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DOMINANCE OR TERRITORIALITY? THE COLONISATION OF TEMPORARY LAGOONS BY *CAIMAN CROCODILUS* L. (CROCODYLIA)

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ABSTRACT

The behaviour of 51 individually known spectacled caimans (*Caiman crocodilus*) was studied in the Llanos savannahs during the first half of the rainy season. At the onset of the rains caimans left their dry season refuge, a permanent pond, to colonise the appearing temporary lagoons. Caimans less than one year old did not leave the pond. Despite reports of territoriality in this species, no indication of territorial behaviour was found during the colonisation of lagoons. Ninety per cent of the caimans were nomadic. Their movements between water bodies included the permanent pond. Residence in a study lagoon was up to one week long and was followed by prolonged periods of absence. During their residence time in the lagoon, some caimans showed site fidelity, others did not. There was considerable overlap of caiman ranges in the lagoon, but caimans showed spacing behaviour when simultaneously in the water. Priority of access to resources in caimans and other crocodilians is apparently determined by the body size of competitors and not by the site of agonistic encounters. It is argued that the social behaviour of crocodilians is characterised by an absolute dominance hierarchy based on body size, rather than territoriality.

RESUMEN

El comportamiento de 51 caimanes (*Caiman crocodilus*) marcados individualmente fue estudiado en las sabanas de los Llanos durante la primera mitad de la estación lluviosa. Al comenzar las lluvias, los caimanes abandonaron el charco de aguas permanentes (morichal) donde se refugiaron durante la estación seca y colonizaron las lagunas temporales (esteros) que se comenzaban a formar. Caimanes menores de un año de edad no abandonaron el morichal. No obstante previos informes de territorialismo en esta especie, no hubo ninguna indicación de comportamiento territorial durante la colonización de esteros. El noventa por ciento de los caimanes fueron nómadas e incluyeron el charco permanente en sus movimientos entre lagunas. El tiempo regular de residencia en el estero estudiado fue de hasta una semana, seguido por periodos de ausencia prolongada antes de un regreso eventual. Durante la residencia en el estero solo algunos caimanes se mostraron fieles a un determinado sector. Cuando estaban simultaneamente en el agua los caimanes mostraron especiamiento entre sí, pero el traslapo entre las áreas usadas por cada individuo fue considerable. En caimanes y otros crocodílidos el acceso prioritario a recursos es aparentemente determinado por el tamaño de los competidores y no por la localidad del encuentro agonístico. Se argumenta que en vez de territorialismo, el compartamiento social de los crocodílidos se caracteriza por una jerarquía absoluta de dominio basada en tamaño corporal.

INTRODUCTION

Reports of territoriality among spectacled caimans (*Caiman crocodilus*) may be misleading due to a lack of consistency in the definition of territorial behaviour. Territoriality has been inferred from observations of site fidelity (Medem, 1962; Gorzula, 1978), displacement behaviour (Medem, 1962; Staton and Dixon, 1975) and breeding site defence by captive females (Alvarez del Toro, 1974). Although these are typical elements of territorial behaviour, none are sufficient to demonstrate territoriality according to more recent definitions of the term. Kaufmann (1983) reviewed the concepts of territoriality and dominance, defining the first as a space-related dominance, whereby the territory is '. . . a fixed portion of an individual's or group's range in which it has priority of access to one or more critical resources over others which have priority elsewhere or at another time. This priority of access must be achieved through social interaction . . .'. Territoriality is a form of relative dominance (relative to location of the contestants) whereas an absolute dominance hierarchy (e.g. based on body size) is independent of location and time.

In the savannahs of northern South America, large aggregations of spectacled caimans are found in the scarce permanent ponds during the dry season (Staton and Dixon, 1975; Marcellini, 1979). During the rainy season, extensive areas of grassland are flooded, forming temporary lagoons. Caimans move from their dry season refuge to the new lagoons and return to the permanent ponds when the lagoons dry out (Staton and Dixon, 1975; Gorzula, 1978). The present study describes the behaviour of 51 individually known

