REPRODUCTIVE STATUS AND NESTING ECOLOGY OF THE ORINOCO CROCODILE (*Crocodylus intermedius*) IN THE COJEDES RIVER SYSTEM, VENEZUELA

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ABSTRACT

During 1996-1997, ninety-one reproductively active Orinoco crocodiles (males and females) were estimated for the Cojedes River System (CRS), Venezuela. In those years at least 48 different female crocodiles nested in 45.7 km of surveyed sections of the CRS. The reproductive population was mostly found in Caño de Agua (63.2%) and in the lower Sarare River, areas with the best quality nesting habitat. Egg-laying starts during the months of lowest precipitation (January-February) and hatching takes place at the onset of the rainy season (late April-early May). Mean number of hatchlings per pod was 26.0±13.9. Nest distribution along the rivers suggests a polygynous system, in which dominant males form groups with two or more females. Lack or scarcity of good nesting substrate seems to be an important factor determining the current distribution of the species in the CRS. Most frequently selected nesting sites are composed of a high proportion of sand (>70%). There was no evidence of nesting toward the south end of Cojedes and in La Culebra, river sections with relatively poor nesting habitat. Several km of good nesting habitat have been lost since 1991 due to river diversion. Recent data collected from 1998 to 2002 indicated a high variability in hatching success, presumably related to changes in river water levels at the end of the incubation period.

KEY WORDS: adult nesting density, clutch size, *Crocodylus intermedius*, nest density, nesting chronology, nesting habitat, Orinoco crocodile

RESUMEN

Durante 1996-1997 se estimó en 91 el número de cocodrilos del Orinoco reproductivamente activos (machos y hembras) en el sistema del río Cojedes (SRC), Venezuela. En esos años al menos 48 hembras de cocodrilos anidaron en 45,7 km muestreados del SRC. La población reproductiva se concentra en Caño de Agua (63,2%) y en la sección baja del río Sarare, áreas con los mejores hábitat de anidación. La postura de huevos comienza en los meses de precipitación más baja (enero-febrero) y la eclosión ocurre al comienzo de la estación lluviosa (finales de abril- comienzos de mayo). El número medio de crías nacidas por nidada fue 26.0±13.9. La distribución de nidos a lo largo de los ríos sugiere un sistema polígamo, en el cual un macho dominante se agrupa con dos o más hembras. La falta o escasez de buen sustrato de anidación parece ser un factor importante en la determinación de la distribución actual de la especie en el SRC. Los lugares de anidación más frecuentemente utilizados están compuestos de una gran proporción (>70%) de arena. No hay evidencia de que la especie se reproduzca en la sección sur del Cojedes y en Caño La Culebra, seccionescon baja calidad de hábitat de anidación. Varios km de buen hábitat de anidación se han perdido desde 1991 debido al desvió del río. Datos colectados entre 1998 y 2002 indican una gran variabilidad en el éxito de eclosión, presumiblemente debido a cambios en el nivel del río en la etapa final del periodo de incubación.

PALABARAS CLAVES: cocodrilo del Orinoco, *Crocodylus intermedius*, cronología de anidación, densidad de adultos anidantes, densidad de nidos, hábitat de anidación, tamaño de nidadas

RESUMO

Durante 1996-1997 determinei em 91 o numero de crocodilos do rio Orinoco reprodutivamente ativos (machos e fêmeas) no sistema do rio Cojedes (SRC), Venezuela. Nesses anos pelo menos 48 fêmeas de crocodilos fizeram ninho em 45,7 km percorridos no SRC. A população reprodutiva se concentra em Caño de Agua (63,2%) e na parte baixa do rio Sarare, ambas áreas com os melhores habitats para aninhamento. A deitada de ôvos começa nos meses de precipitação mais baixa (janeiro-fevereiro) e a eclosão acontece no começo do periodo das chuvas (fim de abril – começos de maio). A distribuição dos ninhos na beira dos rios sugere um sistema polígamo, onde um macho dominativo se agrupa com duas ou mais fêmeas. A falta dum bom substrato para o aninhamento parece ser um fator importante na distribução atual da espécie no SRC. Os lugares de aninhamento mais frequentemente utilizados se compoem de uma grande proporção (>70%) de areia. Não ha diferença entre a reprodução da espécie no lado Sur do Codejes e no Caño La Culebra, ambas partes com baixa qualidade de habitat de aninhamento. Varios km de bom habitat para aninhamento tem se perdido desde 1991 por causa do desvio do rio. Dados colheitados entre 1998 e 2002 indicam uma grande variabilidade no êxito da eclosão, possivelmente pela mudança no nivel do rio na etapa final do periodo de incubação.

PALAVRAS CHAVE: crocodilo do Orinoco, *Crocodylus intermedius*, cronologia de aninhamento, densidade de adultos ninhantes, densidade de ninhos, habitat de aninhamento, tamanho das ninhadas

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Little has been published on the reproductive ecology of the Orinoco crocodile (*Crocodylus intermedius*), one of the most critically-endangered crocodilian species of the world (Ross 1998). Basic information on this regard was published by Medem (1981, 1983). Thorbjarnarson and Hernández (1993*a*,*b*), working both with captive and wild crocodiles, shed some light on several aspects of the reproductive ecology of the species.

