

# Reproductive Ecology of the Orinoco Crocodile (*Crocodylus intermedius*) in Venezuela.

## II. Reproductive and Social Behavior

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**ABSTRACT.**—The assertion display of male Orinoco crocodiles consisted of a stereotyped series of head-slaps and roars. It was principally an early morning activity, and coincided seasonally with courtship during the end of the rainy season and the beginning of the dry season. Courtship and mating activity involved visual, acoustic, and tactile elements similar to those of other crocodylians. Mating took place about two months prior to nesting. Nesting in captivity and nest opening behaviors are described.

Among wild crocodiles in the Capanaparo River, similar nest opening behaviors were inferred from tracks at nest site. Neonates form cohesive groups that are attended by an adult. In the Capanaparo, dry-season adult breeding groups averaged one male per 2.2 females and were centered on deep pools in the otherwise shallow river.

**RESUMEN.**—El despliegue de aserción de los machos del caimán del Orinoco consiste de una serie estereotipada de 1-3 golpes mediante la cabeza contra el agua, y 2-5 bramidos fuertes. Este despliegue se produce principalmente cerca al amanecer, y a través del año entero pero con mayor frecuencia durante el época de celo (final de la estación lluviosa y principio de la estación seca). El cortejo y apareamiento consisten de elementos visuales, acústicos, y táctiles parecidos a los previamente reportados para otras especies de crocodrilidos. Apareamiento sucede principalmente en diciembre, dos meses antes de nidificación. Se describe los comportamientos de nidificación y eclosión en cautiverio. Basado en los rastros dejados en los nidos en el río Capanaparo, se inferó comportamiento semejante. Crías recién nacidas forman grupos atendidos por un adulto. En el río Capanaparo durante la estación seca, grupos adultos de reproducción consisten de un macho y un promedio de 2.2 hembras, ubicados cerca a los pocos pozos profundos.

Crocodylians are arguably the most behaviorally complex of the reptiles, with intricate social systems and a diverse behavioral repertoire (Garrick and Lang, 1977; Garrick et al., 1978; Lang, 1987; Vliet, 1989). However, investigations have been done on only a few of the 23 extant species, notably *Alligator mississippiensis* (Garrick and Lang, 1977; Garrick et al., 1978; Vliet 1989), *Crocodylus niloticus* (Modha, 1967; Hutton, 1984), *C. acutus* (Garrick and Lang, 1977), and *Caiman crocodilus* (Alvarez del Toro, 1969; Staton and Dixon, 1977). Interspecific differences in signaling behavior, in social organization, and in reproductive behaviors are evident (Garrick and Lang, 1977; Lang, 1987; Vliet, 1989), but there are few reports describing the reproductive and social behaviors of most crocodylians. The true diversity of crocodylian behavior may only be apparent once investigations have been undertaken on a greater variety of species.

The Orinoco crocodile (*Crocodylus intermedius*) is a large species restricted to the Orinoco River drainage of Venezuela and Colombia (Thorbjarnarson and Franz, 1987). Its ecology is outlined in the pioneering studies of Medem (1958, 1981, 1983). In Venezuela, previous studies have dealt with status and distribution (Godshalk, 1982; Franz et al., 1985; Ramo and Busto, 1986; Thorbjarnarson and Hernández, 1992). As part of a conservation program sponsored by the Venezuelan Fundación para la Defensa de la Naturaleza (FUDENA), we began work on this species in 1984. In this paper we delimit the reproductive and social behaviors of Orinoco crocodiles.

### METHODS

Observations were made from November 1984 to June 1989 on a captive group of adult crocodiles (3 males:13 females) at Hato Masaguaral, in the central Venezuelan llanos (8°34'N, 67°35'W). The crocodiles were observed for a total of 43.5 h, either from small blinds situated around four 25 m × 25 m breeding enclosures, or from a second floor balcony adjacent to a main enclosure. Most courtship observations

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were made during morning observation periods (0530–0800 h), but intermittent observations (ad libitum sampling, Altmann [1974]) were made throughout the day. The principal study animals were a pair of crocodiles (male 3.85 m TL, female 3.02 m TL) housed in one enclosure. Additional observations were made on two other adult males (3.7 m, 3.2 m TL) maintained with a group of 12 females (adult and subadult; 1.7–2.8 m TL) in three interconnected enclosures.

