

## Social Signals and Behaviors of Adult Alligators and Crocodiles

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**SYNOPSIS.** We compare and contrast the signalling systems and social behaviors of *Alligator mississippiensis*, *Crocodylus acutus*, and *Crocodylus niloticus*. Our qualitative analysis focuses primarily on the behaviors of adults during three phases of reproduction: I. Defense of Territory and Courtship, II. Nesting and Incubation, and III. Hatching and Post Hatching. Signals and signal elements are very similar among the three species. For example, all have vocal, non-vocal acoustic, and visual signals, some transmitted through air or water and others through both media. In addition, each species' repertoire is composed of discrete, graded and complex signals. A few signals are unique to each species. However, their signalling systems differ in the temporal organization of the behaviors, and in the relative frequency in which certain functional groups of signals occur or in which signals occur in a particular sensory mode. Apparently, the signalling systems of *C. acutus* and *C. niloticus* are more similar to each other than either is to the signalling system of *A. mississippiensis*. The signalling systems of the crocodile species appear to be adapted to open water habitats in which visual signals are advantageous and to high density breeding groups and post-copulatory intersexual contact. In contrast, the *Alligator* signalling system appears adapted to a marsh habitat in which vocal signals are likely favored and to low density breeding groups.

### INTRODUCTION

Advances in the study of crocodilian behavior and ecology now allow us to compare the behaviors of three species. This paper attempts to compare and contrast the signalling systems and social behaviors of these species, and introduces a consistent nomenclature for the social sig-

nals of crocodilians. Our analysis focuses on the reproductive behavior of the adults; the similarities and differences among species are here discussed in terms of the ecological and environmental factors which may have shaped them.

Recent reviews of reptilian social behavior contain meager information about crocodilians (Blair, 1968; Brattstrom,

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1974), but a number of behavioral studies are now available. We have studied adults of two of the species, the American alligator (*Alligator mississippiensis* Daudin) and the American crocodile (*Crocodylus acutus* Cuvier) (Garrick, 1974, 1975b; Garrick and Lang, 1975; Garrick *et al.*, 1977; Lang, 1975, 1967b, unpublished). For behavioral comparisons with the Nile crocodile (*Crocodylus niloticus* Laurenti), we rely on the descriptions of Cott (1961, 1968, 1975), Modha (1967, 1968), Pooley (1962, 1969, 1974, 1976), and Pooley and Gans (1976).

#### GENERAL CROCODYLIAN BIOLOGY

The 21 species of extant crocodylians are usually assigned to three families (Mertens, 1943): the Alligatoridae with 4 genera and 7 species, the Crocodylidae with 3 genera and 13 species, and a single species of Gavialidae (though Cohen and Gans, 1970 postulated an alternative classification). They are the survivors of an adaptive radiation of eusuchian crocodylians which began in the late Cretaceous (Sill, 1968; Langston, 1973). Their phylogenetic affinities are with the advanced diapsid forms, the Archosauria, which includes the major groups of Mesozoic dinosaurs, as well as the ancestors of the present day Aves (Colbert, 1965).

In general, crocodylians inhabit tropical and subtropical regions, are late maturing, long-lived, and semi-aquatic. Their visual system is adapted for nocturnality (Walls, 1942). As adults they have relatively few predators besides humans, to which many species are usually inoffensive.

#### SPECIES CHARACTERISTICS

*A. mississippiensis*, hereinafter referred to as AM, is distributed from Texas to S. Carolina in the southeastern U.S.A. There are major population concentrations in Louisiana and Florida where the species inhabits fresh and brackish water marshes, ponds, and river systems. Adults are black dorsally with yellow or white crossbands on the back and tail. The average size of adults is 2-3.5 m (McIlhenny, 1935;

Joanen and McNease, 1971, 1973; Brazaitis, 1974).

*C. acutus*, (CA), is a New World species which is broadly distributed along continental and island coastal and estuarine habitats in the Caribbean Sea and tropical Pacific Ocean. It still exists in some numbers in the Greater Antilles where the species inhabits lakes, salt ponds, mangrove swamps, rivers and their estuaries (Garrick, unpublished observations). Adults tend to be tan to dark brown in coloration with darker crossbands on the back, sides, and tail. Average adult size is 2.5-3.5 m (Ogden and Singletary, 1973; Alvarez del Toro, 1974; Brazaitis, 1974).