The largest population of the Orinoco crocodile is found in the Cojedes River System (CRS), at the periphery of the Orinoco crocodile distribution (Seijas and Chávez 2000). Ayarzagüena (1987) and González-Fernández (1995) reported data on the reproductive status and ecology of the Orinoco crocodile in the CRS, an area currently under heavy

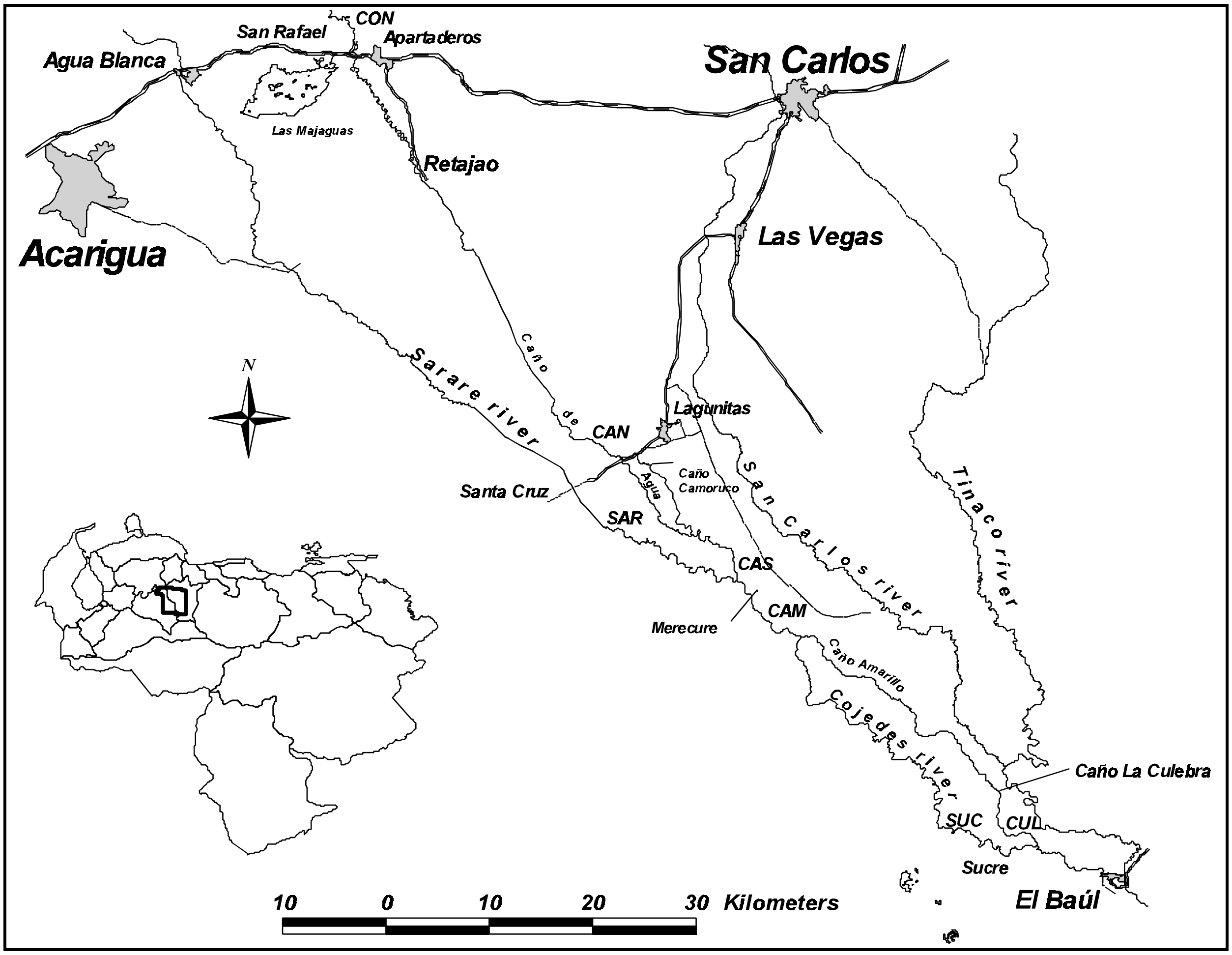

Fig. 1. Map of the study area (Cojedes river system) Venezuela, indicating the position of landmarks, reference points, and main river reaches surveyed.

anthropogenic pressure due to its proximity to some of the important agricultural, urban and industrial centers in the country (Ayarzagüena 1987, 1990; Godshalk 1978, 1982; Seijas 1998). In the last 40 years, human activities have changed the characteristics of the Orinoco crocodile habitat in the CRS. Some changes have modified the water quality of the river. Others have altered the physical characteristics of the river through damming, dredging, and canalization (Seijas 1998). To what extent have these alterations affected reproduction of the Orinoco crocodile? It has been suggested (Ayarzagüena 1987) that dredging and canalization, for example, have a negative impact on crocodiles because they destroy nesting beaches. This should translate into a reduced nest density in modified sections in comparisons to sections where the river maintains its meanders.