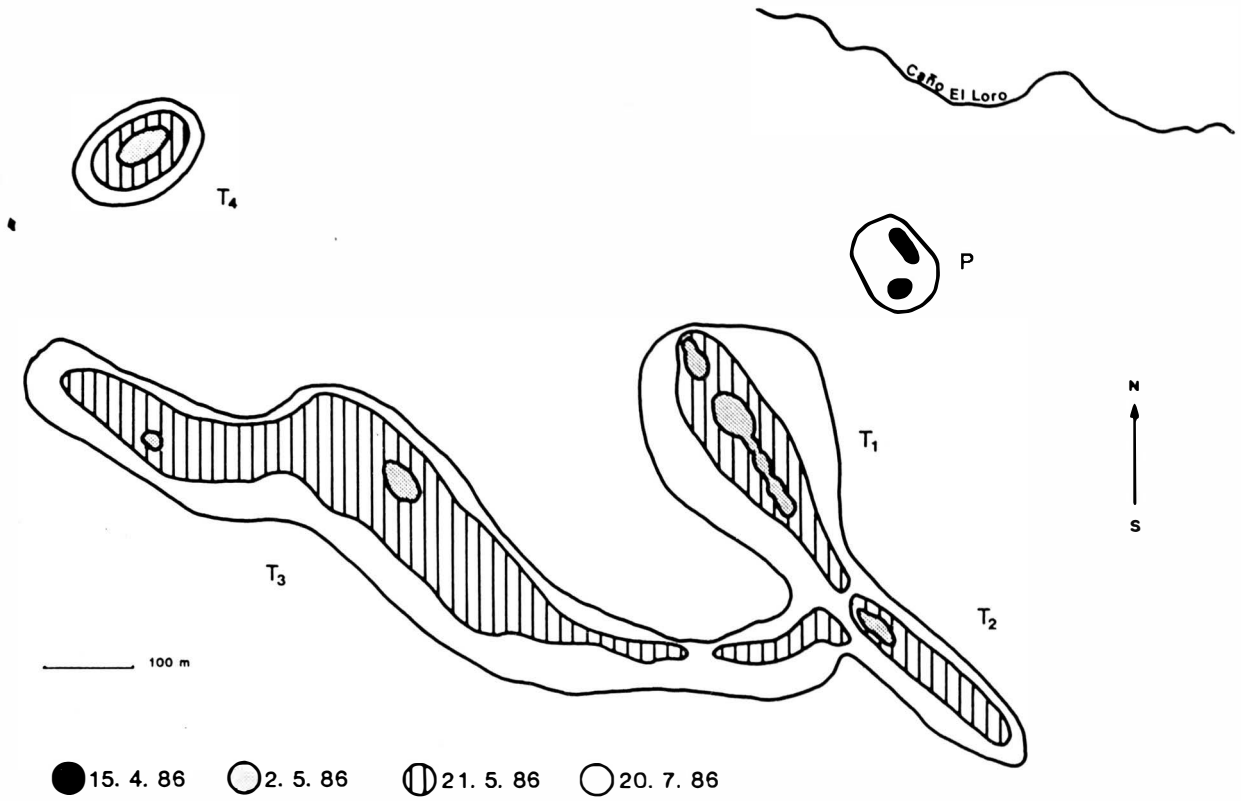

Fig. 1 The study site, showing the permanent pond P and the growth of the temporary lagoons T over the course of the rainy season. T1, T2 and T3 are considered together in the text as the temporary lagoon of the study. They became a continuous water body in June. T4 was visited sporadically and not included in the nightly census. The next temporary lagoon (T5, not on the map) was located 1km to the northeast of P.

caimans during their colonisation of temporary lagoons. The study period corresponds to the mating season of caimans in this environment (Staton and Dixon, 1976). The inadequate use of the concept of territorial behaviour is discussed in respect to former reports of territoriality in this species and other crocodilians.

METHODS

The study took place at the Hacienda Los Naranjos (4° 13′ N, 73° 16′ W, 400m above sea level) in the Colombian Llanos. The Llanos is the seasonal grassland savannah located northeast of the Andean range, both west and east of the Orinoco river. For descriptions of this region see publications by Hueck (1966), Staton and Dixon (1975) and Cabrera and Willinck (1980). There is a single rainy season usually from April to November, and a dry season from December until March. Average annual rainfall in the study area is 3438m and the average temperature is 25.7°C (written comm. HIMAT, Bogotá). The data were collected daily between 12 April 1986 and 20 July 1986. This period corresponds to the first half of the rainy season. Rainfall at the study site was recorded daily.

The spectacled caiman (*Caiman crocodilus* L.) is common in the study region, where it is sympatric with two other *Alligatoridae* species: *Paleosuchus palpebrosus* and *Paleosuchus trigonatus* (Medem, 1981). The study population was never hunted for commercial purposes. During this study 19 female, 22 male and 10 unsexed (juvenile) caimans were captured, measured, marked and released. Their size range was 16.6cm to 75.1cm snout-vent-length (SVL, measured to the anterior end of the cloaca). Three age categories were defined using growth data for free-ranging spectacled caimans published by Gorzula (1978):

- — Juveniles (13): SVL <36.0cm. Animals less than three years old.
- — Immatures (26): SVL 36.0cm-50.0cm.
- — Adults (12): SVL >50.0cm. Animals 7 years in age or more. Females sexually mature (Rivero-Blanco, 1974).