The loud headslaps and vocalizations associated with the assertion display could readily be heard during the day or night. This allowed the relative incidence of crocodile assertion displays to be noted over a 24 h period throughout the year. Headslap-roars were recorded using a Marantz Superscope Model CD-330 cassette recorder with a Sennheiser MKH-815T microphone.

The number and distribution of adult crocodiles in the Capanaparo River was derived from repetitive aerial surveys, and diurnal and nocturnal boat censuses (Thorbjarnarson and Hernández, 1992). The number and distribution of breeding females was determined from nesting data collected from 1987–1992 (Thorbjarnarson and Hernández, 1993).

#### RESULTS

**Assertion Display.**—The principal assertion display of male Orinoco crocodiles consisted of a combination of headslaps and loud roars (which together we refer to as a headslap-roar; Fig. 1). The sequence of behaviors involved in the display was typically as follows. Prior to the assertion display, males would slowly swim in a "high float" posture, with the body inflated, head held high in the water, and the dorsal surface of the body and tail exposed (Fig. 1a). While patrolling in this posture males would occasionally produce short bursts of sub-audible vibrations (SAV; Garrick et al., 1978) causing the water on or over their backs to vibrate upwards (water dance in Vliet, 1989). These low frequency SAVs (ca. 15 Hz, K. Vliet, pers. comm.) were below the range of human hearing, but could be felt by transmission through the water and ground. Infrequently, males headslapped while patrolling in the high float posture.

To display, a male typically moved into shallow water and oriented its body perpendicular to the shore with its head 0.5–1.0 m from the shoreline. From this position the head and the distal two-thirds of the tail were raised obliquely until they were lifted almost entirely out of the water (Fig. 1b, c). From this head emergent, tail arched posture, the male would usually "tail wag" briefly (Fig. 1d), then forcefully slap his

upper jaw against the surface of the water, simultaneously closing his mouth, increasing the force of the impact (Fig. 1e). This headslap produced a loud distinctive noise and was usually performed twice in rapid succession ( $\bar{x}$  = 2.17, range = 1–4,  $N$  = 359; Table 1). Immediately following a headslap, the male raised its snout, angling the head upwards with the mouth agape, and roared 2–4 times ( $\bar{x}$  = 2.86, range = 1–7,  $N$  = 373; Table 1). The low-frequency SAVs were also a component of the assertion display; males were observed to produce SAVs prior to headslap-roaring (Fig. 1b), and while producing roars (Fig. 1f).

Roars had a deep, throaty, sonorous quality, and were given with a slowing cadence and decreasing volume. The sound energy of the roars was concentrated between 50 and 250 Hz (Fig. 2), and did not possess any of the harmonic qualities of *A. mississippiensis* bellows (Garrick et al., 1978). Associated with each roar, the male would lower his body in the water and raise the tip of his snout (Fig. 1g). Between roars males raised their bodies and dropped their heads slightly (Fig. 1f). A full sequence of two headslaps and 3–4 roars typically lasted 8–10 sec (Fig. 2). Males everted their mandibular glands while roaring (Fig. 1g), adding an olfactory component to the display. After roaring, the male dropped his head and tail to water level, and frequently exhaled through his mouth, producing bubbles (Fig. 1h). Occasionally the crocodile ended the display by forcefully sculling his tail in the water. There were individual differences in the number of headslaps and roars given by the three males at Masaguaral (Table 1). Assertion displays appeared to be contagious, with one male's display eliciting headslap-roars from the other males. A male *C. acutus* in a nearby pen was also observed to respond by producing a similar display (Thorbjarnarson, 1991).

Headslap-roars were heard throughout the day, with a sharp peak around dawn (Fig. 3a). Only 139 of 1054 headslap-roars (13.2%) were recorded during daylight hours (0700–1800 h). Headslap-roars were produced throughout the year, but had a well-defined peak during the courtship and mating season (September–February, Fig. 3b). Overall, 88.4% of the observed bellows ( $N$  = 1056) occurred during these five months, peaking in December (24.7%).

Females were never observed to headslap-roar. A single headslap was produced by a female on 28 May 1989 associated with nest defense. Nevertheless, females have the capability to roar and have been heard to do so in response to loud noises (e.g., explosions).