The main objectives of this study were: 1) to answer basic questions on the reproductive ecology of *C. intermedius* in the CRS in reference to nesting habitat, clutch and pod size, nest chronology, location and success, and nesting population size, and 2) to discuss the reproductive ecology of the species in the context of the anthropogenic modifications of the CRS.

STUDY AREA

This study was conducted in the mid- and lower- reaches of the Cojedes River System of northwestern Venezuela (Fig. 1). In the CRS rivers flow from northwest to southeast through several types of landscapes that vary in relief, land-cover types, and main human activities. In the northern part of the CRS, agricultural lands (rice cultivation) dominate the landscape and are interspersed with large-and medium-sized urban centers and cattle ranches. The southern part of the region (south of the Lagunitas-Santa Cruz road) is a matrix of forested savannas and cattle pastures intermixed

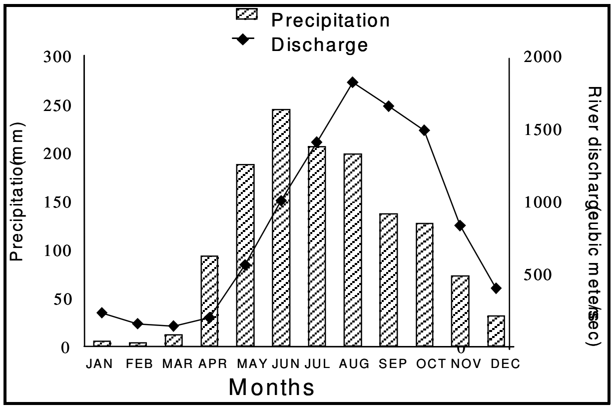

Figure 2. Pattern of precipitation in the Cojedes River System area of Venezuela

with forest relicts, scattered agricultural lands, wetlands, and other less extensive land-cover categories. The CRS has zones of relatively high human population densities in the north, where the cities of San Carlos (>80,000 people) and Acarigua (~200,000 people) are located and the rivers there have been modified by damming, canalization, dredging, contamination, and deforestation. Human population densities are smaller to the south downstream, with El Baúl (~6,000 people) as the largest town, where human impact is less apparent.

There are two clearly-defined seasons in the study area. The rainy season extends from May to October, and the dry season from December to March. April and November are transitional months. Annual mean precipitation (1975-1996) is 1323 mm in the middle part of the study area and a little greater (1514 mm) toward the south at El Baúl (MARNR 1997). During the rainy season river discharge increases (Fig. 2) and frequently overflows its banks and inundates the floodplain, particularly in the southern portion of the study area. Annual range between absolute minimum and maximum temperatures is 11.6˚C (21.7˚-33.3˚C) (MARNR 1995).

METHODS

Potential Nesting Habitat

A part of the river shore was subjectively considered as potential nesting habitat for *C. intermedius* if it had one or more of the following characteristics: 1) it consisted mostly of lightly compacted material and generally had excavations made by other reptilians such as iguanas (*Iguana iguana*) or turtles (*Podocnemis unifilis*), species with similar nesting requirements in terms of soil texture; 2) the shore was bare or sparsely covered by vegetation; 3) it was 1.5 m or more above the water level, and 4) there was a record of previous utilization of the site by nesting crocodile females.

Three river segments were examined in 1996 and 1997 for the presence of potential nesting habitat (Table 1): 1) A 4.7 km section of Caño de Agua south of Puente Nuevo (PN). There, the river was very narrow (8-12 m) and has numerous meanders despite having been dredged an unknown number of times in the past. Both margins of the river have been deforested and grasses and bushes cover the banks down to the water's edge. Most of this part of the river (60%) was lost during the rainy season of 1996 (see below); 2) Caño de Agua Sur (CAS) is also very narrow (in general less than 12 m) and it is the most meandering river segment of the entire study area. Most of the banks were forested and grasses were less abundant than in the PN section and usually did not reach the water's edge. Scattered groups of logs and branches of fallen trees were found along the river. Dense clumps of the riparian shrub (*Alchornea castaneifolia*) also were frequently found along the river edge; 3) The part of the Cojedes River from Merecure to Caño Amarillo opening (CAM), where the Cojedes River was relatively wide (15-20 m) with ample meanders and banks covered mostly by forest. The shrub *A. casteneifolia* was very common in this part of the river. In the remaining downstream part of this river section grasses and Heliconia plants were abundant and reach the water's edge (see Fig. 1).

In early February 1997, a small number of beaches (15) from CAS and CAM were more carefully scrutinized to determine their use by iguanas and turtles.

Nesting Substrate Texture

Soil composition was determined for substrate samples from nesting and non-nesting beaches (according to the preceding criteria). The proportion of silt, clay and sand in those samples was estimated following the hydrometer method of Bouyoucos (Foth 1978) at the Universidad Nacional Experimental de los Llanos Occidentales 'Ezequiel Zamora' (UNELLEZ) in Guanare, Venezuela.

Wider Range Surveys

During nocturnal spotlight surveys and daylight reconnaissance over 45.7 km of the CRS in 1996-97 (Table 2), we collected information on clutch and pod size, nesting and hatching chronology, and nest sites.

