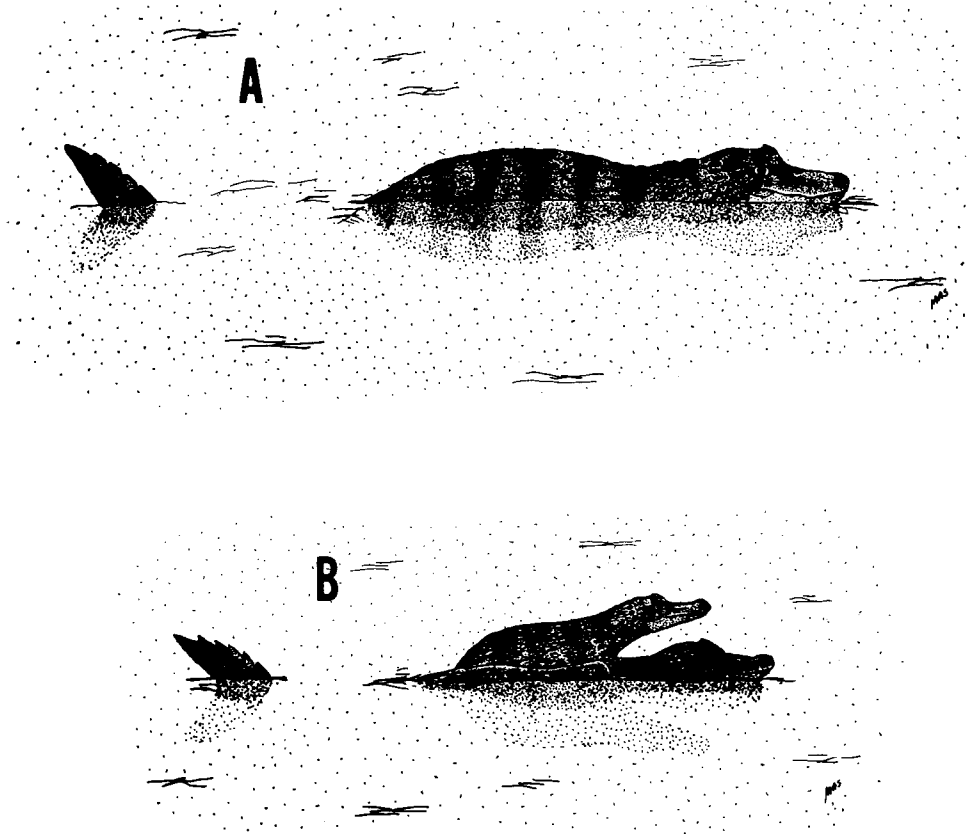
Fig 4. Copulatory positions of *Caiman crocodilus:* (A) position under conditions of normal water depth (male); (B) altered position under conditions of low water depth (female above, male below).

Another observation of behavior possibly representing copulation was made on 13 June as follows: at 0603 h, a displaying male began to move his tail vertically and laterally in association with the display. A smaller caiman, presumably a female, mounted the back of the male, which immediately began to swim around, often changing directions vigorously. It appeared that the larger individual was trying to dislodge the smaller one. The female's body angled over the male's back with the cloacal region inverted beneath the male's, their vents apparently juxtaposed (Fig. 4B). The male paddled with his tail (again only to the right side), and they swam for about 5 min in that manner. Becoming stationary, the tail display was repeated for about 2 min. The female then dismounted and swam away. This observation came 2–3 weeks after copulation had first been observed. Water levels in the lagoon dropped drastically during that time as the water pump to the

lagoon had been stopped. Maximum depth during mid-June was only 30–50 cm. It is possible that this environmental variable elicited a different copulatory position; Alvarez del Toro (1974) noted a pre- and post-copulatory variant of the behavior of *C. c. chiapasius* when water depth is shallow.

Ovarian Development

Observations on ovarian development were made only for individuals killed by autos, or for individuals killed for stomach analysis. Three adult females showing no ovarian development were collected on 8 April at a site some 80 km W San Fernando de Apure in habitat very similar to that of La Guanota. Ovarian development commenced during late April or May; on 31 May, 4 June, and 15 June, adult females possessed enlarged ovarian eggs measuring

10.5–32.0 mm ($\bar{x}$ = 23.2, n = 8), 5.1–23.8 m ($\bar{x}$ = 16.0, n = 76), and 7.8–25.8 mm ($\bar{x}$ = 17.7, n = 58) in diameter, respectively. Another adult dissected on 3 August contained full-sized oviducal eggs with semicalcified shells. Thus there is an approximate 3-month interval between commencement of ovarian development and breeding, and first nesting.

Minimum Size at Reproduction

The smallest nesting female, found 16 October, measured 70.0 cm snout-vent length and 130 cm total length. The smallest reproductively active female, encountered 31 May, measured 67.7 cm snout-vent length and 129.1 cm total length. This female contained 8 yolked ovarian eggs (Dia. = 10.5–31.5 mm, $\bar{x}$ = 26.9 mm); as her oviducts were not distended, the developing clutch was probably her first reproductive effort. A female measuring 52.0 cm snout-vent length and 105 cm total length on 19 July 1974 (well into the breeding season) showed no ovarian development or oviducal enlargement.

These observations agree with Bustard's (1970) generalization that *C. crocodilus* females reach sexual maturity at 125 cm total length. Well-fed captive specimens reach 1 m in total length in 3 years (Blohm 1973; Chirivi-Gallego 1973; Rivero Blanco 1974) and would probably reach 125 cm by 4 years of age. Assuming equal growth under natural conditions, females probably mature sexually in their 4th year. *C. c. fuscus* from Colombia is known to have reproduced at 1.08 m total length (Chirivi-Gallego 1973), but this would be exceptional for Llanos caimans.

Nesting

Period of nesting. At Hato Masaguaral, the first nest of the 1974 breeding season was found on 15 August by a ranch worker; the following day it contained eggs. Within 3 days, three nests in construction were found. At Hato La Guanota during the 1973 breeding season, the first hatchlings were found on 24 October; assuming an incubation period of 70–75 days (See Incubation and Embryonic Growth), first nesting period occurred in the 2nd week of August. Oviposition continued until the 3rd or 4th week of October, and incubation extended through late December or early January. Most nesting occurred in September.

The period of mid-August through late October coincides with the latter half of the rainy season. Rainfall in August 1973 exceeded normal and was greater than that of any month except July (Fig. 5). September and October are usually months of intermediate rainfall, but rainfall during these months in 1973 at San Fernando de Apure exceeded normal and approached normal August levels.

The 1974 rainy season at Hato Masaguaral was initially dry, and it is possible that nesting would have begun earlier under more normal conditions. Nevertheless, it is obvious that nesting by Llanos *C. crocodilus* coincides with periods of high water levels, which is unlike *C. crocodilus* from other parts of its range. At Puerto Carreno, Colombia, less than 200 km S San Fernando de Apure, in the gallery forests surrounding the Orinoco River, females examined during the rainy season showed no signs of reproductive activity, no nests were found, and according to locals, nesting takes place toward the end of the dry season (Chirivi-Gallego 1973). Elsewhere in Colombia, breeding takes place year-round, with the exception of the first 2 months of the rainy season (Medem 1958, 1960, 1962; Chirivi-Gallego 1973). At Parque Nacional Isla de Salamanca, Departmento de Magdalena, Colombia, most nesting takes place during an early peak of the rainy season, incubation during an intermittent dry spell, and hatchlings emerge during the much more intense second peak of the rainy season.