*C. niloticus*, (CN), is distributed throughout the African continent (except for the Sahara) and offshore islands including Madagascar (Pooley and Gans, 1976). Although originally a resident of diverse aquatic habitats, presently this species can only be seen in numbers comparable to earlier years near Murchison Falls, Uganda, and at Lake Rudolf, Kenya. Adults are olive-green to brown in coloration with dark crossbands on the back, sides, and tail. Average adult size is 3.0-4.5 m (Cott, 1961; Graham, 1968; Brazaitis, 1974).

Additional life history data related to reproduction for the three species may be found with references in Table 1.

#### STUDY AREAS AND METHODS

We studied American alligators and crocodiles at a commercial exhibition known as "Gatorama" (26°55'N, 81°17.5'W), located 3 km SE of Palmdale near Lake Okeechobee, Florida. About 40 adults of each species were housed separately in two adjacent enclosures; each enclosure contained about 0.9 ha of water and was surrounded by land that provided suitable basking and nesting areas. The alligators were obtained locally in the 1960s, and the crocodiles were captured from wild populations in Jamaica in 1967-8.

The social behaviors of AM were recorded by LDG and JWJ during the spring and late summer of 1974, and the

TABLE 1. Social organization and social behaviors during three reproductive events.

## A. COURTSHIP AND MATING

Age of participants: adults; habitat requirements: open, shallow water

Sp.	Mating system <sup>a</sup>	Aggregation, Numbers <sup>b</sup>	Dominance hierarchy		Territorial defense		Size of $\sigma$ 's territory <sup>c</sup>	Sex ratio $\sigma$ : $\varphi$ <sup>d</sup>	
			$\sigma$	$\varphi$	$\sigma$	$\varphi$	(ha)		
AM	P (7,9, 12,14) i	+, < 10 (13)	+	-	+	rare (7)	0.3-0.8 (14,17)	1:2.4 (7)	
CA	P (16)	+, > 25 (8)	+	+	+	- (16)	0.1-0.9 (1,16)	1:3.5 (16)	1:2 (1)
CN	P (5,19) M (27)	+, c.500 (19,20)	+	n.d.	+	- (5,19,27)	0.3-1.2 (5,19)	1:2.6 (5)	1:4.8 (19)

## B. NESTING AND INCUBATION

Age of participants: adults; habitat requirements: suitable nest material, shade, proximity to water

Sp.	Nest Material <sup>e</sup>	Nest Spacing <sup>f</sup>	Nest Site <sup>g</sup>	$\varphi$ Nest Defense		$\sigma$ near $\varphi$ or nest	$\sigma$ with Territory		
				Intraspecific	Interspecific				
AM	V (7,11,18)	S (7,11,18)	+	+	+	+	-	-	
				Pre-laying (7)	Post-laying (8)	+,rare (6)	(11)	(13)	(13)
CA	S (2,8,16,21)	S (1-2,16,21)	+	+	+	+	+	+	
		C (8)		(1,16)	(1)	(1,16)	(1)	(1,16)	
CN	S (3,5,19,22-24)	C (3,5,19,22-24)	+	+	+	+	+	+	
			(3,5,20,24)	(27)	(19)	(5,19,23)	(19)	(3,19)	

## C. HATCHING AND POST-HATCHING

Age of participants: adults, hatchlings; habitat requirements: quiet water, adequate cover

Sp.	$\varphi$ liberates hatchlings	$\sigma$ present near young <sup>h</sup>	Intraspecific defense of young <sup>h</sup>	Interspecific defense of young	Duration of parental association with young <sup>h</sup>
AM	+	-	n.d.	+	24 mos. (6)
	(10,11,18)	(13)		(15,18)	
CA	+	n.d.	n.d.	+	$\geq$ 5 wks. (1)
	(21)			(1)	
CN	+	+	+	+	12 weeks (5,27)
	(23,24-27)	(27)	(19,27)	(4,5,19,25-27)	

<sup>a</sup> Polygamous (P) vs. monogamous (M).<sup>b</sup> + = present in species; - = absent in species; n.d. = no data.<sup>c</sup> Water area only; one hectare (ha) = 10,000 m<sup>2</sup>.<sup>d</sup> Ratios for AM and CA derived from observations of the number of  $\varphi$ 's associated with a territorial  $\sigma$ ; ratios for CN equal the number of territorial  $\sigma$ 's to the number of nests (= inseminated  $\varphi$ 's).<sup>e</sup> Sand, soil (S) vs. vegetation (V).<sup>f</sup> Colonial (C) vs. solitary (S).<sup>g</sup> + = same nesting site(s) utilized by  $\varphi$  in successive years.<sup>h</sup> Data incomplete; additional observations required.<sup>i</sup> Key to references:

- |                             |                               |
|-----------------------------|-------------------------------|
| 1—Alvarez del Toro, 1974    | 15—Kushlan, 1973              |
| 2—Campbell, 1972            | 16—Lang, 1975                 |
| 3—Cott, 1961                | 17—Lang, unpubl. obs.         |
| 4—Cott, 1968                | 18—McIlhenny, 1935            |
| 5—Cott, 1975                | 19—Modha, 1967                |
| 6—Fogarty, 1974             | 20—Modha, 1968                |
| 7—Garrick, 1975b            | 21—Ogden and Singletary, 1973 |
| 8—Garrick, unpubl. obs.     | 22—Pooley, 1962               |
| 9—Garrick and Lang, 1975    | 23—Pooley, 1969               |
| 10—Herzog, 1975             | 24—Pooley, 1973               |
| 11—Joanen, 1970             | 25—Pooley, 1974               |
| 12—Joanen and McNease, 1972 | 26—Pooley, 1976               |
| 13—Joanen and McNease, 1973 | 27—Pooley and Gans, 1976.     |
| 14—Joanen and McNease, 1976 |                               |

late winter of 1975. CA were studied by JWL in the fall of 1973, the spring of 1974, and the late winters of 1975 and 1976. Animals were observed primarily during daylight hours. For night observations we used passive night vision scopes. Garrick *et al.* (1977) contains further details of the study population, environmental setting, and methods of observation and analysis.

Cott (1961) studied Nile crocodiles in nature along the 18 mile stretch of Victoria Nile from Murchison Falls to the Lake Albert delta (Uganda) and at game reserves in Zululand (South Africa). Modha (1967) studied a wild population of crocodiles from 1965-67 at Lake C (about 65 ha in area) on Central Island in Lake Rudolf (Kenya). And Pooley observed CN in rivers, lakes, and swamps primarily in eastern South Africa and southern Mozambique, and pioneered observations in large enclosures.

Behavior at Gatorama was sampled *ad libitum* in the sense discussed by Altmann (1974). The assignment of behaviors to males or females was based on: 1) observations of marked and sexed AM and CA and subsequent comparisons of the behaviors of unmarked animals to those of known sex, and on 2) the classification of adults into apparent size classes with the largest animals assumed to be males. Apparently, a method similar to 2) above was used by Pooley, Cott and Modha.

With the exception of a few terms, *e.g.*, bellowing, which are part of the literature of crocodilian behavior, the nomenclature is our own. We have named the signals of AM and CA descriptively rather than functionally, *e.g.*, "snout lifting" not "appeasement display." CN signals which have been named functionally by previous workers are identified by quotation marks.

#### SOCIAL BEHAVIORS AND REPRODUCTIVE EVENTS

Reproductive functions change through the breeding season, and corresponding shifts in the social structure and habitat accompany these changes. The behaviors are described within this context. Each

reproductive activity occurs at a specific location within the broader habitat. For example, crocodilians copulate in shallow water, and nest where adequate nest material, shade, and water are available. And following incubation, the hatchlings require secluded shallow waters. These particular environments, then, are the focal areas for breeding, nesting, incubation, hatching and post-hatching behaviors.

Figure 1 correlates the timing of the major reproductive events with the rainfall pattern at the localities where the studies took place. The following points require emphasis: 1) courtship is lengthy, often extending 6-8 weeks; 2) the peak of courtship precedes nesting and egg laying by about one month; 3) incubation lasts 7-12 weeks; 4) the eggs hatch during a period of seasonally high water; 5) in CN there is much overlap in the timing of reproductive events; and 6) even though AM and CA are breeding at the same locality, the crocodiles mate during the months of February and March, a reproductive pattern similar to that seen in some Jamaican CA populations (Garrick, unpublished observations).

The social organization and summaries of reproductive activities relevant to the expression of social behaviors in AM, CA, and CN during three periods—territorial defense and courtship and mating, nesting and incubation, and hatching and post-hatching, respectively—are presented in Table 1.

In the following sections we compare the reproductive behaviors of these species during each period.