Individuals smaller than 100cm total length were captured by hand, seizing the neck and the base of the tail simultaneously. Larger caimans were hooked around the neck against the ground, then secured with a noose to pull them out of the water. Captured caimans were weighed, restrained on a board and then sex was determined by cloacal probing (after Brazaitis, 1968) and/or visual examination of the cloaca with an otoscope. After taking morphometrical data, the caimans were individually marked using a code of holes punched into the proximal vertical scales of the tail and a number painted on their backs with fast drying metallic paint for model airplanes. This number remained recognisable for about six weeks. An attempt to mark the caimans using reflective tape was unsuccessful. The different coloured dots attached to

the craneal plate with cyanoacrylate bonder fell off within one week due to shedding of the *Stratum corneum*. A detailed description of scars, injuries and other conspicuous marks was recorded on each individual's file. Within one hour of capture the caiman was released at the capture location. Data on morphometry, injuries, population structure, and habitat choice will be published elsewhere.

The present study was carried out at night for two reasons: 1. The assumption that during the rainy season caimans are most active at night. 2. Close approach for identification and eventual capture of submerged caimans during the day is almost impossible due to the shyness of the animals. Data on the activity of caimans in the dry season indicate that over 80 per cent of the individuals are found in the water between 2000h and 200h at night (Marcellini, 1979). Nightly water temperature variation between 24.3°C and 29.6°C at the time of censusing did not correlate with caiman activity (Staton and Dixon, 1975). Comparable data for the rainy season is not yet available.

Caimans can be easily located at night using spotlights since their *Tapetum lucidum* reflects the light intensively reddish to orange and, at close range, white. Night censuses have been estimated to record over 90 per cent of the caimans in a pool (Staton and Dixon, 1975). The study lagoon (Fig. 1, T1 + T2 + T3) was censused within 15 minutes between 1900h and 300h each night. The time depended on weather conditions. The position of each caiman was recorded using compass triangulation and landmarks around the lagoon. Approach and identification of marked individuals and the capture of unmarked ones were performed after finishing the census. During rains the water surface became rough and submerged caimans could not be seen, making identification difficult. Successful identification was achieved in 52 per cent of all sightings (N= 189). Data on the relative positions of caimans and censuses at the permanent pond are excluded from the analyses, because observations here became inaccurate as cyperaceous vegetation increased. Statistical analyses, unless otherwise indicated were performed using the software statistics package Minitab (C) at the Computer Main Frame of Cambridge University (UK).

RESULTS

1. Colonisation of temporary water bodies

At the onset of the rainy season in mid-April temporary lagoons started to appear in the vicinity of the single permanent pond of the study area (Fig. 1). At the beginning of observations (12 April 1986) 30 caimans were counted in the 0.14 ha permanent pond. Thereafter, a successive decline of caiman numbers was recorded. Five weeks after the initial census less than three caimans could be regularly found in the permanent pond. The first lagoon appeared on 22 April 1986 with an area of less than 0.2 ha. Five nights later three caimans were sighted in it.

Ten caimans, less than one year old, were marked in the permanent pond during the first three weeks of the study. They were often resighted in the same pond, but never in the temporary lagoon. The two year old female F-7 (SVL = 26.9cm) was the youngest caiman recorded covering the 180m which separated the permanent pond from the adjacent lagoon (Fig. 1). A similar result is reported by Gorzula (1978), who found caiman hatchlings only in permanent ponds of a seasonal savannah in Venezuela (but see Ouboter and Nanhoe, 1988, for swamp forest habitat).

Out of 27 caimans (yearlings included) marked in the permanent pond between 15 April 1986 and 4 June 1986, 22 per cent were resighted during that period in the same pond, 44 per cent were resighted in the adjacent lagoon, and 34 per cent were not seen again. No caiman identified in the temporary lagoon between 26 April 1986 and 28 May 1986 was resighted in the permanent pond (N = 13). Thus, during the first month of the rainy season caimans moved from the permanent pond to temporary lagoons, but apparently not in the opposite direction. Later in the season, however, movements from the lagoon to the permanent pond were observed (see below).

Although vegetation in the permanent pond made the nightly censuses from June onwards inaccurate, sightings in June included two adult females, two adult males, one immature male and several juveniles. This shows that during the rainy season the permanent pond was still used by caimans of all age categories and both sexes.

2. Movements between lagoons

Twelve instances of movements from the permanent pond to the lagoon by known individuals were recorded. Movements between lagoons or from these to the permanent pond were recorded five times. One example of such movements was the immature male M-9 (SVL = 47.5cm), marked in the permanent pond on 28 April 1986, resighted there on 29 April 1986 and 5 May 1986, then seen in the lagoon T3 on 12 May 1986 and, one month later, in lagoon T4 (Fig. 1). Short distance movements between the lagoons T1, T2 and T3 (Fig. 1) when these were still discrete water bodies are considered as movements *within* the study lagoon. Thirty caimans recorded for an average total time of 2.4 days in the study lagoon, out of 76 days of observations (see below), are assumed to have moved between distant water bodies including a brief stop at the study lagoon. Caimans were seen travelling through the savannah on two occasions during daylight (900 hours, 1000 hours) and once in the evening (1900 hours). No individual from the marked population sample was resighted in the temporary lagoon T5, located 1km away from the permanent pond, but spectacled caimans have been reported to travel overland distances of 2.4km and 5.0km (Gorzula, 1978; Marcellini, 1979).