The nesting habits with regard to rainfall patterns adopted by these other populations of *Caiman crocodilus* allow young to emerge when water levels are rising or high, and it is characteristic of other crocodilians such as *Crocodylus niloticus* (Cott 1961) and *Crocodylus porosus* (Derayinagala 1953). It is adaptive in that survival of the young is undoubtably enhanced under flooded conditions. However, it cannot be the strategy of Llanos *Caiman crocodilus* because for hatchlings to emerge during the early or middle rainy season, all or some nest building and incubation would have to be performed during the dry season. This timing would require that the female oviposit during the stressful dry season; that she guard the nest at a time when no shade or water for cooling and protection is available; and that she construct the nest of dry material since little green vegetation remains during the late dry season. Nesting earlier in the dry season would not ensure a flooded environment for the emerging hatchlings and would still require protection of the nest under dry conditions. The present nesting strategy avoids the early months of the rainy season when water levels are rising and might flood the nests. It also allows the adult to remain near and guard the nest and provides the hatchlings grassy shallows for their first 1 or 2 months.

Nest Material. Caimans use the material closest to the nest site to construct the nest (Alvarez del Toro 1974). At Hato La Guanota, caimans nested in two decidedly different situations which is
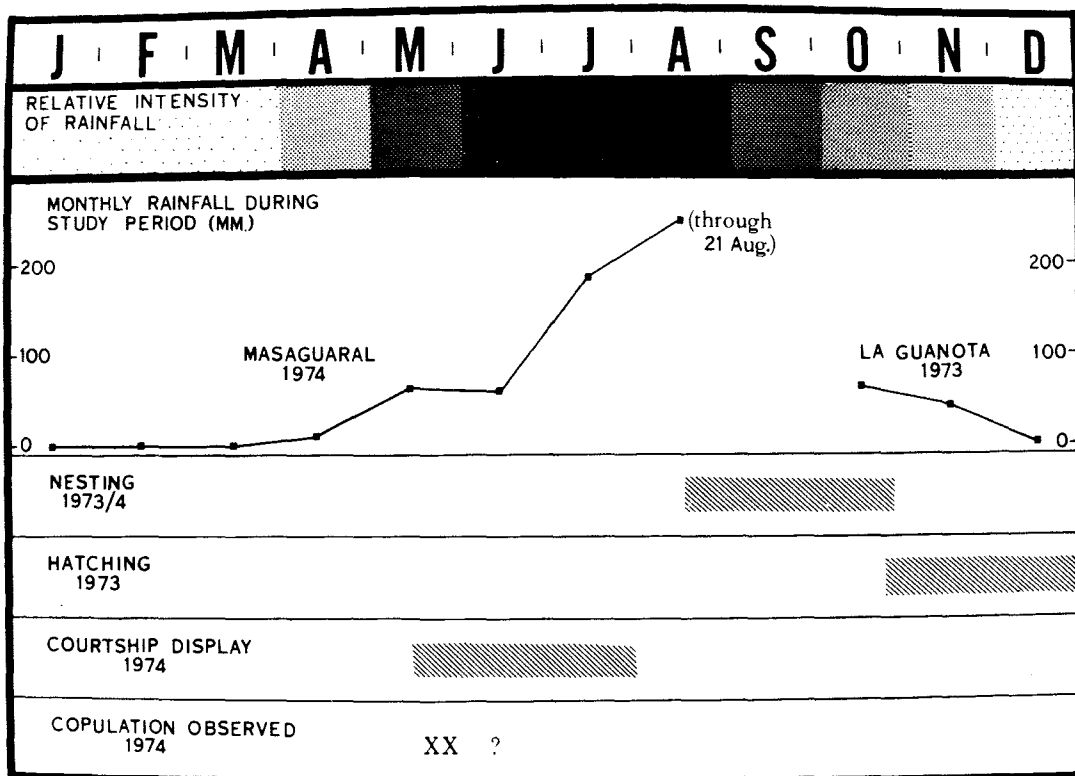
Fig. 5. Events in the breeding biology of *Caiman crocodilus* in relationship to seasonal rainfall in area of study.

reflected in the nest material used. Nests constructed in the open savanna were of *Paspalum fasciculatum*, consisting entirely of this grass and some soil. Nests constructed near or in gallery forest consisted of leaves, twigs, and soil. Of 40 nests encountered, 33 (82.5%) were of *Paspalum* or a similar grass; 5 (12.5%) were of leaves, twigs, and soil; and 2 (5%) were intermediate. At Hato Masaguaral, where the savanna is more wooded, nests were beneath small clusters of trees *(Capernicia, Fiscus* sp. and *Fagara* sp.*)* dispersed over the savanna. These nests (n = 4) were made of palm fronds, twigs, various grasses, and soil.

Nest construction and oviposition. Observations on nest construction by *Caiman crocodilus* were made on recurrent visits to nests in various stages of construction. Nest material was never added during the day.

A nest in construction found on 16 August consisted of a mound of twigs, dirt, and grass (dry and fresh materials) about 15 cm high. By the following day, more material had been added to the nest. A distinct indentation on top of the mound indicated that the female had crawled over the nest. On 18 August this nest was destroyed by feral pigs, but by 21 August it was rebuilt to its former dimensions and on 23 August it contained eggs. Another nest in construction, 30 cm high on 17 August, received additional material on the night of 20 August. It was found destroyed on 23 August. Females were not seen at these nests.

On 19 August a female was found actively constructing a nest at dusk (2015 h). On 20 August this nest measured 1 m × 1 m × 20 cm, and the following day it contained eggs. The bottom of the previous chamber was distinctly lower than the 20-cm-high mound of the previous day. Apparently the female constructed a platform as the first step in nest construction and then developed the egg chamber

before oviposition. Following egg deposition, the female evidently added material and repacked the outer layer of the nest by crawling over it.

These observations agree with those of Alvarez del Toro (1969) and Hunt (personal communication) who indicate that captive *Caiman crocodilus* build a mound several days before oviposition. Alvarez del Toro (1974) stated that under normal conditions the nest is constructed 2 to 6 days before oviposition. Contrary to our observations, Alvarez del Toro (1974) believed nest construction to take place during the early morning and late afternoon hours. This may vary greatly.

Nest size. Length, width, and height of 22 nests from La Guanota averaged 117.0 cm (90-200), 104.5 cm (80-150), and 44.5 cm (30-65), respectively. They are nearly dome-shaped and almost circular at the base (Fig. 2A). No correlation was found between nest size and clutch size or nest size and adult (female) size.

Position of the nest relative to water. The nest's position relative to water is an important factor in its fate. Of 28 nests observed during October and November (1973 at La Guanota), 5 (17.9%) were flooded and all eggs drowned. The cause must be attributed to human influence since flooding occurred in areas controlled by a dike system and water pumps. However, natural flooding may also influence the nest's success. Nine nests (33.1%) were in water 3-20 cm deep and 14 (50%) were on dry land. Nearly all nests were eventually preyed upon, and predation occurred after water levels receded completely or to shallow depths. Predators such as the tegu lizard *(Tupinambis tequixin)* or foxes *(Cerdocyon thous)* may find foraging more difficult under flooded conditions. In addition, the adult would be more likely to remain near the nest a greater portion of the time if water were nearby for thermoregulatory and hiding purposes.