**Courtship and Mating.**—Orinoco crocodile

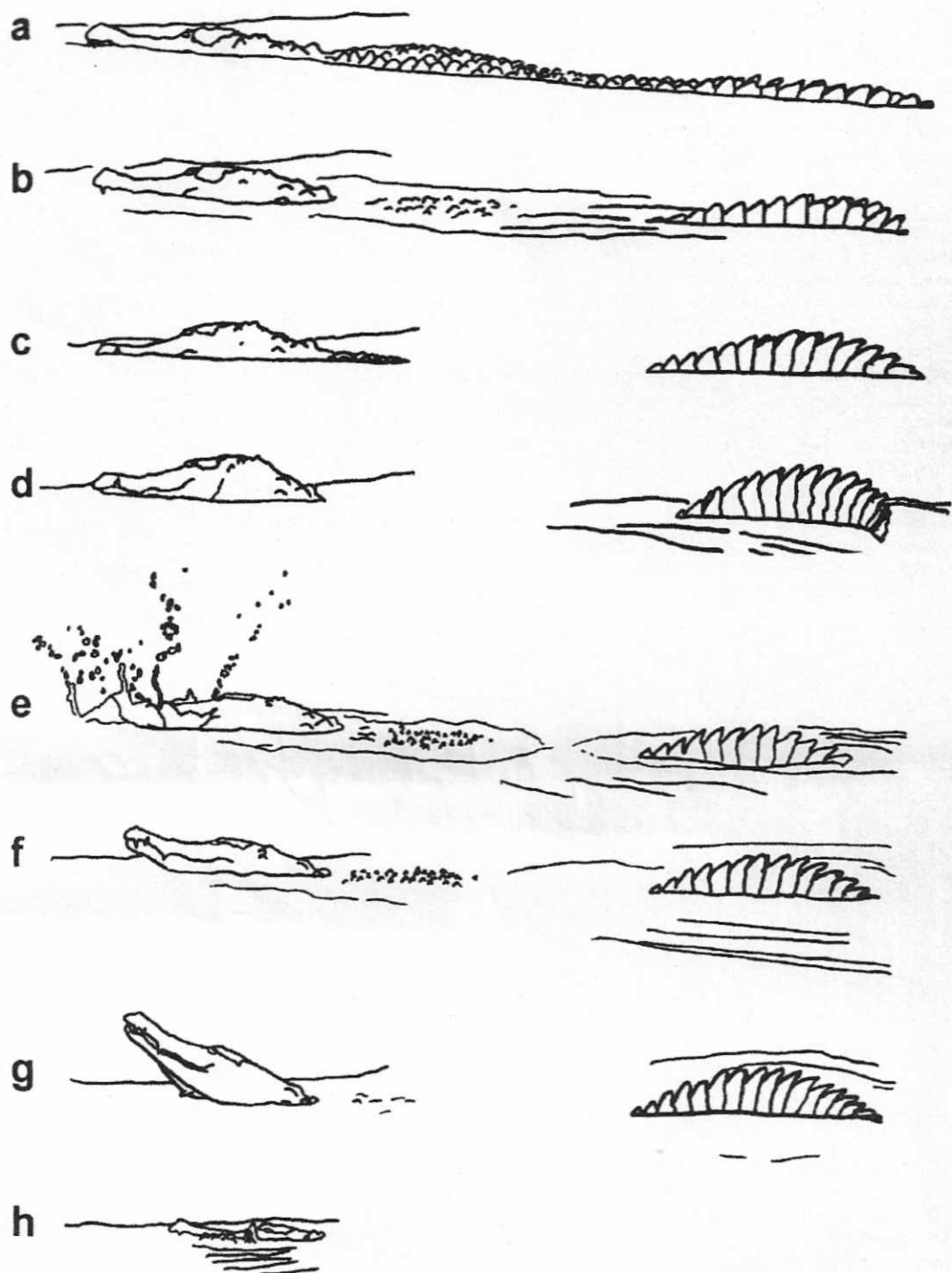


FIG. 1. Sequence of body postures of a 3.8 m TL male *C. intermedius* during the headslap-roar display: (a) high float, (b) beginning of head emergent, tail arched posture and subaudible vibrations (SAV; visible as a disturbance in the water over the crocodile's back), (c) head-emergent, tail arched posture with (d) a tail wag, (e) headslap, (f) lower head posture during roars (with SAV), (g) raised head posture while roaring (mandibular glands everted), and (h) bubbling following the roars. Tracing made from photographs.