The behaviour of the caimans during the first half of the rainy season can be characterised as nomadic. After the appearance of temporary lagoons and their colonisation by caimans, resightings of known individuals in neighbouring water bodies indicated that they did not become sedentary in the new lagoons, but rather moved between them. Such movements were made by caimans of all age and sex classes, except

	N	*proportion resighted*	*median value of resightings/caiman*	*range of resightings/caiman*
Males	22	15 (68%)	3.0	0 - 23
Females	19	12 (63%)	2.0	0 - 9

Table 1: Resighting rates of male and female spectacled caimans during the study.

for yearlings (see above). No significant difference in the resighting rates of males and females was observed (Table 1). Each caiman apparently moved between lagoons independently of other conspecifics, since no two or more individuals visited and left the study lagoon simultaneously.

The movement between water bodies ceased during the last week of the study, when high caiman numbers were consistently attained during the nightly censuses, and the same individuals recorded each night in the study lagoon. The average number of caimans counted in the lagoon increased from two individuals per night over the last six weeks, to 10 individuals per night during the week thereafter. This change was not related to changes in the rainfall pattern. It probably corresponds to the onset of the breeding season when adult females become sedentary and build nests (Staton and Dixon, 1976). This study did not verify if this sedentary behaviour persisted until the end of the rainy season.

3. Total time present in the lagoon

Fig. 2 shows the frequency distribution of the total number of days that each caiman (N = 33) was recorded in the lagoon during the study (76 observation days considered). The observed mean was 3.9 days. In order to correct for the unknown number of caimans which did not visit the lagoon at all, a mean of 3.0 days was chosen to calculate the random Poisson distribution. Each observed value in Fig. 2 represents a minimum value since individuals were only identified in 52 per cent of the sightings (N = 189). The observed distribution was not significantly different from the Poisson (Fig. 2, $P < 0.1$, chi-square = 9.12, $df = 4$). The large value of chi-square is due to three individuals who significantly exceeded 12 days in the lagoon (Fig. 2, $P < 0.0001$ in the Poisson distribution). If they are omitted from the sample the mean time in the lagoon is 2.4 days and the value of chi-square drops to 1.19 ($df = 3$, NS) in a comparison with a random Poisson distribution with a mean of 2.0.

Three male caimans, M-1 (SVL = 41.6cm), M-5 (SVL = 41.5cm) and M-11 (SVL = 50.2cm), were identified in the lagoon on 16, 17 and 24 days respectively. Since their time recorded at the lagoon was significantly higher than that of 30 other caimans, the former are referred to as *residents* (10 per cent of the sample) and the latter as *visitors* (90 per cent of the sample). The residents M-1 and M-5 visited the lagoon in bouts of several consecutive days, but M-11 was more or less constantly present (Fig. 3). The unusual behaviour of M-11 may have been related to a severe snout wound evidently inflicted with a machete by a