Ants. Ants were found in 15 of 27 nests (55.6%) that were examined for their presence. Similarly, Chirivi-Gallego (1973) and Medem (1969) report the presence of ground termites (Isoptera) in *C. crocodilus* nests. Joanen (1969) and Pooley (1969) report ants in the nests of *Alligator mississippiensis* and *Crocodylus niloticus*, respectively.

In the Llanos, the nest apparently provides a dry residence for the ants during the rainy season. Eggs cracked while incubating in captivity were entered and eaten by ants. Cracked eggs were occasionally found in natural nests and some of these suffered the same fate. On two occasions, pipped eggs in natural nests were eaten by ants. Ants may act as cleansing agents, ridding the caiman nests of fungal growths, and cracked eggs that might otherwise omit odors that would attract predators. In this respect, there

may be some element of symbiosis, the caimans furnishing the dry platform and the ants cleansing the eggs and nests.

Eggs

Clutch size. One nest contained only nine eggs when first discovered, probably the result of partial predation (See Maternal Care of the Nest and Predation). Thirty other nests contained from 17 to 38 eggs. The average of 28.6 eggs per clutch (0.91 SE) is slightly lower than the mean of 29.1 reported by Rivero Blanco (1974) from 170 nests at the same site. Linear regression analysis of clutch size and adult female size (n = 6) was nonsignificant (r = 0.557). Medem (1958) stated that clutch size depends on adult female size in *Caiman crocodilus* but did not support his statement with data. Cott (1961) demonstrated this relationship in *Crocodylus niloticus*, and it seems likely that sufficient data will substantiate Medem's belief.

Egg size. Eggs vary in shape from elliptical to almost spherical. The mean and range of egg length, width, and weights are 63.8 mm (56.5-72.8, n = 323), 40.7 mm (37.2-43.7, n = 323), and 59.9 g (48.7-77.4, n = 241), respectively. The range in values of clutch averages (30 nests) of egg length, width, and weight in each is 59.8-68.8 mm, 38.3-42.5 mm, and 52.5-69.8 g, respectively. Linear regression analysis of these parameters was significant (Table 1).

There was no seasonal trend in variation in clutch size. However, average egg weight per clutch changed during the 3-month nesting period (Fig. 6), heavier eggs (and therefore larger, heavier young, Fig. 13) being produced earlier. Assuming hatchling size to enhance the survival of young in the dry season, a mechanism thus exists for natural selection to act on success during the dry season (and eventual production of young).

Artificial incubation and dimensional changes of eggs. Eggs were incubated in artificial nests composed of *Paspalum fasciculatum* collected from natural nests and the growth of eggs in four nests was monitored. Clutch I, II, and III were placed in grass-filled closed plastic bags 40 × 50 cm at the base and 30 cm high. Clutch IV was kept in a mound of freshly cut *Paspalum fasciculatum* 40 cm high and 75 × 75 cm at the base. This nest was moistened by adding 15-20 liters of water to it. Average temperatures at egg level for clutches I-IV were 29.0, 27.3, 27.1, and 26.8 C, respectively. Minimum temperatures in clutches II-IV were between 23.0 and 24.0 C, and the lowest temperature recorded for clutch I was 27.2 C. Maximum temperatures did not exceed natural nest temperatures. Nest humidities were checked irregularly. Relative humidity in

Table 1. *Regression equations between average values of egg length, width, and weight for 16 clutches of* Caiman crocodilus. *For each clutch, data were available for 6 to 37 eggs (usually exceeding 10 eggs).*

Independent variable (X–Axis)	Dependent variable (Y–Axis)	
	Mean width	Mean weight
Mean length	$Y=26.692+0.2203X$ $r=0.554^{a}$	$Y=+50.345+1.7362X$ $r=0.865^{b}$
Mean width	----------------	$Y=-110.960+4.1983X$ $r=0.832^{b}$

[a] Correlation significant at 0.05 level

[b] Correlation significant at 0.01 level

clutches I-III varied between 88 and 95%—almost exactly that of natural nests. Clutch IV was subjected to nest humidities as low as 71% because of air flow throughout the nest due to the lightly packed grass. Humidities of 90% or greater were maintained only during rainy or cloudy conditions. Water was repeatedly added to this nest to raise and maintain humidity.

Clutches I and II changed little in weight. Thirteen eggs of these two clutches hatched; one died in the egg after pipping; another died fully developed without

Fig. 6. Seasonal variation in the average egg weight (per clutch) of *Caiman crocodilus* during 1973. Each triangle represents one clutch.

pipping; and the remaining egg was sterile. All clutch III eggs were rotten and averaged 4.1 g (2.3-7.6) weight loss after 36 days of incubation. After 4 days of incubation, clutch IV eggs averaged 12.2 g (9.6-16.7) weight loss. Four of the six eggs produced young with human aid; one fully-developed young died within the egg without pipping; and the remaining egg rotted. Besides the 6 clutch IV eggs for which data were recorded, 10 others (from the same clutch) were incubated in the same nest. Of the 16 eggs total, 5 eggs contained fully-developed young which did not pip and died within the egg. The average weight loss for these eggs was 13.8 g, significantly greater than the 10.1-g weight loss averaged by eggs containing fully developed young and hatched with human assistance. Clutch IV young were surrounded by a gritty mucous which appeared to be the excretory wastes of the allantois in a semisolid form. Wastes under such conditions, presumably resulting from low humidity, would undoubtedly be extremely concentrated and possibly weaken the young. In contrast, 21 eggs from various nests which had pipped and hatched without assistance averaged only 1.7 g weight loss during incubation. Only one of the latter eggs lost over 3.5 g during incubation and 7 eggs gained from 0.1 to 1.7 g. Weight loss during incubation is an important factor in determining the vigor of the hatchling at the termination of incubation. Humidity is a critical factor in determining weight loss, hence the importance of maintaining high and constant humidity in natural nests (See Nest Humidity).