TABLE 1. Headslaps and roars as components of assertion displays performed by captive male Orinoco crocodiles ( $N = 3$ ) at Hato Masaguaral, during four successive breeding seasons (January 1985–December 1988).

	Number of headslaps			
	1	2	3	4
Male 1	65	66	13	0
Male 2	7	38	14	1
Male 3	2	10	105	1
Unid. male	5	27	4	1
Total	79	141	136	3
% total	22.0	39.3	37.9	0.8

	Number of roars						
	1	2	3	4	5	6	7
Male 1	14	45	41	21	11	1	1
Male 2	2	20	26	48	2	0	0
Male 3	2	46	63	1	0	0	0
Unid. male	5	5	11	8	0	0	0
Total	23	116	141	78	13	1	1
% total	6.2	31.1	37.8	20.9	3.5	0.3	0.3

courtship was comprised of a series of stereotyped behaviors, whose overall sequence was similar to that reported for *C. acutus* (fig. 3b in Garrick and Lang, 1977). Courtship was frequently initiated by the female as a response to the male bellowing in the principal study pair, but courtship in the other breeding group was typically initiated by the male actively approaching the female and producing sub-audible vibrations from a high float, or head emergent, tail arched posture.

During courtship, unreceptive females remained immobile on the surface or submerged. If the female was receptive, courtship activity began with the pair slowly swimming in circles or engaging in snout rubbing. Upon initial con-

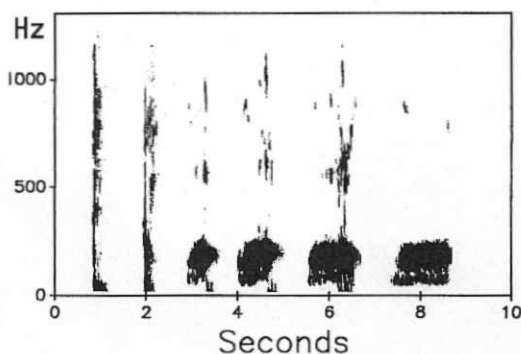


FIG. 2. Sonogram of a male assertion display showing two headslaps and four roars produced by a 3.7 m TL male on 10 February 1985 at 0555 h.

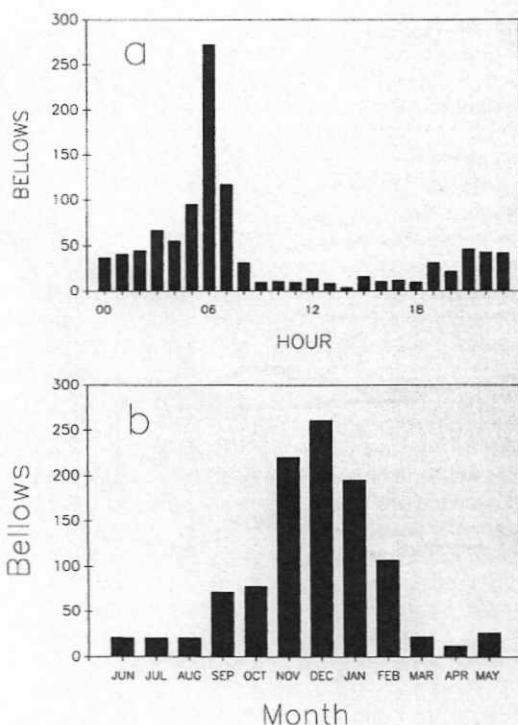


FIG. 3. Relative frequency of bellows by (a) hour of day and (b) month of year; data collected from January 1985 to December 1988.

tact both male and female frequently emitted snorting sounds, which may serve as recognition signals, or the female would obliquely angle her snout upwards (fig. 2g in Garrick and Lang, 1977). While snout rubbing, the female moved the tip of her snout along the lateral surface of the male's jaws. At times this was followed by the female placing her head atop the male's cranial table, nuchal region, or snout, occasionally pressing him underwater (pressing behavior of Vliet, 1987). Females were also observed rubbing the ventral surface of their jaws along the dorsal surface of the male's neck, back or pelvic region.