Clutch and Pod Size-. After hatching from the nest, neonates remained in well-defined groups or 'pods' for several weeks. During nocturnal surveys, the location and number of pods, and the number of hatchlings in each pod were recorded. When a particular pod was counted more than once, the maximum number of hatchlings recorded was taken as the pod size.

A preliminary measure of hatching success was obtained by comparing the mean number of hatchlings per pod against the mean number of eggs per clutch. Mean clutch size was extrapolated combining our own data with information from

Table 1. Number of beaches considered as potential nesting habitat in three river reaches in the Cojedes River system.

Place	Length (km)	Number of Beaches	Beaches per km
Caño de Agua, downstrem From Puente Nuevo (PN)	4.7	16	3.40
Caño de Agua Sur (CAS)	5.2	20	3.85
Merecure-Caño Amarillo (CAM)	8.4	9	1.07

Table 2. Number of Orinoco crocodile females that nested in several riversections of the Cojedes river system during 1996 and 1997.

River Section	Length (km)	Nesting Females	Density (Females/km)
Caño de Agua Norte (CAN)			
Retajao[a]		1	
Doncella-Guamita	5.5	4	0.73
Guamita-Puente Nuevo	10.5	12	1.14
Caño de Agua Sur (CAS)			
Puente Nuevo-Carama[b]	4.7	8	1.70
Pte Lorenzo-Confluence	7.6	12	1.58
Merecure-Caño Amarillo (CAM)	9.0	4	0.44
Sarare (SAR)	8.4	7	0.83
Totals	45.7	48	1.03

[a]The nest from Retajao was a casual observation in a non-surveyed section. It was not considered for the calculation of density.
[b]Most part of this river section disappeared during the 1996 flooding

the literature. Due to predation and dispersion of hatchlings, pod size decreases with time, so only those pods found in April or early May were considered in the analyses. Presence or absence of an adult crocodile in proximity of a pod was recorded and taken as an indication of parental care.

Nesting Chronology and Nest Sites-. The nesting chronology of the species was determined based on reports of Ayarzagüena (1987) and González-Fernández (1995) and our own observations on dates of nest construction, egg banding, hatching period, hatchling total length, presence of egg tooth, and umbilicus size of hatchlings. During 1996 and 1997, the position of each nest (or pod of hatchlings) was recorded with a Global Positioning System (Magellan 4000 and 4000xl). We assumed females to nest in the same spot year after year, a behavior that is well-documented for many crocodilian species (Garrick and Lang 1977, Ogden 1978, Thorbjarnarson and Hernández 1993*a*).

Nesting Success-. From 1994 to 2002, nesting success (number of successful nests per river length surveyed) (nests that produced hatchlings) in the CRS was monitored repeatedly (but only partially due to logistical problems) along the lower part of Caño de Agua Sur and the Cojedes River from its confluence with the Sarare river and Caño Amarillo, a continuous section of about 20 km.

Size of Nesting Population-. For estimation of the nesting population size we included observations from an even wider survey of 153 km of the CRS. The minimum number of nesting females in the survey area was estimated by comparing the relative position of nests and pods from 1996 and 1997. Size of the reproductive population was estimated based on the number of nesting females.

The number of dominant males was estimated as one per female for relatively isolated nesting females, and up to one male for every four females for localities with several females, depending on the relative proximity of nests. The last estimate is conservative if we take into account the sex ratio reported by Thorbjarnarson and Hernández (1993*b*) of 1:2.2. In non-surveyed sections of the CRS the number of nesting females was subjectively estimated based on the characteristics of the section and known nest densities in contiguous upper and/or lower reaches of the river.

Data Analysis

Median pod size differences between river sections was estimated with a Kruskall-Wallis test. A contingency table analysis was used to estimate the dependence of parental care of hatchling pods on river sections under different human pressure.

RESULTS

Potential Nesting Habitat

Table 1 shows the number of potential nesting beaches found in each of the three sections surveyed. Most of the beaches classified by us as potential nesting habitat along the CAM section were found approximately in the first 4 km downstream from Merecure. In the remaining downstream part of this river section appropriate beaches were almost nonexistent.

In the sections of the river that had been canalized, river banks that fulfilled the criteria as potential nesting beaches were scarce or absent. Caño de Agua Norte (CAN), upstream from Puente Nuevo, has been dredged and partially canalized over the last 20 years but in some parts has recovered its meandering condition. In those latter reaches the characteristics of the river were the same as downstream from the bridge, but in the river segments that remained canalized, banks were very steep and nesting beaches were absent. In the southern part of the study area near Sucre (SUC) and at Caño La Culebra (CUL) adequate nesting habitat was also scarce.