Seventy-eight eggs incubated in a variety of nests 21 to 48 days averaged changes of +1.12 mm (-3.7 to +2.1) in length and +0.03 mm (-1.6 to +1.0) in width. Extreme changes may represent procedural errors. Of the 78 eggs, 54% and 52% of the changes in length and width, respectively, were positive; 27% and 37%, respectively, were decreases; and 20% and 11%,
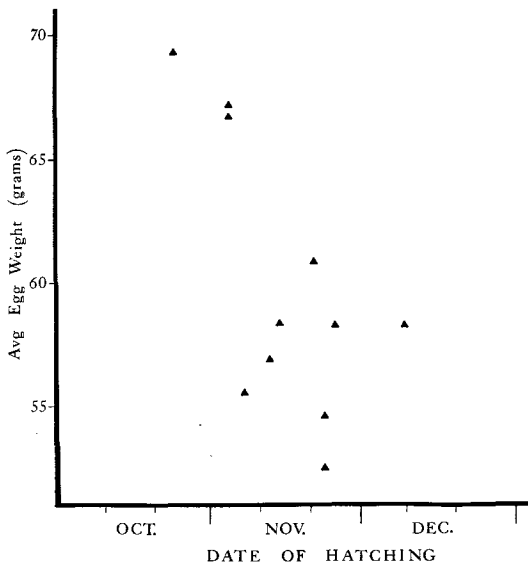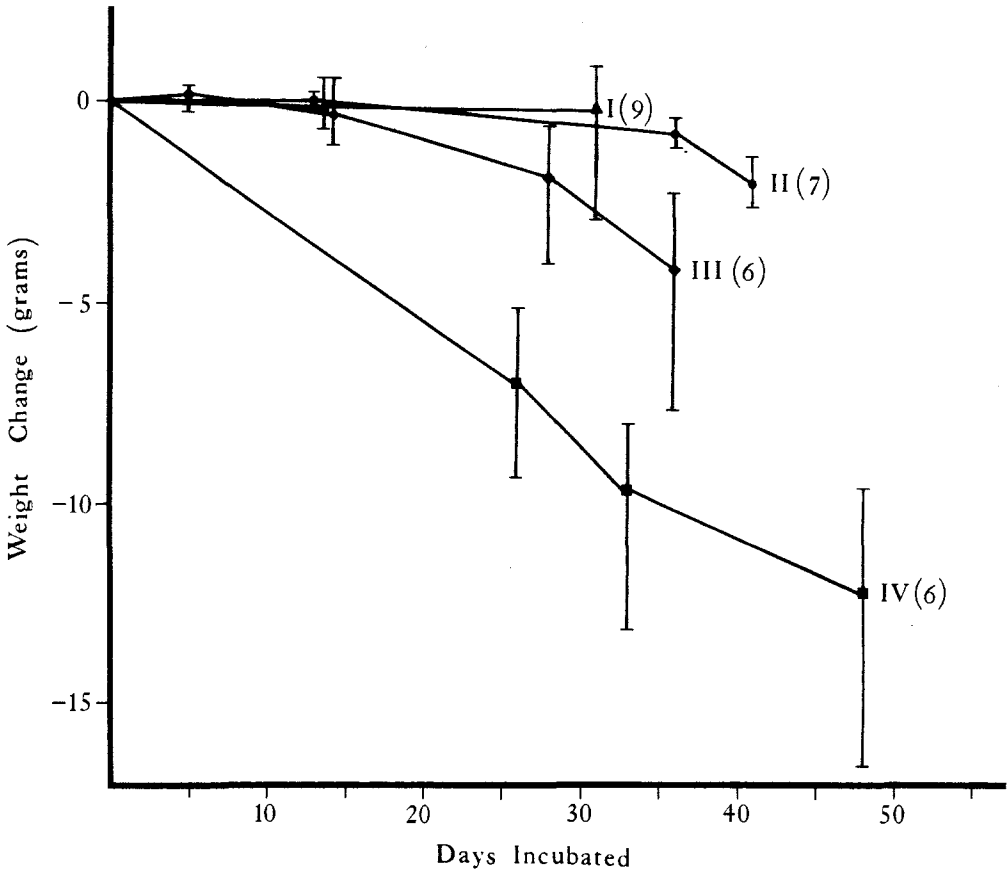
Fig. 7. Mean and range of weight changes in four clutches of *Caiman crocodilus* eggs incubated under different conditions of humidity.

respectively, were recorded as no change. Thus the majority of eggs became slightly longer and/or wider during incubation or did not change.

Maternal Care of the Nest and Nest Predation

Thirty-two of the 40 nests encountered for the first time (all during daylight hours) were intact, seemingly having never been preyed upon. Another had recently been raided but still contained eggs. Of the 32 intact nests, 3 contained no eggs and were either false nests, nests in which eggs would soon be laid, or nests which had been raided and remade by the adult. Two of these three nests were tended by the adult. One nest being guarded had flooded and all eggs had drowned. Of the 30 nests with eggs, 13 (42.4%) were guarded by an adult. This is probably an underestimate since nesting female *C. crocodilus* do not always make themselves obvious in the presence of humans at the nest. We tried to capture adults at the nests, and this usually frightened the adult from the area, resulting

in fewer observations of adults on subsequent visits. One adult captured on our first visit to a nest was never again seen in over 50 subsequent visits. Females were seen on only 6 of 22 subsequent visits (22.3%) to other undisturbed nests during the daylight hours. Only once was a female seen at a nest following initial capture and release. In one instance, no attempt was made to capture an adult consistently present at the nest. On 76 visits to this nest during daylight, the adult was not seen; however, of 34 visits to the nest on 35 nights she was near the nest, usually within 2-3 m, 29 (85%) times. Undoubtedly she was present but undetected on many of the day visits.

Fourteen nests were partially or completely destroyed by predators on visits subsequent to the first. One nest was raided twice and another three times before all eggs were eaten. Partial predation has also been reported on nests of *Crocodylus niloticus* (Modha 1967; Pooley 1969) and *Alligator mississippiensis* (Joanen 1969). Although partially raided nests were never found remade by the adult, five visits to four nests which were eventually raided

Table 2. *The fate of 40* Caiman crocodilus *nests encountered at Hato La Guanota during the 1973 breeding season.*

Fate	N	Percent
Raided by humans	5	12.5
Eggs removed by investigators	3	7.5
Destroyed by cattle	3	7.5
Caged off from predators by investigators	2	5.0
Flooded	5	12.5
Contained no eggs	3	7.5
Hatched	3[a]	7.5
Destroyed by predators	16	40.0

[a] Eggs of one removed by investigators after female abandoned nest.

revealed that these had been reworked by the adult since a prior visit. Evidence of this was fresh grass or fresh indentations made on top of the nest.

There is little doubt that nests of *Caiman crocodilus* are tended by adults of the species. Functions at the nest include remaking it after predation and, undoubtedly, protection from predators. The degree to which the latter is displayed is not known and may be subject to the experience of the females involved. All (six) adults captured at nests were females.

Of 40 nests encountered at La Guanota during the 1973 breeding season (Table 2), only those that hatched successfully (3) and those preyed upon (16) can be used in estimating prenatal mortality (nest predation) as other factors were directly or indirectly human-induced. These data show that nesting success was 15.8%, whereas 84.2% of the nests were preyed upon. If females abandoned the nests due to our visits, the predation estimate may be high. Estimates of predation on crocodilian nests vary substantially and predation rates undoubtedly vary with nesting densities, predator density, the availability of other food items to the predator, maternal care given, and other factors. Pooley (1969) and Joanen (1969) rate nest predation at less than 20% in certain populations of *Crocodylus niloticus* and *Alligator mississippiensis*, respectively. However, nest predation in *Crocodylus niloticus* is also known to be much higher. Pooley (1969, 1973) stated that during early stages of incubation, predation has been as high as 33.8% (22 of 65 nests) and 49.4% (38 of 77 nests). Since "the peak danger period of nest predation occurs at hatching," (Pooley 1969:33), mortality in these populations might be as high as 85% (as in our study).