Continued courtship consisted of circling behavior, snorting, snout-rubbing, bubbling, and repeated submerging and re-emergence. When re-emerging, the male occasionally expelled air from his lungs, creating a loud bubbling noise which continued into a loud hiss as his head reached the surface. More violent activity, usually associated with the introduction of food into the pen, included energetic swimming and mock biting. Under these conditions the female frequently snout-lifted, with the head angled out of the water at approximately a 45° angle.

While submerged, or less frequently while at the surface, the male rode atop the female and

assumed a copulatory posture (fig. 15 in Vliet, 1987). The pair then would rise to the surface where copulation would occur. Because intro-mission took place underwater, it was difficult to confirm copulations. Early in the courtship season (September–October) pairings usually did not result in apparent copulation, which was characterized by the male sliding laterally and bending his tail under the female's. During attempted copulations the female remained below the male (alternately below or above the water's surface), with her snout angled upwards and off to one side. While below the surface the female occasionally expelled air through her mouth, producing bubbles.

At Masaguaral, apparent copulation was frequently preceded by very little courtship activity, and was seen most frequently during mid-December. The mean date of twelve apparent copulations was 17 December (SD = 15.6 d; 24 November–17 January).

*Nesting Behavior and Parental Care.*—The footprints of crocodiles on Capanaparo River nesting beaches indicated that females began making nocturnal visits and trial excavations on potential nest sites up to 4 wk prior to nesting. In captivity, as well as at the Capanaparo, oviposition was usually preceded by several nights of increased digging activity. During oviposition, captive females were positioned over the nest hole with their ventral surface pressed close to the ground, head cocked up in an "alert" posture with the mouth opened slightly, and hind legs folded back along the ventro-lateral surface of the tail. Slow, irregular contractions of the abdomen were interspersed with deeper muscular contractions and a slight uplifting of the pelvic/cloacal region when an egg passed through the pelvic canal. In 1987, the observed interval between these deep contractions increased from 30 to 75 sec during oviposition. After laying, females pushed soil into the nest hole using the hind legs alternately. When the hole was almost filled, females repeatedly compacted the nest soil using their rear feet in a slow walking motion before scraping more soil onto the nest.

Observations of nest opening behavior were made on Masaguaral on 11–12 May 1985, the only year eggs were left in the breeding enclosure. The female crocodile made nocturnal visits to the nest site for several days prior to opening the nest. On the night of 11 May, she emerged from the water prior to 2200 h, and was observed excavating the nest at 2232 h. The female used her front feet to dig soil out of the nest cavity, and the rear legs to remove this material from the vicinity of the nest site. Digging was intermittent, and between bouts the female rested her throat on the soil atop the

nest, or backed off slightly and placed her snout in the nest hole. The muffled vocalizations of the young within the nest were heard intermittently from the beginning of the observations (2232 h).

To pick up hatchlings, the female rotated her head laterally approximately 90 degrees, opened her mouth, and gently grabbed the hatchling with her jaws. Usually, several attempts were necessary to secure each neonate, who was then flipped back into the gular region of the mouth using an inertial feeding motion of the head and neck. The female produced occasional snorts during the excavation of the nest, to which the young responded by vigorously grunting. The female also inverted her mandibular glands periodically during the nest opening.

The female parent carried eighteen hatchlings a distance of three meters from the nest to a pond within the breeding enclosure. She made seven trips over a period of five hours. While carrying the first group of four hatchlings into the water, the female swam around the shoreline adjacent to the nest for eight minutes, submerging twice for short periods, before finally releasing the hatchlings in an area of emergent grass near the nest. The male crocodile which lived in this breeding enclosure was not observed to participate in nest opening.

Interpretation of signs left at wild nests in the Capanaparo indicates that females open nests, carry young to the water, and release them in shoreline areas covered by overhanging vegetation, usually under the dead branches of a fallen tree or under dense growths of riparian shrubs (particularly *Coccoloba obtusifolia*). At one nest in 1992, hatchlings were encountered 50 m upstream of the nest site together with three eggshell membranes, suggesting that the young, together with eggshell remains, had been carried there by the female. In another instance, hatchlings and egg membranes were found at the mouth of a burrow (>3 m deep) inhabited by an adult crocodile (presumably the female parent) 50 m upstream of the nest site.