In the more intensive iguana and turtle survey of February

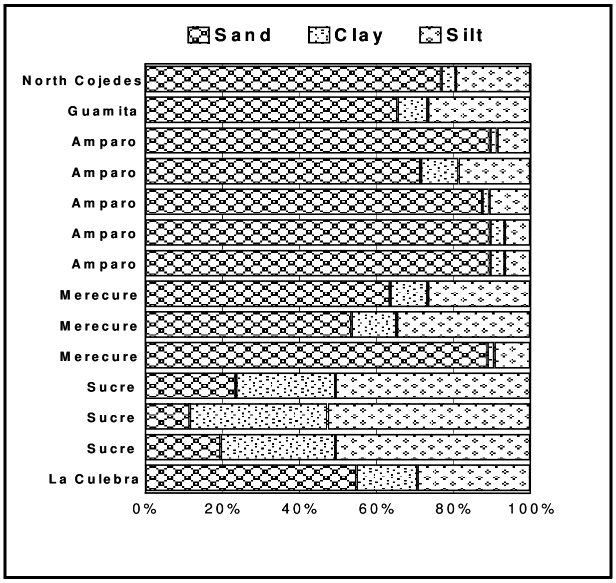

Figure. 3. Texture of river bank soil samples collected at different locations along the Cojedes river system, Venezuela. Locations are ordered from north to south (top to bottom).

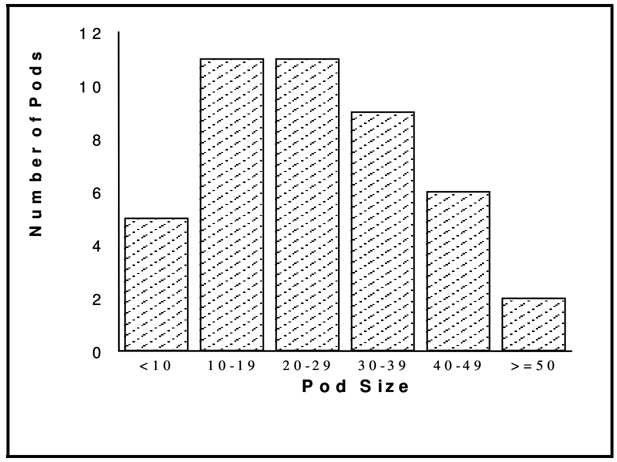

Figure 4. Frequency distribution of pods of Orinoco crocodile hatchlings according to number of individuals in Cojedes Rriver System, Venezuela. Large pods may result from integration of hatchlings from more than one female.

1997, 20% of the beaches (CAS and CAM) had clutches of turtles' eggs (*Podocnemis unifilis*). Most of these beaches (73.3%) also had nest excavations made by iguanas. In a nocturnal survey conducted from La Batea to Merecure on 27 April 1997, the remains of eight turtle nests were found. However, turtles or turtle nests were never observed in the northern part of the study area at CAN or Cojedes Norte (CON).

In SUC, turtles were seen frequently basking on logs or branches of fallen trees. They may nest in that area, although nesting was never observed. Iguanas were very rare in this part of the river, even though its banks were profusely covered by trees. In CUL iguana presence was also rare.

Nesting Substrate Texture

Although vast parts of the study area were not evaluated for their suitability for nesting, a pattern of decrease in substrate quality of riverbanks from north to south was apparent. Samples from northern sections of the study area showed a preponderance of sand (65.5-89.5%; Fig. 3). In two samples from CAS, close to Merecure, sand accounted for 58.5% on average. A lesser percentage of sand was found in La Culebra (54.8%), and the smallest percentages of sand of all samples were obtained from Sucre (range 11.5 to 23.5%).

Clutch and Pod Size and Parental Care

Mean number of hatchlings per pod was 26.0 $\pm$13.9 SD of 44 pods observed the first month of hatching season (Fig. 4). Median pod size was greater in the SAR section ($\bar{x}$=35.5) than in the CAN ($\bar{x}$=24.0) or CAS+CAM sections ($\bar{x}$=22.1)(H=6.2; gl=2; P=0.045).

According to our own data, and that reported by Ayarza-güena (1987) and González-Fernández (1995), the mean number of eggs per clutch in the CRS is 38.2 $\pm$11.0 (n=12), which is below the typical range (40-70) mentioned for the species by Thorbjarnarson (1992). Mean pod size found in our study (26.0) represents 68% of mean clutch size, which could be taken as a preliminary measure of hatching success.

In 47.7% of 44 pods, an adult crocodile, presumably the mother of the hatchlings, was seen in close proximity. Pod attendance by adults was dependent on river section, being lowest in CAN (X^2=4.48, gl=2, P=0.034).

Nesting Chronology

The earliest observation of hatchling crocodiles was 12 April, during the 1996 hatching season. Morphological characteristics of hatchlings found in 72 pods observed from 1991 to 1997, suggest that most hatching occurred from mid-April to early-May. In captivity, under ideal conditions, the incubation period lasts some 80-85 days (Lugo 1995, Ramo *et al.* 1992, Seijas and González 1994, Thorbjarnarson and Hernández 1993*a*), so construction of nests may start as early as mid January. Most nesting, however, occurs in late January and early February. The earliest nest ever examined