The main predator of *C. crocodilus* eggs was the abundant tegu lizard, which dug a distinctive burrow when raiding a nest. Only *Tupinambis*, which accounted for at least 11 of the 16 raided nests (68.8%), partially raided nests. Joanen (1969) believed recurrent raids to be an intentional strategy on the part of raccoons *(Procyon lotor)* preying on eggs of *Alligator mississippiensis*. Such may also be true for *Tupinambis*. Other raids were probably by the fox; this predator completely destroyed the nest when feeding on the eggs. Rivero Blanco (1974) considered the Crested Cara-Cara *(Caracara plancus)* to be the major predator on caiman eggs, but it seems unlikely that this bird, even with its powerful legs and claws could tear open the tightly packed vegetation of a caiman nest. It seems more likely that this bird may scavenge on the remains of eggs left by predators.

Nest Temperatures

Nest temperature data were recorded on 225 occasions (Fig. 8). The outer layer of the nest absorbed heat during the morning and generally paralleled the increase in air temperature; afternoon temperatures in the outer layer of the nest usually exceeded air temperatures. Inner nest temperatures increased at much slower rates, reaching a peak by 1500–1600 h. By this time, outer nest and air temperatures decreased rapidly; nest temperature at egg level decreased slowly. By 2000 h both air and outer nest temperatures were lower than inner nest temperature; by 0800–0900 h the following morning they again exceeded inner nest temperature, which remained relatively constant throughout the night.

Grass nests *(Paspalum fasciculatum* and *Pennisetum* sp.) were built in open sunny locations. Nests of twigs, leaves, and dirt were built beneath some form of cover, shading them from the sun. Grass nests possessed higher temperatures during most of the daylight hours (Table 3). Until midmorning, outer and inner nest temperatures were statistically equal for each of the nest types. By 1100 h, however, all three temperatures were significantly higher in grass nests than in nests of leaves, twigs, and dirt. This remained true until about sundown, and by 2000 h,
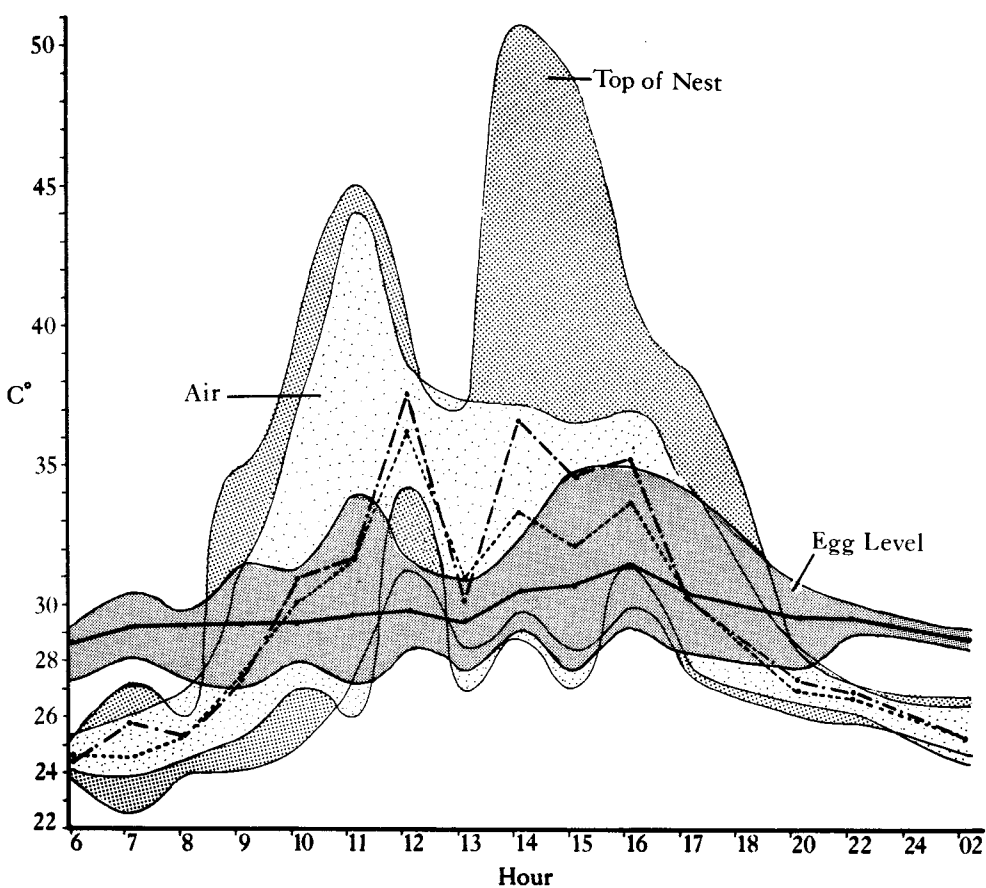
Fig. 8. Hourly average and range of 225 sets of temperature data for nests of *Caiman crocodilus*. Solid line = mean internal nest temperature; dashed line = mean air temperature; bar/dot line = mean outer nest temperature.

values of air and outer nest temperature were approximately equal. At that time, however, inner nest temperatures of grass nests were still significantly higher than those of nests of twigs, leaves, and dirt. By 2200 h, temperatures were approximately equal in and out of the nest. Air temperatures around nongrass nests are significantly higher than those around grass nests at 2200 h; this probably is the result of more rapid cooling in the open grass nests than in the covered nongrass nests. Fig. 9 compares outer and inner nest temperatures of a grass nest (*Pennisetum* sp.) with one of twigs, leaves, and dirt. The trends evident for these individual nests agree with the overall trends previously described.

Crocodilian nests possess thermoregulatory qualities in that they maintain relatively constant internal temperatures at egg level, as compared with external fluctuations in temperatures (i.e., nest

surface temperature and air temperatures). Such a thermoregulatory ability has been demonstrated for the nests of *Alligator mississippiensis* (Chabreck 1973) and *Caiman crocodilus* (Rivero Blanco 1974; present study). Modha (1967) reported relatively constant temperatures in the hole nests of *Crocodylus niloticus*. Additionally, McIlhenny (1935), Derayinagala (1939), Medem (1971), and Neill (1971) reported natural nest temperatures of *Alligator mississippiensis*, *Crocodylus porosus*, *Paleosuchus palpebrosus*, and *C. novaeguinae*, respectively. Internal nest temperatures of these crocodilians varied from 23.3 to 38.9 C, but generally fell between 28 and 34 C. Developing *Crocodylus novaeguinae* embryos cannot withstand low temperatures of 23 and 26 C, were most successful at 32 C, and although hatching at 38 C, hatchlings were weak and possessed deformed tails (Bustard 1971b). This suggests that this species can tolerate a relatively wide span of

Table 3. *Comparison of temperature and humidity between* Paspalum *nest (upper number) and those of leaves, twigs, and dirt (lower number) at selected times of the day by Student's t-test. Sample sizes are in parentheses.*