Hatchling crocodiles in the Capanaparo remained together in a tight group, or "pod," following hatching. An adult crocodile was usually seen together with pods of neonates. Both in captivity and in the wild, hatchlings were observed to bask on the head and/or back of the adult. During the 1985 observations at Masaguaral, the male was never observed attending the pod, but was usually kept well away from the hatchlings by the aggressive behavior of the female. In the Capanaparo River, attending adults were presumed to be females based on size ( $\leq 3.5$  m TL). Adult crocodiles with pods of hatchlings were observed 1–2 wk after hatching in 1987 and 1992, and 8 wk after hatching

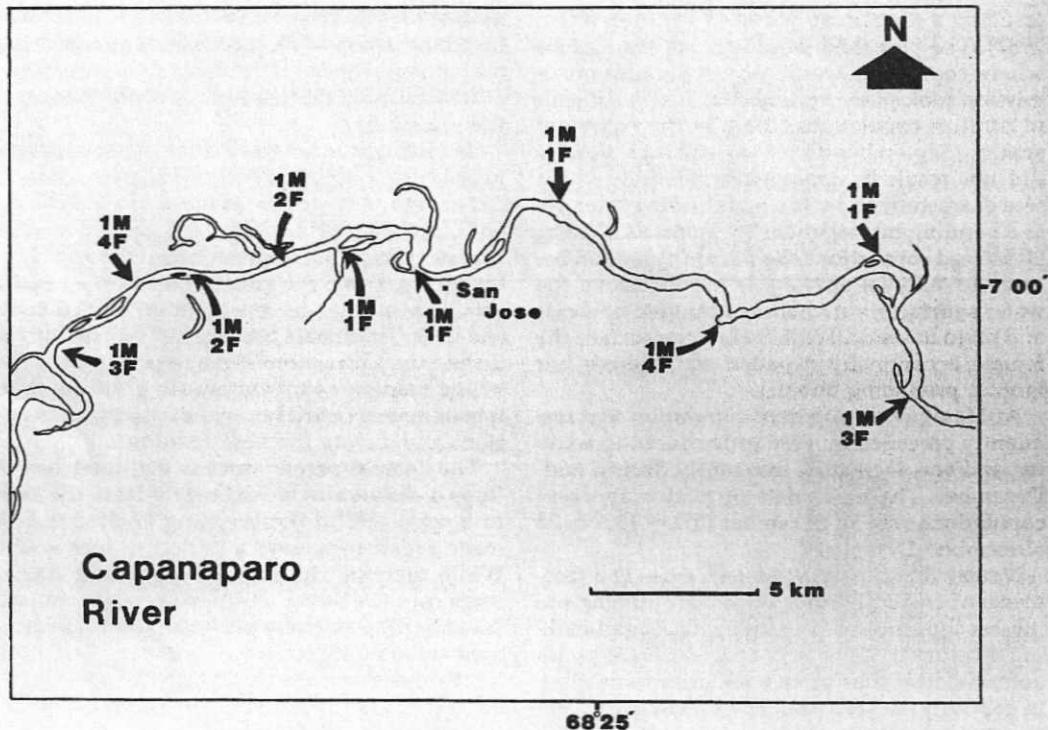


FIG. 4. Distribution of adult breeding groups along a 37 km stretch of the Capanaparo River. M refers to male, and F is the number of females present. Juvenile and subadult animals not included. The river flows from left to right.

in 1991. We made similar observations of adult crocodiles attending pods in other areas (Tucupido River, April 1986, three wk post-hatching; Camatagua Reservoir, June 1986, four wk post-hatching).

In captivity the pod of hatchling was very cohesive during the 3.5 mo it remained in the breeding enclosure in 1985. Pod cohesion was especially notable during the day when the group was frequently seen basking together, usually near or on the female. Within four wk of hatching the individual members of the pod began to disperse at night and scattered around the entire 20 m  $\times$  20 m lagoon. However, by the following morning the young would again form into a pod adjacent to the nest site. This pattern of activity continued until the hatchlings were removed from the breeding enclosure (September 1985).