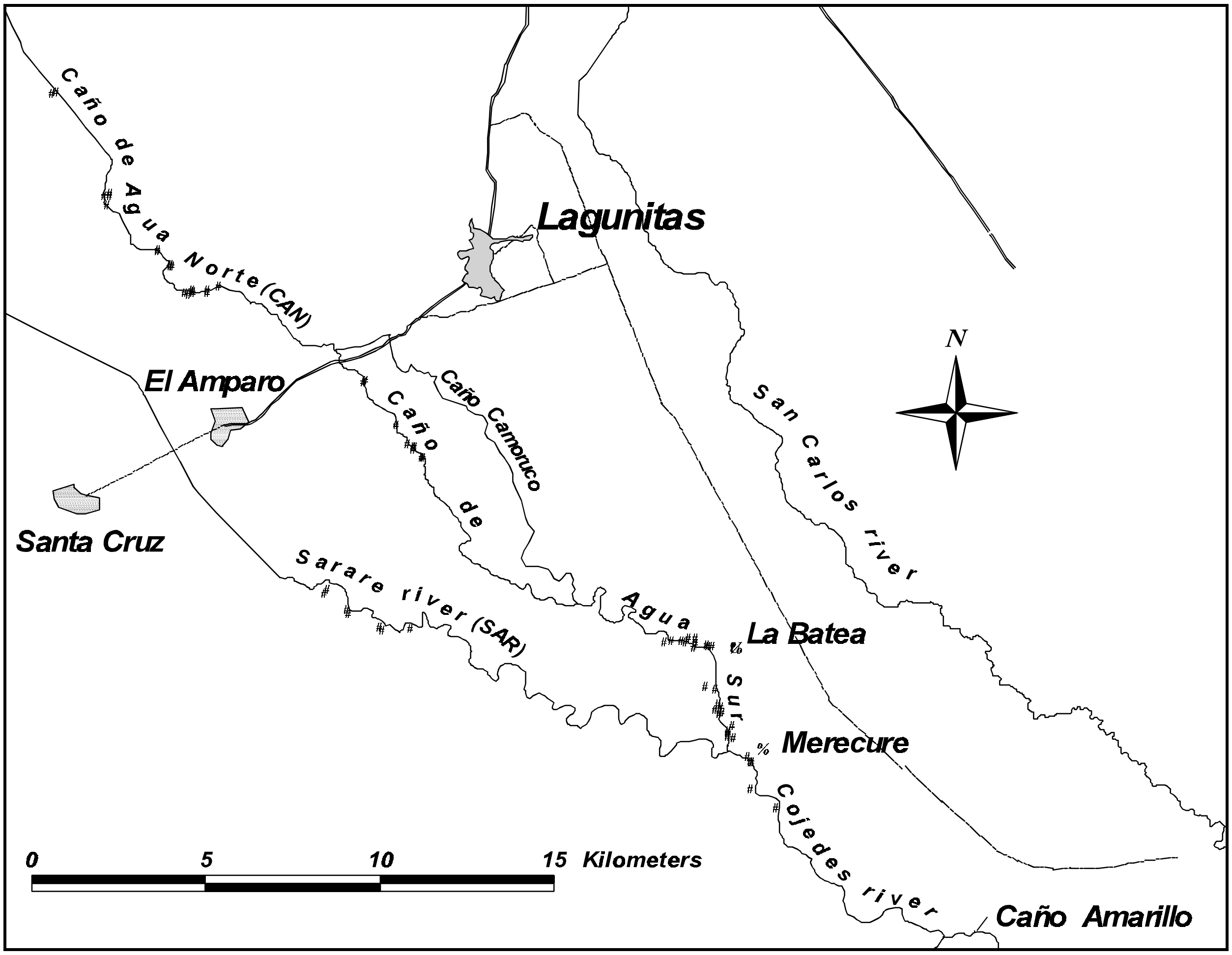

Figure 5. Orinoco crocodile nests (#) found during 1996 and 1997 in the Cojedes river system, Venezuela. Nest tend to occur in clusters, indicating the presence of a dominant male a one or more females.

by us, on 5 February 1997, and those found by Ayarzagüena (1987) support this conclusion.

Nest (Pod) Density

Based on comparisons of nest and pod locations from 1996 and 1997, we estimated at least 48 nesting females in the 45.7 km surveyed, or a density of 1.03 nests (or nesting females) per km (Table 2). Although Cojedes Norte was never surveyed during the time when hatching occurs (late April to early May), the size of many of the crocodiles seen there indicated that successful reproduction has taken place in that part of the river in previous years, even though this section is isolated from the rest of the study area by a dam that effectively blocks entrance of crocodiles from downstream.

Nesting females were not uniformly distributed along the river. In the river section La Doncella-Guamita only four nests (0.73 nest/km) were observed. This river reach was completely canalized and had steep banks. Downstream from it, in the Guamita-Puente Nuevo section of Caño de Agua, the river had recovered its meandering conditions. Nest density there increased to 1.14 per km.

The greatest density (1.7 nesting females/km) was found in 1996 in the 4.7 km of Caño de Agua south of Puente Nuevo. However, most of that river section (approximately 60%) was lost during the rainy season of 1996 due to river diversion after a severe flooding event, when the river changed its course and diverted into smaller branches toward Caño Camoruco. The fate of eight nesting females from that part of the river is not known. Two nests found near Puente Nuevo in 1997, just north of the diverted river section, might have belonged to some of these females.

Four km of CAS, between Camoruco mouth and Puente Lorenzo (Fig. 5), were not surveyed for nests or hatchlings. Considering that the characteristics of that river section were very similar to the ones found immediately downstream, in

Table 3. Number of nests of Orinoco crocodile that produced hatchlings in lower Caño de Agua Sur and Cojedes between Camoruco and Caño Amarillo. Data for 1994 was taken from González-Fernández (1995); data for 1998 and 1999 were taken from Chávez (2000).