Hour	Temperature (C)			Humidity (%)	
	Ambient air	Outer nest	Inner nest	Air	Inner nest
0900	28.3 (9)	28.6 (8)	29.7 (9)	68.3 (9)	90.7 (9)
	26.9 (11)	26.4 (11)	29.1 (11)	76.0 (11)[a]	91.3 (11)
1100	32.9 (25)[b]	33.5 (25)[b]	30.0 (28)[c]	67.3 (28)	90.4 (28)
	28.4 (11)	27.6 (11)	29.0 (11)	71.4 (11)	91.0 (11)
1300	35.2 (2)[b]	34.0 (2)[c]	29.7 (2)	63.0 (2)	89.5 (2)
	30.7 (12)	29.5 (12)	29.4 (12)	64.1 (12)	90.1 (12)
1500	34.3 (10)[b]	40.2 (10)[b]	32.1 (10)[b]	57.9 (10)	89.0 (10)
	30.1 (10)	28.9 (10)	29.5 (10)	64.0 (10)	90.2 (10)
1700	31.4 (13)[b]	32.2 (13)[a]	31.2 (13)[a]	62.8 (13)	90.2 (13)
	29.2 (11)	29.0 (11)	29.7 (11)	69.0 (11)	89.6 (11)
1930	26.7 (7)	27.4 (7)	30.3 (7)[a]	82.4 (7)	90.7 (7)
	27.1 (12)	27.3 (12)	29.4 (12)	84.4 (12)	91.5 (12)
2200	26.1 (6)	26.9 (6)	29.9 (6)	82.7 (6)	90.8 (6)
	26.7 (8)[c]	26.9 (8)	29.6 (8)	82.9 (8)	91.8 (8)

[a] Significantly greater at the 0.01 level

[b] Significantly greater at the 0.001 level
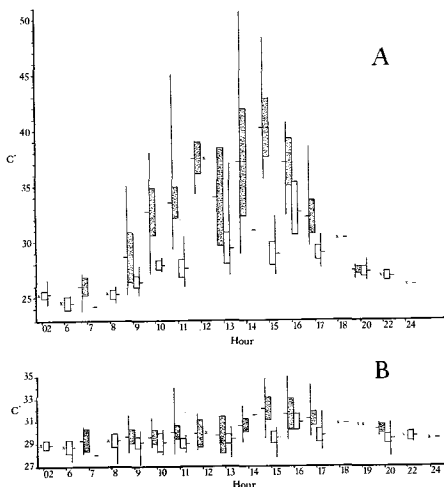
[c] Significantly greater at the 0.05 level

Fig. 9. Twenty-four hour comparison (mean ± 2 SE and range) of outer (A) and inner (B) nest temperatures of *Caiman crocodilus* nests of different construction material. Stipled = grass nest, *Paspalum fasciculatum* and *Pennisetum* sp. (*n* = 1190; clear = nest of leaves, twigs, and soil (*n* = 106). An *x* denotes no observations; a – denotes a single observation.

incubational temperatures, and in view of the wide range of crocodilian nest temperatures reported in the literature, the same is probably true of other species. Nest temperatures of *Alligator mississippiensis* vary from 27.6 to 32.4 C (Chabreck 1973). Similarly, Rivero Blanco's (1974) average temperature for one nest, approximately 27.5 C, was slightly lower than our values.

Neill (1971) contended that the problem in thermoregulation of crocodilian nests was not gaining heat, but in preventing excessive heat exposure of the eggs during midafternoons. Neill indicated that daily air temperatures surrounding the nest reached levels almost intolerable to the adult and surely intolerable to developing embryos. Insulation during midafternoon is undoubtedly a primary function of the nest. However, air temperatures exceed internal nest temperatures for only about 10 h each day (Chabreck 1973; Rivero Blanco 1974; present study, Fig. 8). Prevention of cooling is a thermoregulatory function of the nest during the remaining 14 h of the day. Heat loss can be prevented only after heat has been gained. The amount of heat to which the developing embryos will be exposed has undoubtedly been subjected to natural selection.

Three sources of heat for crocodilian nests have been cited. McIlhenny (1935) believed the temperatures in alligator nests resulted from decom-

position of the organic materials of which they were constructed. This view was shared by Joanen (1969) and Chabreck (1973). Modha (1967:86) states that in hole nests of *Crocodylus niloticus*, which lack detritus to be decomposed, "from the surface downwards the temperature first falls and then rises with increases in depth. The higher temperatures in the egg chamber probably result from heat generated during metabolism." Such a heating source would also be present in a mound nest. Earlier authors, such as Bartram (1791) and Ashe (1808) attributed some heat gain to absorption of solar energy, but this source has apparently been ignored by recent writers.

Bird embryos are poikilothermic and dependent on external heat for completion of incubation (Drent 1967); the same seems likely for reptiles. Drent showed that metabolic heat production by the embryos of the gull *(Larus argentatus)* increased as they grew in size and hence with incubation time. Assuming an equivalent situation in crocodilian embryonic heat production, its effects, if significant, would be greatest in the latter stages of incubation. However, Chabreck (1973) showed that nests of *Alligator mississippiensis* were warmer in the second, third, and fourth weeks rather than the later stages of their 9-week incubation period. The contribution of embryonic heat production thus seems small.

Chabreck's data would, however, substantiate the view that decomposition is important in heating the nests, since during the first few weeks of incubation there is more organic material to decompose. Decomposition, however, is temperature dependent; daily patterns of decomposition follow temperature cycles (Witkamp 1969). Both air temperature and decomposition can apparently influence inner nest temperature.

If decomposition were the only source of heat, inner nests would always equal or exceed outer nest temperatures since the inner nest would be subject to dissipation of heat to the exterior. This is obviously not true since afternoon outer nest temperatures of both nest types are greater than inner nest and air temperatures. In such situations, the inner nest undoubtedly absorbs heat conducted from the warmer surface area. Solar energy thus influences the inner nest temperature. Furthermore, that influence, whether it be through the effect of increasing decomposition or through heat transfer from the outer layer of the nest to the interior, is great enough to give the grass nests in open locations a warmer interior nest temperature than the shaded nests of leaves, twigs, and dirt (Fig. 9; Table 3). Analysis of the situation is further confounded by the fact that grass nests contain more organic matter to be decomposed, but the significance of solar energy in warming the nest cannot be ignored. In conclusion, the heating of a crocodilian mound nest is due to solar energy, the effect of decomposition of organic material, and their interaction.

Nest Humidity

Nest humidities varied little, ranging from 85–95% (Fig. 10). Ambient humidity dropped as low as 46% during the daylight hours but inner nest humidities were usually 90% or greater. Nest humidities increased slightly during the night when air humidity rose to 80–90%. Humidity levels in different nest types were almost identical (Table 3). Air humidities surrounding nests of leaves, twigs, and dirt were greater than those of grass nests during the early morning hours, probably due to evapotranspiration by the trees above them and to the shading of this air from the sun.

Nests are usually associated with the warming of eggs for incubation (such as for birds), and the importance of regulation of humidity levels within crocodilian nests has generally been overlooked. *Caiman crocodilus* nests maintain almost constant humidity levels as do those of *Alligator mississippiensis* (Joanen 1969). *Caiman crocodilus* eggs exposed to subnormal humidities lost weight and had a lower hatching success (See Artificial incubation and dimensional changes of eggs). Likewise, Modha (1967) found that dry nests of *Crocodylus niloticus* had low hatching successes of 0–10.8%. Laboratory experiments with eggs of *Crocodylus acutus* and *C. novaeguinae* (Rand 1968; Bustard 1971*b*, respectively) suggest that the eggs of hole nesters are quite resistant to dessication, apparently due to hydrophilic albumen present in crocodilian eggs (Bustard 1971*b*).