**Breeding System.**—Repetitive aerial surveys (Thorbjarnarson and Hernández, 1992), diurnal and nocturnal boat surveys, and nest counts (Thorbjarnarson and Hernández, *in press*) indicated the presence of 10 breeding groups of Orinoco crocodiles along a 37 km stretch of the Capanaparo River (Fig. 4). The groups were centered on deep pools (>3 m deep) in the otherwise shallow river, and distances between

breeding groups ranged from 1.5 km to 8.0 km ( $\bar{x} = 4.1 \pm 1.9$  km).

At each site, censuses revealed the presence of one large crocodile (>3.5 m total length; presumably male) with one or more smaller crocodiles (2.5–3.5 m TL); both adult females and smaller males. Based on nest counts in the adjacent area (during the period 1987–1992), we estimated the number of adult females in each group. Males formed a monogamous pair at four of the 10 sites, or formed apparently polygynous groups with two (two sites), three (two sites), or four (two sites) females. The average adult male to adult female sex ratio was 1:2.2. Other adult crocodiles (>3 m TL) were observed in oxbow lakes connected to the main river channel, but did not nest and were presumed to represent non-reproductive males.

#### DISCUSSION

The signaling behaviors of Orinoco crocodiles consist of behavioral acts similar to those reported for other crocodylians (Garrick and Lang, 1977; Garrick et al., 1978; Vliet, 1989), but combined in a unique fashion to produce distinctive displays. These complex signals are comprised of visual, vocal, olfactory, and acoustic elements which have species-specific mean-

ings (Lang, 1987; Vliet, 1989). The two most prevalent social displays used by crocodilians are headslaps and roars (Garrick and Lang, 1977; Vliet, 1989). Roars ("bellows") and headslaps are performed separately in American alligators (Garrick et al., 1978; Vliet, 1989), but in Orinoco crocodiles are combined into a single display. The headslap acoustic signal appears to be virtually universal among crocodilians, being reported even in the morphologically and taxonomically distinct *Gavialis gangeticus*, where the narrowness of the snout produces a very weak sound (Whitaker and Basu, 1983).

The inclusion of a vocal component in the assertion display, however, is somewhat more variable. Within the genus *Crocodylus*, several species have an assertion display that consists of the stereotyped head emergent, tail arched body posture followed by headslapping, but typically without roars (*C. acutus*, Garrick and Lang, 1977; *C. niloticus*, Modha, 1967; *C. palustris*, Whitaker and Whitaker, 1984). Nevertheless, roaring has been occasionally reported in these species (*C. acutus*, Alvarez del Toro, 1974; Thorbjarnarson, 1991; *C. niloticus*, Cott, 1961; *C. palustris*, Battye, 1944). The fact that males evert their mandibular glands while roaring suggests that olfactory cues are an important part of the display (Vliet, 1989).

The functions of the assertion display are probably twofold (Garrick and Lang, 1977): establishing and maintaining territories among males (Kellog, 1929; Vliet, 1989), and attracting females for courtship (Joanen and McNease, 1971; Garrick and Lang, 1977; Garrick et al., 1978; Vliet, 1989). The assertion display serves as a system for communicating with other males information regarding territoriality. Male territoriality among crocodilians appears to be in large part a seasonal behavior associated with reproduction (Garrick and Lang, 1977; Lang, 1987). The successful establishment and defense of territories among male crocodiles is related to size and temperament, with the larger and more aggressive crocodiles being dominant (Lang, 1987). An assertion display conveys information regarding the sex, location, size and possibly individual identity of the animal (Garrick et al., 1978), presumably through the inherent properties of the sound produced (e.g., frequency and energy). This same information may be utilized by females for choosing partners.

Studies of crocodilians in captivity and in the wild suggest that prior to nesting females are not territorial, but enter and leave male territories (Modha, 1967; Garrick and Lang, 1977), and that the most prevalent mating system is polygyny: *C. niloticus* (Cott, 1961; Modha, 1967; Kofron, 1991), *C. acutus* (Thorbjarnarson, 1988),

*Gavialis gangeticus* (Whitaker and Basu, 1983); *Alligator mississippiensis* (Joanen and McNease, 1989). The seasonal frequency of Orinoco crocodile headslap-roars suggests a dual role in the establishment of territory and in mate attraction. The seasonal peak of headslap-roars coincides with the height of mating in December. The establishment of reproductive territories precedes courtship and mating (Lang, 1987), and may account for the increase in headslap-roars during September–November at Masaguaral. Nesting at Masaguaral takes place in February and early March (Thorbjarnarson and Hernández, *in press*), when the frequency of headslap-roars is rapidly diminishing. A similar seasonal pattern of bellowing, courtship, and mating has been reported for the American alligator (Joanen and McNease, 1975).