Year	Number of Successful Nests	River Length Surveyed
1994	21	17.6
1996	5	17.6
1997	7	13.6
1998	16	13.6
1999	16	13.6
2000	13	4.0
2001	9	13.4
2002	0	18.0

the section Puente Lorenzo-Confluence, six additional nesting females, not listed in Table 2, could be expected in Caño de Agua Sur.

In the Sarare River, only a stretch of 8.4 km (SAR) was surveyed for nests or pods, resulting in a density of 0.83 nest/km. The river section from there down to the confluence with Caño de Agua has never been surveyed.

No hatchling or nest was ever found in Sucre or Caño La Culebra. The size of crocodiles seen or captured there indicated that they were older than a year, suggesting that crocodiles in these locations may have come from elsewhere, probably upstream.

A detailed examination of crocodile nest distribution revealed a pattern of clustering. Groups of up to four females were found in close proximity, suggesting the presence of a dominant male and a group of females, as has been reported in the Capanaparo River by Thorbjarnarson and Hernández (1993*b*).

Nesting Success

Number of successful nests per river length surveyed indicated a high variability between years (0-21 nests, Table 3).

Nest predation by humans did not seem to be an important factor affecting the viability of the Orinoco crocodile in the CRS. One nest seemed to have been taken by people in the section of Merecure-Caño Amarillo in 1997, but the evidence was equivocal. However, people in Retajao took at least 11 hatchlings from a pod in 1996.

Adult Population

Ninety-one reproductively active crocodiles were estimated for the Cojedes River System, most of them (63.2%) in Caño de Agua (Table 4).

Table 4. Reproductive population of Orinoco crocodiles in the Cojedes River System. The number of dominant males was calculated as one per female for relative isolated females, and one male for every three-four females for places with several females.

Place	Length (km)	Nesting Females	Dominant Males	Total
Cojedes Norte (CON)	7	2[a]	1	3
Caño de Agua Norte (CAN)				
Toma Cojedes-La Doncella	25.5	1	1	2
Doncella-Guamita	5.5	4	1	5
Guamita-Puente Nuevo	10.5	12	4	16
Caño de Agua Sur (CAS)				
Puente Nuevo-Carama[b]	4.7	8	3	11
Camoruco-Pte. Lorenzo	3.7	6[a]	2	8
Pte Lorenzo-Confluence	7.6	12	4	16
Confluence-Caño Amarillo	9	4	1	5
Caño Amarillo-Sucre	51	1[a]	1	2
Caño Amarillo-La Culebra	33.5	1[a]	1	2
Sarare				
Downstream Amparo bridge	8.4	7	2	9
Lower Sarare	12	8[a]	3	11
Totals	153	66	25	91

[a]Not surveyed. Figure estimated based on similarity of appearance with surveyed sections.
[b]Most of this river reach disappeared during the flooding season of 1996.

DISCUSSION

Orinoco Crocodile Density is Adequate in Good Habitat

Although depleted in most of its former range, there is a high density of Orinoco crocodiles in the CRS. There were at least 48 adult females in the surveyed sections of the river (45.7 km), a number that is most probably an underestimation since only a relatively small part of the region was properly surveyed.

The reproductive population is concentrated in the Caño de Agua and in the lower Sarare River, the areas that had the highest quality nesting habitat. There was no evidence that the species reproduces in Cojedes Sur and in Caño Culebra, areas which had lower quality nesting habitat. However, crocodile abundance and nest site quality of many sections of the CRS have not been evaluated, so this conclusion is preliminary.

Adequate Substrate Scarce

However, lack or scarcity of good nesting substrate seems to be an important factor determining the current distribution of the species in the CRS. Soil samples taken from active nests indicated that the most frequently selected nesting sites are composed of high proportions of sand (generally more than 70%).

Use of Turtles and Iguanas as Indexes-. The use of turtle nests and iguana excavations (Feb. 97) as indexes to measure potential crocodile nesting habitat had varying results. Counts of turtle nests were clearly underestimations, because they are harder to find than are iguana excavations. On the other hand, it was probably too early in the nesting season of *Podocnemis* and many turtles may not have nested yet. González-Fernández (1995) found turtle nests in 38% of the beaches with crocodile nests.

The lack of presence of iguanas in SUC, even though riverbanks were profusely covered by trees suggests that iguanas in SUC may be limited by scarcity of nesting substrate. Additionally, in CUL few iguanas were seen but this may be because of a lack of trees there, instead of a lack of nesting habitat. The lack of arboreal vegetation may signify a more important limiting factor for iguanas in CUL.

Clutch and Pod Sizes not Explained

If pollution and other human-related factors affect egg viability in the area studied, that may be reflected in mean pod size. Habitat modification and pollution (Seijas 1998) were greater in CAN than in CAS. Habitat alteration in the surveyed portion of the Sarare River was comparable to that found in CAN, but information on pollution was not available. Mean pod size was greatest in the Sarare River (35.5), as compared to previous data of 31 $\pm$10 (González-Fernández 1995). However, this site was insufficiently sampled. Since there are many factors that can affect pod size, including female size and hatching success, it is difficult to interpret the meaning of these differences in pod size. More detailed studies in this regard are necessary, particularly on the effects of contamination on crocodile reproduction.