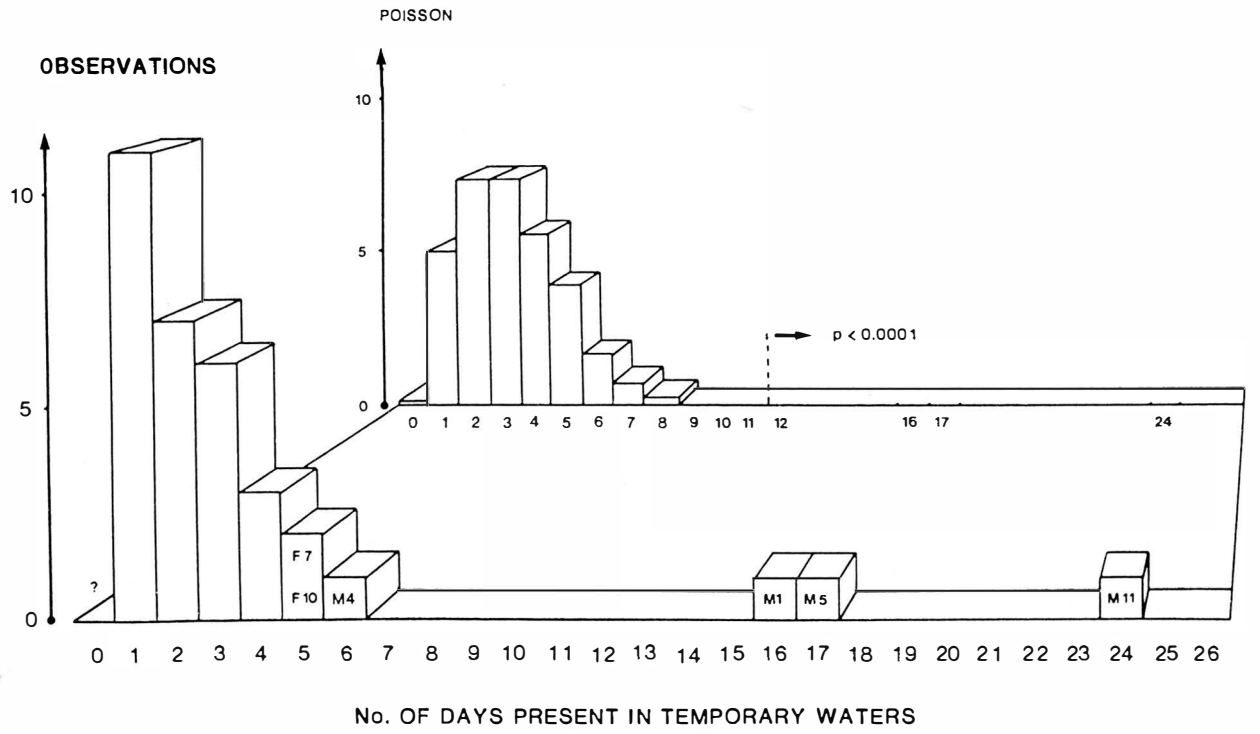

Fig. 2 Frequency distribution of the total number of days that each caiman was recorded in the temporary lagoon over the 76 days of observation. The identity of the six caimans recorded five or more days at the lagoon is indicated. The distribution of the data (foreground) is compared with a random Poisson distribution (background) (see text).

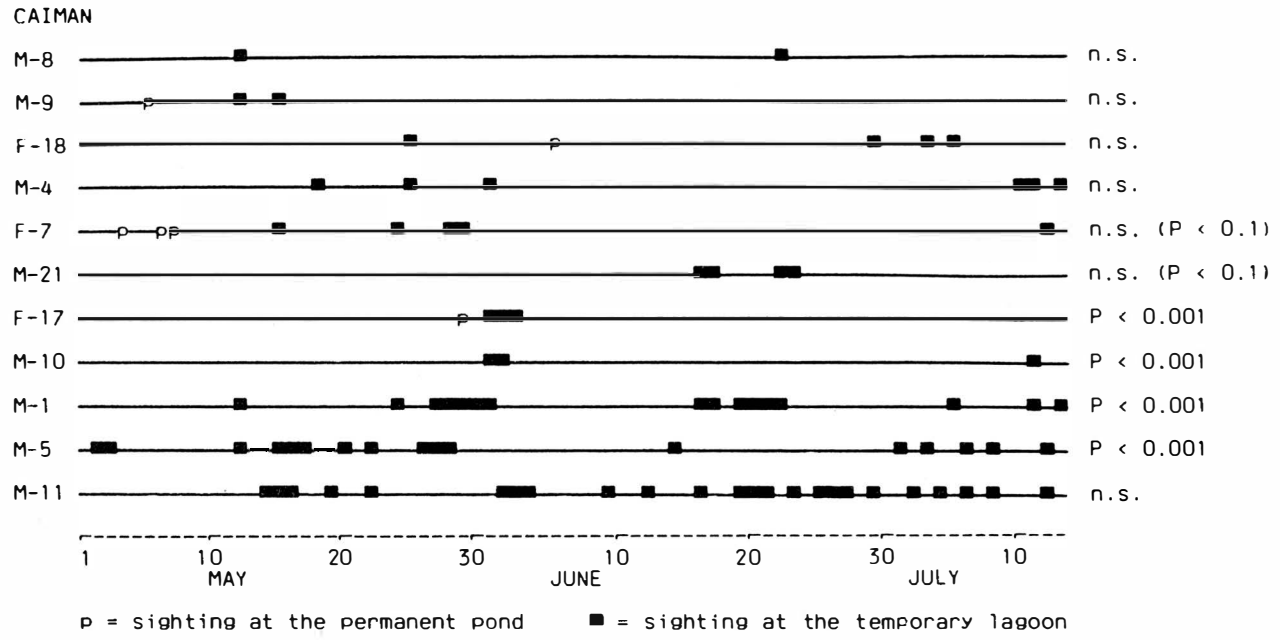

Fig. 3 Occurrence of some caimans at the temporary lagoon. Each square represents one day. This sample was used for a sequence analysis (Siegel, 1958) testing clumpness of each caiman's sightings over time. The significancy of this test is indicated by *P* values for each caiman.

hunter. This wound probably interfered with feeding for a long time, since M-11 had the lowest body condition of the population sample at the beginning of the study. Thirty days after its first capture, M-11 had reached a just below average body condition.