Embryonic Growth and Incubation Period

Total length measurements of embryos taken from the egg at varying intervals during artificial incubation were calculated as a percentage of the average size at hatching for that particular clutch and plotted against the time from sampling until the date of hatching for that clutch (Fig. 11). Length was linearly related to time for embryos within 50 days of hatching. The shape of the curve at smaller embryos lengths is conjectural, and hence, so is our estimate of incubation time. A minimum estimate is 53 days based on the unrealistic assumption that the embryos could achieve 30–40% of their final length at hatching within a few days. A linear extension of the plotted data probably provides the best average estimate possible, yielding 73 days as the incubation period; we do not imply, however, that early embryonic growth is curvilinear. This value of 73 days is close to
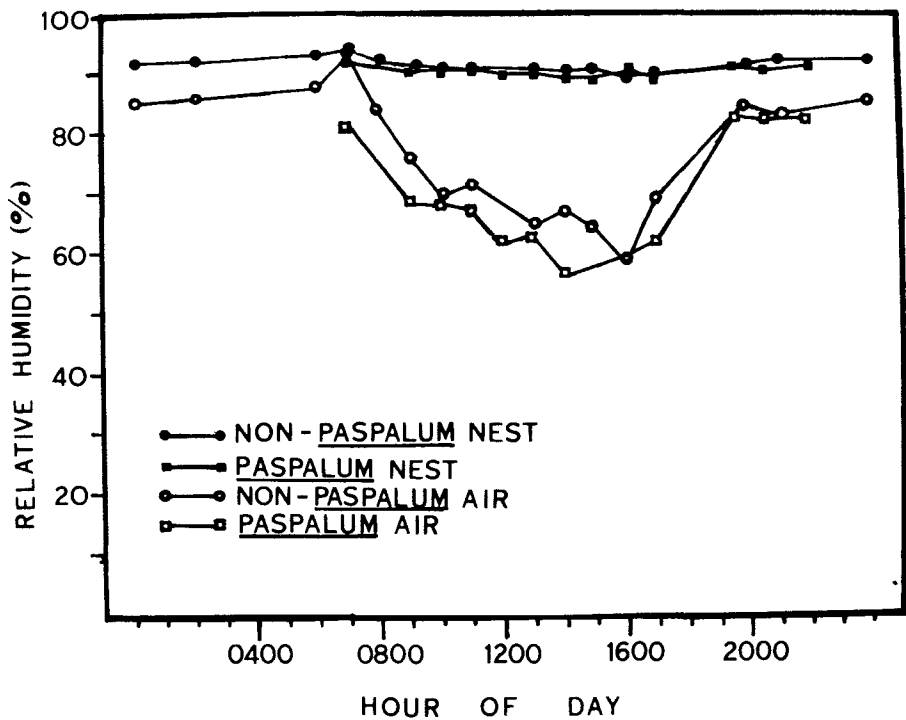
Fig. 10. Twenty-four hour comparison (mean) of nest humidity and air humidity in nests of different construction material. *Paspalum* nest, n = 119; non-*Paspalum* nest, n = 106.

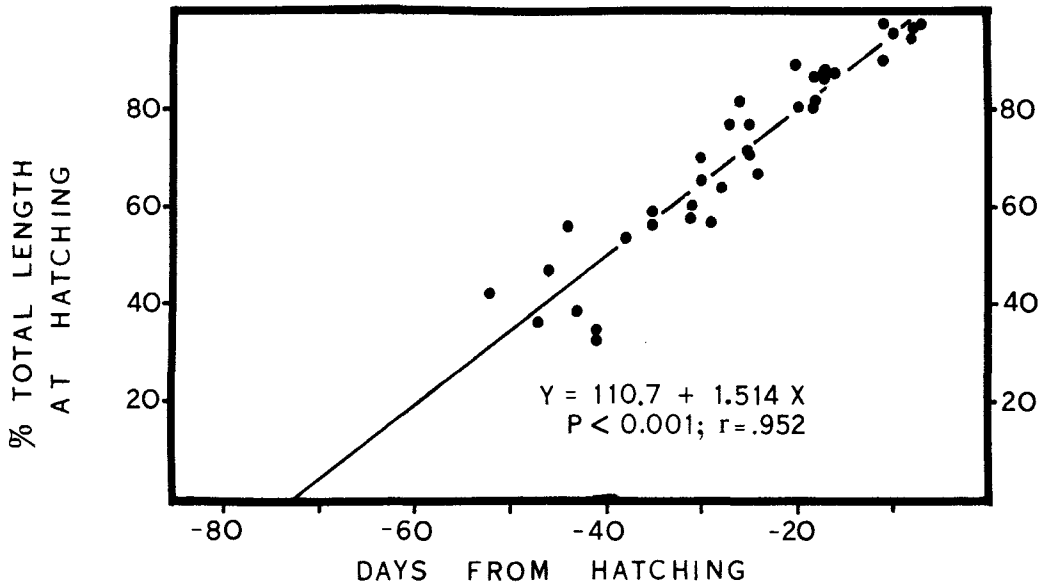$$Y = 110.7 + 1.514 X$$
$$P < 0.001; \ r = .952$$

Fig. 11. Increase in total length (calculated as a percentage of the average total length of young of that particular clutch at hatching) of embryos sampled at different time periods before hatching.

the 75–80 day incubation period of *C. crocodilus chiapasius* from Mexico (Alvarez del Toro 1974).

Hatching and Natality

Young of the year were first seen on 24 October 1973. Most hatching occurred in November, but some hatching extended into late December. One of us (Staton) remained at a nest during hatching on the night of 27–28 November 1973. To avoid disturbing the hatching process, a headlight was used sparingly and limited observations were made during the night.

At 0240 h, the nest was inspected and the top had been pushed back, uncovering several eggs. The adult was nearby and called occasionally, as did several young from within the nest. The female was heard up on the bank at 0320 h, but she returned to the water within 15–30 s. The nest was again inspected and although several empty eggshells had been removed, no additional eggs were open. The adult was heard on land only once again during the night at 0335 h. She remained there for 30–45 s. The nest was inspected with lights again at 0500 h; eight young had emerged, apparently due to the stimulation of and possibly aid provided by the female at 0335 h. However, the manner in which this was performed is not known. Two more young called from within the nest and the adult continued to call until dawn, but no more young hatched. During the day of 28 November the adult was seen by the nest, several eggs had been moved, but hatching did not occur during these daylight hours. Following darkness, the remaining eggs hatched, presumably stimulated by the presence of the female.

Eggs hatched most readily in captivity when the eggs were handled; however, some young caiman pipped and emerged from the egg without apparent stimulus. Pipping was performed by chipping off a small portion of the eggshell and simultaneously or subsequently making one or more slits in the shell membrane. Young sometimes called from the egg before pipping, but called much more frequently after pipping. Frequently, young in eggs which had pipped but not yet hatched, appeared to call back and forth to each other. Such vocality of young just before hatching is known for many crocodilian species and has been termed "communication" between the eggs by Lee (1968:88) in reference to *Alligator mississippiensis*: "I believe that there is communication between the eggs of this reptile. The evolutionary significance of such behavior is obvious. Young alligators emerging long before the mother opens the nest might suffocate. Individuals remaining within the egg, even for a few hours after the nest is opened, would be subject to attack by predators." A more simple interpretation is that the communication is between young and the adult opening the nest (Campbell 1973). This view complements the intricate nature of adult behavior during the hatching process and does not invoke group behavior by the young. In addition, Campbell (1973) notes that the evolutionary significance pointed to by Lee is lost if hatching does not occur simultaneously for all eggs.