Parental Care Underestimated-. The observance of females nearby only half the pods is surely an underestimation, because the disturbance produced by the noisy approach of the boat, powered by an outboard engine, might have caused many females to disappear from sight.

Human Disturbance Affected Pod Attendance-. There was a significant difference in what was interpreted as maternal care or pod attendance between Caño de Agua Norte and Caño de Agua Sur-Caño Amarillo. This may be a consequence of higher human interference in Caño de Agua Norte (Seijas, 1998, 2001), as has been reported for *Caiman yacare* in Brazil (Crawshaw 1987). Another possibility is that females in Caño de Agua Norte were relatively new colonizers of the area and probably younger and less- experienced than females in southern locations.

Nesting Chronology Pattern Normal

Nesting chronology documented in this study agrees with the general pattern described for the species (Medem 1981, 1983, Ramo *et al.* 1992, Thorbjarnarson and Hernández 1993*a*): egg-laying starts during the months of lowest precipitation (January-February) and hatching takes place at the onset of the rainy season (late April-early May). Nesting (and consequently hatching) occurs earlier in the captive breeding facilities of the Universidad Nacional Experimental de los Llanos (UNELLEZ), and later in the breeding facilities of Masaguaral Ranch, in response to different precipitation regimes in those areas (Ramo *et al.* 1992, Thorbjarnarson and Hernández 1993*a*). Eggs laid late during the nesting season are under a high risk of being lost due to flooding. The high nesting success reported by González-Fernández (1995) for a reach of the Cojedes River (Merecure-Caño Amarillo) in 1994 may be the result of delay of flooding events in that year.

Nest Success Varied between Years

The number of successful nests per year showed a high variability in hatching success, probably related to changes in water levels at the end of the incubation period (late April). Flooding in late April or May has a devastating impact on nest success.

A flaw in this method of calculating hatching success is that nests that fail to produce hatchlings could not be detected, and so are not included in the calculations. There is no information on other wild Orinoco crocodile populations to compare these results.

Egg or hatchling collection did not seem to be a factor that affects Orinoco crocodile survival in the CRS, at least where most of the nesting occurs, although anecdotal information indicated that this kind of human intervention occurs sporadically (pers. observ. González-Fernández 1995) and probably was common practice in the past (Godshalk 1978). Human settlements are generally several kilometers away from river banks, and the CRS is not inhabited by people exploiting the river resources, as is the case in the Capanaparo River (Thorbjarnarson and Hernández 1992). González-Fernández (1995) reported that 2 of 27 (7.4%) nests analyzed by him were destroyed by a dredge, but no predation by humans was reported.

Nest Densities Stable

Reproductive data from this study, compared to data in the literature (Ayarzagüena 1987, González-Fernández 1995), suggest that the number of nesting females has remained stable over the last 10 years. Globally, the total density of nests was the same as found by González-Fernández (1995) in part of the study area (1.04 nest/km). Ayarzagüena (1987) estimated some 25 nesting females in Caño de Agua Sur, which was roughly the same number found in this study for the same part of the CRS. Nest density of the *C. intermedius* population in the Capanaparo River studied by Thorbjarnarson and Hernández (1993*a*) ranged from 0.24 to 0.36 nests/km.

Nest density in the CAM (0.44 nest/km) was relatively low when compared with the 1.4 nests/km obtained in 1994 by González-Fernández (1995). The results obtained by González-Fernández may be exceptional, because that year the rainy season started late, with the lowest combined precipitation for April-May (129.7 mm) for the period 1975-1996 (MARNR 1997). Compared to other years, a smaller number of nests (if any) may have been lost in 1994 due to flooding.

Some river sections that have been dredged repeatedly in the last 20 years had relatively high density of nesting. Dredging may have an immediate negative impact because it destroys nesting beaches (González-Fernández 1995) but the river seems to recover after several years. One of the smallest nest densities was found in La Doncella-Guamita, a stretch that has been channelized. Channelization may have a greater impact on reproduction and on the population as a whole because it reduces the habitat for the species, eliminates most beaches, and increases the river flow speed, which may have a negative impact on pod cohesion and hatchling survival.

The distribution of nests or nesting females along the river indicated that in the Cojedes River the Orinoco crocodile showed the same social structure described for the species in the Capanaparo River, in which dominant males form polygynous groups with two or more adult females (Thorbjarnarson and Hernández 1993*b*).

However, the 91 adult crocodiles estimated in our study represents a minimum since: 1) some parts of the river were poorly surveyed and, conservatively, a low density of adults was assigned to them, and 2) not all the adult females nest every year.

Future Research Needs

The impact that damming, channelizing and water diversion in the CRS may have on nesting and reproductive success of the Orinoco crocodile has not been properly studied. Several kilometers of good nesting habitat have been lost due to flooding and river diversion in the last 10 years. The wise management of the Las Majaguas reservoir and of the future Las Palmas reservoir, to avoid sudden rises of water levels and loses of nests, will be crucial for the survival of the species.

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