4. Temporal pattern of visits to the lagoon

Each caiman visited the temporary lagoon at intervals (see Fig. 3 for an exemplary subset of data). The days between visits to the lagoon are referred to as the absence interval. The sample is composed of the pooled absence intervals of 22 caimans recorded more than once in the lagoon. The frequency distribution of the absence intervals recorded was bimodal (Fig. 4) and differed significantly from the expected geometric distribution ($P < 0.001$, chi-square = 70.3, $df = 14$). This difference was still significant at the 0.1 per cent level, when the three resident caimans were removed from the sample. The large value of chi-square is due to the high number of very short absence intervals (one to two days) and very long absence intervals (longer than 34 days). In general, caimans visited the lagoon in bouts up to one week with brief absence intervals within bouts, and there were prolonged absence intervals between bouts. Out of 30 caimans recorded at the temporary lagoon, 12 (40 per cent) returned to the lagoon after an absence period of at least two weeks.

This pattern is supported by sequence analysis (Siegel, 1956) of the presence and absence days of 10 single individuals seen in the lagoon at least three

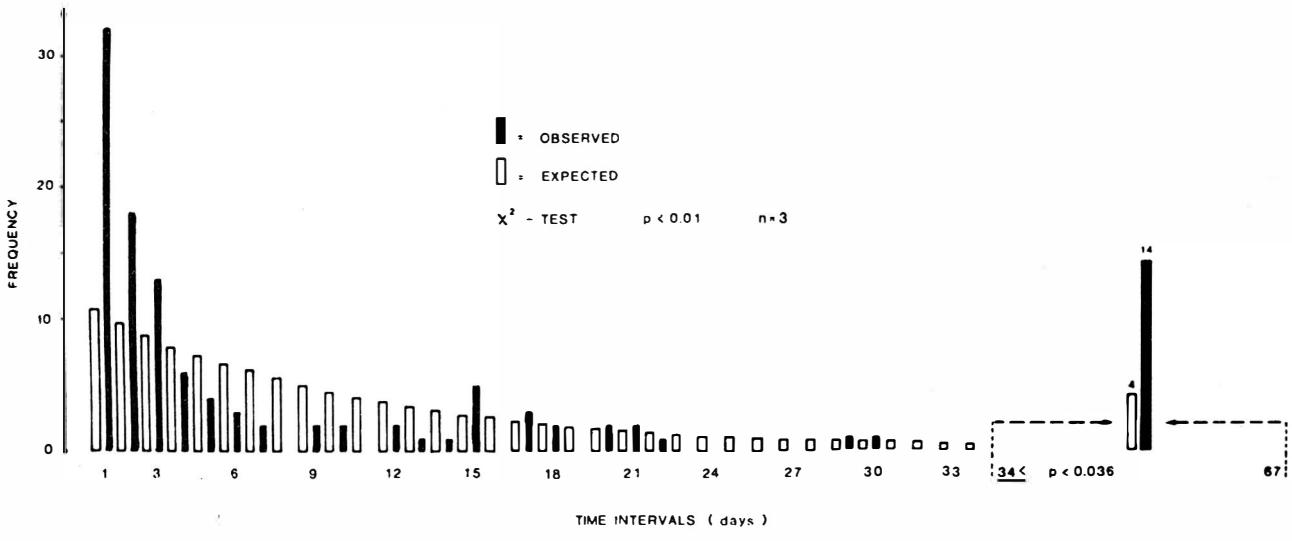

Fig. 4 Frequency distribution of absence intervals between two sightings of the same individual at the temporary lagoon (33 caimans pooled). Absence values between 34 and 67 days are pooled. The distribution of observed values is bimodal and differs significantly from a calculated geometric distribution.

times. The days present were significantly clumped in time for four caimans (Fig. 3): the resident males M-1 and M-5, and the visitors male M-10 (SVL = 67.0cm) and female F-17 (SVL = 53.5cm). They displayed the pattern of short visits followed by prolonged absence intervals. The visits of four other caimans were sporadic events. Because the resident immature M-11 rarely left the lagoon, its days of presence were not clumped in bouts.