In the wild, dropping water levels may signal the establishment of Orinoco crocodile reproductive territories, followed by courtship and mating. At this time, crocodiles are forming dry season concentrations in the major river channels. Our observations suggest that males defend reproductive territories in the Capanaparo River centered on deep pools. The consistent observation of similar number of animals and nests in these specific areas year after year implies that individual group composition changes only on a long-term basis. Other large crocodiles (>3 m TL) were seen in prime feeding areas (oxbow lakes), but where no nesting takes place. Because the annual nesting effort of females is quite high (ca. 80%; Thorbjarnarson and Hernández, 1993), it is possible that these isolated animals were subordinate males excluded from breeding by dominant individuals.

However, the nature of the breeding system is almost certainly related to population density (Garrick and Lang, 1977). Under high density conditions in captivity (Lang, 1987), or in the wild (Modha, 1967; Kofron, 1991), crocodilians form dominance hierarchies, with one or a few of the largest males doing most of the breeding. Kofron (1991) even reports temporal separation of breeding activities by dominant males. Under lower density conditions the breeding system changes (Lang, 1987), and crocodilians may form distinct breeding groups or be monogamous. In the wild, the type of breeding system may reflect natural species-specific differences in population density, or recent changes in population density due to human-related factors. The present reproductive system in the Capanaparo River (part monogamous, part polygynous) may reflect natural variability in Orinoco crocodile mating systems, or the depleted status of this crocodile population due to past hunting (Thorbjarnarson and Hernández, 1992). At the very low population densities which presently

characterize this species throughout most of its distribution, monogamous pairs may be the rule, as was reported by Medem (1981) for parts of Colombia. Natural variability may be based on territory quality, or inter-male differences in reproductive performance. However, due to recent protection and the undertaking of a head-starting program (Thorbjarnarson, 1992), the Capanaparo crocodile population is thought to be increasing. The continued monitoring of the Capanaparo River crocodile population should provide interesting information on the density-dependent nature of breeding systems in this crocodile.

Orinoco crocodiles exhibit a highly developed system of parental care, which appears to be a characteristic feature of crocodylian reproduction (Ferguson, 1985; Shine, 1988). Although adult male involvement in parental care has been reported (Alvarez del Toro, 1969; Lang et al., 1986), most cases involve maternal care. Size estimates (direct observation or size estimation from footprints) of crocodiles attending adults in the Capanaparo River suggest that this is an exclusively female activity.

Nest opening by adult crocodylians has been noted in all species studied to date (Ferguson, 1985; Shine, 1988). Although hatchlings of some mound-nesting species can escape from the nest without maternal assistance (Kushlan and Simon, 1981), nest opening behavior is apparently essential in hole nesters (Pooley and Gans, 1976). A variety of sensory modalities are used for communication between females and the young during nest excavations. Fully developed young within the nest vocalize in response to vibrations from the approaching footfalls of the female. The vocalizations of the young elicit the nest opening behavior of the females (Pooley and Gans, 1976; Kushlan and Simon, 1981; Kushlan and Mazzotti, 1989). During the nest excavation process, vocalizations by the young and the female continue, and the inverting of the female's mandibular glands during this process also suggest that chemical olfactory cues may play an important role.

Diurnal variation in pod cohesion (grouped during the day, dispersion at night) is similar to reports for other species of crocodylians (Deitz, 1979; Cintra, 1989) and probably results in increased foraging opportunities for neonates. In the Capanaparo, females remained close to the pod, and may play an important role in protecting them against certain predators such as wading birds or the giant river otter (*Pteroneura brasiliensis*).

The impetus for initiating the ecological studies of Orinoco crocodiles began with the Venezuelan Fundación para la Defensa de la Naturaleza (FUDENA) and T. Blohm. In particular, we would like to thank C. Blohm, G. Medina-Cuervo, and M. de Lourdes Acedo de Sucre at FUDENA for their invaluable support. K. Vliet freely shared with us his considerable knowledge of crocodylian behavior.

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