In 1971, Rivero Blanco (1974) found 1,970 nests within a 2,000-ha area at Hato La Guanota. Nesting density at this site can thus be calculated as 0.085 nests/ha/breeding season. Using this figure and the average of 28.6 eggs/clutch, natality could be estimated as 2.43 hatchlings/ha, not considering predation. However, 84.2% of the nests were preyed upon, reducing the natality estimate to 0.39 young/ha/breeding season or 2.58 ha/hatchling.

Size of Hatchlings

A total of 100 young were hatched from artificial nests. Weights of hatchlings averaged 41.5 ± 0.63 g (SE) and ranged from 31.0 to 51.2 g. The maximum difference of weights within one clutch was 7.4 g. Snout-vent length averaged 11.29 ± 0.053 cm (SE) and varied from 9.8 to 12.3 cm; maximum range in a single clutch was 1.4 cm. Total length ranged from 19.1 to 23.8 cm and averaged 21.49 ± 0.12 cm (SE). No clutch varied more than 2.4 cm. Snout lengths varied between 0.60 and 0.80 cm ($\bar{x}$ 0.73 ± 0.005 cm, SE); maximum variation of a single clutch was 0.15 cm. Correlations between clutch averages for these variables are diagrammed in Fig. 12.

Hatchling weight was linearly related to original egg weight (Fig. 13). The clutch deviating most from the regression line was Clutch IV (See Artificial incubation and dimensional changes of eggs), incubated under conditions of low humidity.

Postnesting Period

After escaping the nest, hatchlings stayed together in the area of the nest. In the only instance when detailed observations were made, the adult female was consistently found with the young for at least 2 weeks after hatching, during which time the young and adult hid amongst aquatic vegetation. When approached by men, the adult female swam about and vigorously splashed the water with her head as she surfaced. She once swam underwater to within 1 m of the investigator and splashed loudly. However, the female never attacked the observer, even when a hatchling was captured. The adult sometimes called when humans approached and the young become highly wary, sometimes called, and often submerged. Four months later in March 1974 (dry season), this female was in the same pond with her seven remaining young. Attempts to catch them
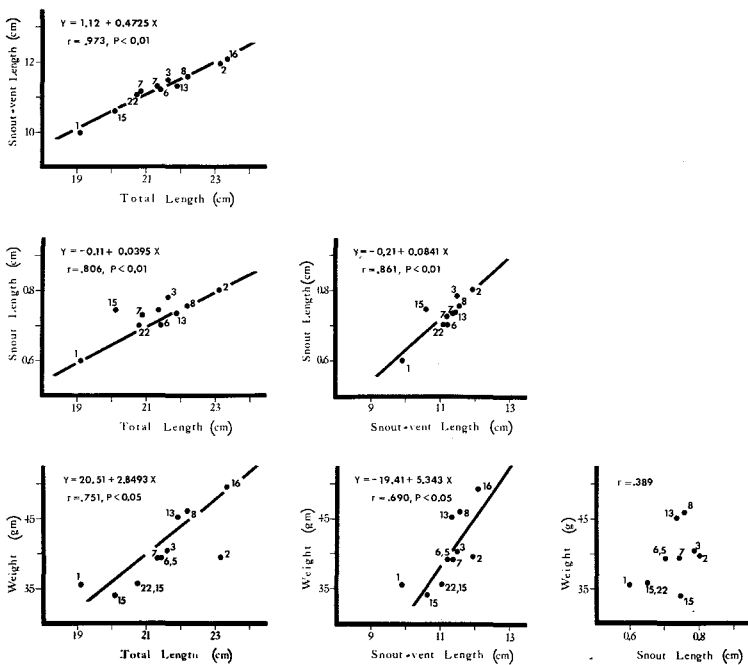
Fig. 12. Correlation between mean values (per clutch) of total length, snout-vent length, snout length, and weight of *Caiman crocodilus* hatchlings from clutches incubated under artificial conditions. Each dot represents one clutch. Sample sizes are equal for each pair of variables except where different values are indicated.
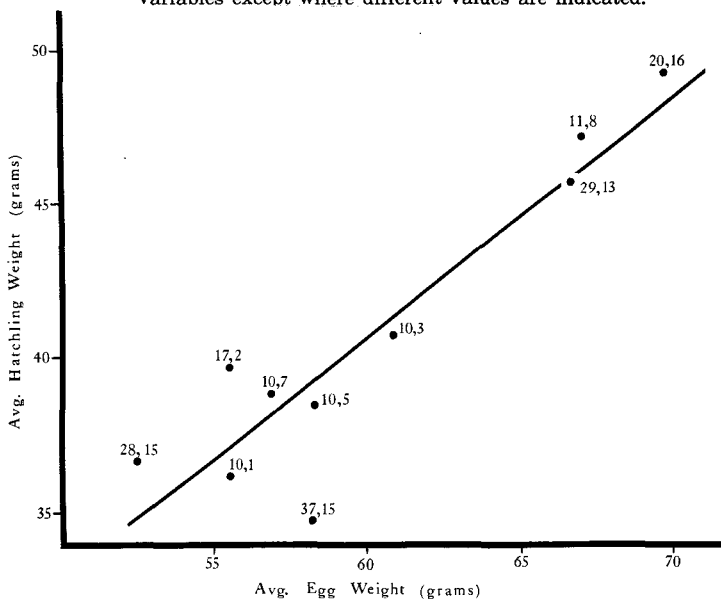

Fig. 13. Relationship between average egg weight and average hatchling weight from clutches of *Caiman crocodilus*. Sample sizes of egg weight and hatchling weight, respectively, are indicated adjacent to observations. Each dot represents one clutch.

resulted in the same vigorous swimming by the adult; however, she did not call or make attempts at aggression.

During the dry season, other pods of hatchlings were found which offer insight into postnatal maternal care. One female at La Guanota observed with her clutch in December was found with her young again on 7 January 1974. On both occasions she showed the same defensive behavior described previously. Two other pods of hatchlings found in the dry season were not tended by the adult. These young were at the edges of rapidly drying lagoons. The young called as several were captured, possibly a warning to others.

Observations on a final group of caimans is especially pertinent. A pod of hatchlings was found in a permanent pond located beneath a water pump. The adult was present and reacted similarly to other adults. In addition, the pond contained young caimans of 1- and 2-year size classes. It seems possible that these were offspring of the same adult from previous years. Protection was given only to the young of the year.

Postnatal care is described for a number of crocodilians (Alvarez del Toro 1969, 1974; Cott 1971b; Hunt 1975; Kushlan 1973; McIlhenny 1935; Pooley 1974; Viosca 1960). The degree to which it is displayed, however, is a matter of controversy. Postnatal behavioral patterns for *Caiman crocodilus* from the Llanos seem to be governed by water availability in the area where the adult and young are located. Seemingly, the adult female remains with the young until the water dries up. At that time she seeks other water, abandoning the young to care for themselves.

Acknowledgments

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