5. Ranges within the temporary lagoon

Seven nightly focal observations of 85 to 555 minutes duration were made on the resident caiman M-11. These indicated that there was no consistent ranging pattern within the lagoon. Movement rates varied between 7m/h and 180m/h (median value = 42m/h, $N = 7$). The absolute distance covered during the 555 minutes observation was 875m, and the longest straight line between two locations for the same night was 338m. Values obtained from two other individuals lay in the same range. The caimans used to move parallel and close to the shore. In general, they swam submerged in short bursts followed by prolonged stops at the water surface, usually facing the shore or parallel to it. These stops could last for several hours. When caimans were stationary the body hung down vertically and the tail tip rested on the ground as a point of support. Caimans usually were not stationary in water deeper than a body length, since tail movements were required to keep the eyes and nostrils above the water surface. Caimans often crawled through the grass along the shore in a water depth of about 5cm, leaving a trail of flattened grass with a serpentine shape.

The average distance between the location of a caiman on one night and its location the night after was 180m (SD = 214, range 25-940m, $N = 30$, eight caimans pooled). Capture and handling did not induce caimans to leave that area of the lagoon. The mean distance from the capture site to the location the following night was 184m (SD = 183.2, $N = 7$), while the mean distance for caimans identified but not captured was 182m ($N = 21$).

The maximum distance covered between two locations over seven days, in which the caiman was sighted three or more times, was measured. This value corresponds to the range covered within the lagoon during an average visiting bout. The median for eight caimans was 240m (range 25-800m). The size of the seven-day-ranges compared with the average moving rate of 180m/night and the size of the lagoon (Fig. 1) suggests that caimans showed fidelity to the lagoon portion chosen at the start of a visiting period. This is referred to as short term site fidelity.

There was no consistency in the area of the lagoon chosen after a prolonged absence (i.e. absence of more than seven days). Some individuals showed long term site fidelity, for example the adult female F-9 (SVL = 54.4cm), which returned after 35 days absent to a site within 50m of its last location. Others were resighted hundreds of metres away from their last location. The male M-8 (SVL = 63.9cm) was found 650m away from the site of the last record after 34 days of absence. Values obtained from 11 more caimans lay between these two extremes.

Sufficient location data was obtained from the resident caimans to estimate ranges within the lagoon for the three month observation period. M-1 ($N = 16$) prefered the eastern part of the lagoon (Fig. 1, T2), but occasionally visited the western areas also. M-5 ($N = 17$) and M-11 ($N = 24$) were mostly found along the western side of the lagoon (Fig. 1, T3), but were also sighted in eastern areas. Considerable overlap between ranges was observed. Most visitor caimans were recorded within the ranges of residents. However, few caimans were seen in the temporary lagoon during most censuses (median = 3 caimans, range 0-22, $N = 66$). Hence, range overlap did not necessarily mean simultaneous use of an area. If caimans occurred simultaneously in an area, they showed spacing behaviour (see below).

6. Spatial distribution of caimans in the lagoon

The spatial distribution of immature and adult caimans in the temporary lagoon, was analysed using a computer program for spatial analysis written by D. Brown (Statistics Group, Cambridge University, UK). The lagoon was subdivided into two equal size sectors (Fig. 1, T1 + T2 and T3). The sample was 11 cases in which four to nine caimans occurred simultaneously in the lagoon sector analysed. For eight cases the probability calculated by the simulation indicated regularity, showing a significant tendency for regularity in the spatial distribution of caimans ($P < 0.01$, combined probabilities test, Fisher, 1958).

The shortest nearest-neighbour distance between two stationary caimans was 15m, but more commonly a minimum nearest-neighbour distance of 30m was observed. This distance may depend on the body sizes of the individuals concerned, but such a relationship was not analysed due to the small sample size. Quantitative analysis of social displacement was not possible because only three social interactions between caimans were observed during the study.

DISCUSSION

There was no indication of territoriality among caimans in the Llanos during the first half of the rainy season. Observations on the reproductive biology of caimans in the Venezuelan Llanos (Staton and Dixon, 1976) suggest that the study period corresponded to the mating season. According to Kaufmann (1983), a territorial individual is expected to be almost continuously in its territory, in order to displace intruders and guarantee its priority access to resources. Caimans in the studied lagoon system did not fulfil this elementary condition for territoriality: 1. Most caimans were nomadic between lagoons. 2. Visits to a lagoon were brief, lasting a maximum of one week. These visits were often interrupted by some nights of absence. 3. Some caimans did not show any preference for any location, while others did remain within a certain sector of the lagoon during their visit. Ranges within the lagoon overlapped considerably. During the short absence periods within a visiting bout caimans may have been in the vegetation next to the lagoon.

Caimans in captivity are known to rest in the vegetation for several days after a substantial meal (Pachon, pers. comm.). During the long absence periods between visits to the study lagoon caimans presumably seeked distant lagoons as supported by three observations of movements across the savannah and five resightings of marked individuals in water bodies other than the study lagoon. Movements between lagoons were not unidirectional, as indicated by 40 per cent of the caimans returning to the study lagoon after a minimum of two weeks absent.

The nomadic behaviour of caimans may be partly related to differences in frog availability between lagoons. Frogs are probably the most common food item in the study lagoon (pers. obs.). Alternative food items found in similar environments, such as fish, snails or crabs (Staton and Dixon, 1975; Gorzula, 1978; Seijas and Ramos, 1980), were not found in the study lagoon. Prior to the start of the rainy season, caimans were found in high densities in the permanent ponds. With the onset of the rains, the calling activity of a common frog, *Physalaemus neglectus dunni*, at the permanent pond increased noticeably. However, as lagoons appeared in the vicinity, the calling activity of frogs decreased to zero in the permanent pond and became deafening in the newly formed lagoons (pers. obs.). Most caimans were found in these lagoons from then onwards. Caiman numbers and calling activity of frogs were particularly high in new lagoons on nights following heavy rainfall (pers. obs.). As the lagoon level rose, caiman numbers and the calling activity of frogs decreased. Two weeks after the onset of the rains, the number of caimans seen in the lagoon was no longer related to rainfall. Although caiman movements between temporary water bodies have been reported before (Gorzula, 1978; Marcellini, 1979), the nature of this behaviour is still not understood.

The nomadic behaviour of caimans during the study suggests that access to resources in the lagoon was not determined by a site-dependent dominance hierarchy (territoriality, *sensu* Kaufmann, 1983). Instead, the distribution of the caimans in the lagoon was probably determined by a body-size dependent hierarchy (Staton and Dixon, 1975), which resulted in spacing behaviour. Spacing behaviour may be a response to potential cannibalism and the aggressive nature of agonistic encounters, which can lead to severe injuries (Staton and Dixon, 1975; Gorzula, 1978).

A site-dependent hierarchy is likely if opponents have a similar body size, as is the case among adult mammals, birds and many arthropods. But similar sized opponents seldom meet among crocodilians due to the large variance in body size. In spectacled caimans, a young sexually mature female can increase its body weight threefold before reaching full size. A fully grown adult caiman achieves 100 to 200 times the weight of a juvenile (Rivero-Blanco, 1974; Medem, 1981). Since most agonistic interactions involve different sized caimans, the outcome of such interactions is generally determined by a body size determined absolute dominance, rather than the location of an encounter. The present study shows lacks of territoriality during a limited period. The theoretical considerations above predict also lack of territoriality during the rest of the year, when caimans are sedentary around breeding sites or in permanent ponds during the dry season.

Territorial behaviour has been reported for other crocodilians, such as *Crocodilus niloticus* (Modha, 1967; Pooley and Gans, 1976; Hutton, 1982), *Crocodilus acutus* (Lang, 1975) and *Alligator mississippiensis* (Garrick, 1975; Garrick and Lang, 1977). Most of these reports use the term 'territory' for an area defended by adults and mention body-size dependent displacements. The defence of an area cannot be termed territoriality, unless the outcome of fights depends on the site of the encounter and is largely independent of body size. So far there is no evidence for site-dependent hierarchies among crocodilians. Even if such a hierarchy existed among fully grown males defending mating areas or females defending breeding sites, the proportion of displacements determined by the site of the encounter rather than the body-size of opponents would still be low. Considering the large variance in the body size of contestants and the accumulated evidence for body-size dependent displacements, the social system of crocodilians is more adequately regarded as an absolute dominance hierarchy in which body size determines access to resources.

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A LATE PLEISTOCENE HERPETOFAUNA FROM BELL CAVE, ALABAMA

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ABSTRACT

Three stratigraphic units in Bell Cave, northwestern Alabama, have yielded fossil herpetofaunas that are mainly analogues of the modern ones in the area. Two of the fossiliferous zones have been dated by the Carbon 14 method; Zone 1/2 at 11,820 +480 to -500 BP and Zone 4 at 26,500 +870 to -990 BP. An intermediate unit (Zone 3) did not yield a Carbon 14 date, but is faunistically nearly identical to Zone 1/2. Excessive damage was present in many of the fossils due to predators and gnawing scavengers, thus only 18 per cent of the 3,953 herpetological fossils could be identified to the generic or to the specific level. The wide variety of habitats represented by the fossils (small, clear streams; larger, slower streams; marshy wetlands; waterfalls and associated talus seeps; woodlands and woodland edges) is attributed to transportation by palaeopredators. None of the amphibian or reptile species is extinct, in contrast to the mammalian fauna which has several extinct taxa. Zone 1/2 has at least 24 species, including one northern and two slightly eastern extralimital ones. Zone 3 has at least 24 species, including the same three extralimital species that occur in Zone 1/2. Zone 4 has 13 species, including only two slightly eastern extralimital ones. It is difficult on the herpetological remains to suggest a palaeoclimate much different from the climate of the area today. Certainly, the presence of many egg-laying turtles, lizards and snakes in all units negates a tundra-like or boreal-like interpretation of the palaeoclimate.