#### *Territorial defense, courtship and mating*

In all three species, combat between males contesting for dominance precedes the establishment of mating territories (in CN: Pooley and Gans, 1976). However, combat takes different forms. Although *mock biting* of limbs or tail (holding a body part in the mouth without biting it) occurs between two CA, it is not observed between fighting AM. In CN, males received

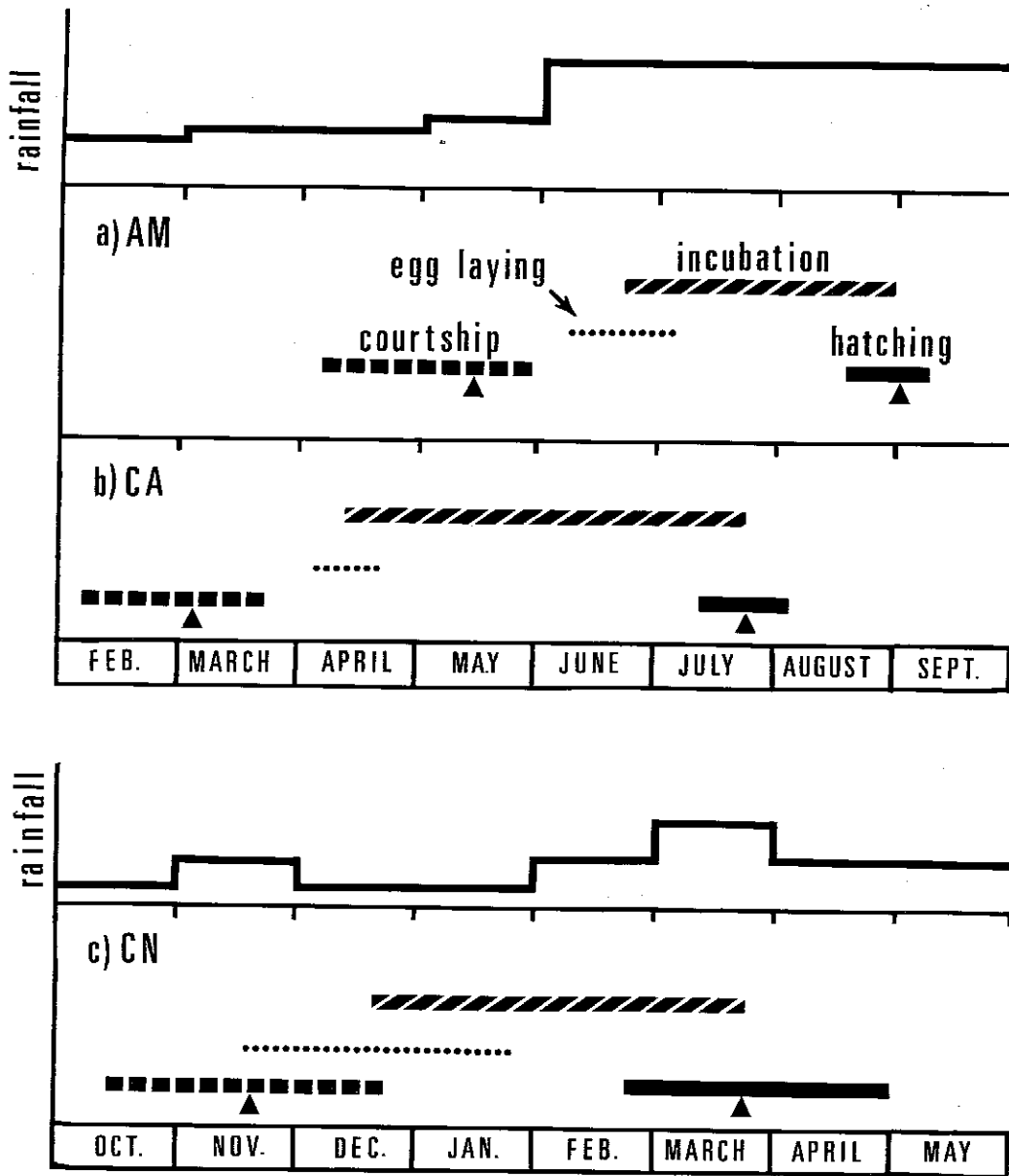


FIG. 1. Timing of reproductive events in relation to rainfall patterns for a) *A. mississippiensis* (AM) and b) *C. acutus* (CA) at "Gatorama" in south central Florida, and for c) *C. niloticus* (CN) at Central Island in Lake Rudolf (data from Modha, 1967). Triangles denote courtship and hatching peaks.

many injuries (Cott, 1961), presumably during disputes over precedence and access to females.

Males defend their territories against non-territorial (subdominant) and other territorial males but tolerate the proximity of females. Females are not exclusively associated with a particular territorial

male, and they move freely among territories (in CN: Modha, 1967).

Territorial males dominate the breeding groups. In AM, for example, the alpha male interrupted courtship of subdominants. Females display submissive behavior in the presence of territorial males. However, females may also form dominance

hierarchies. For example, certain female CA defer to other females with appropriate submissive behavior. Only one female, an alligator, defended a territory from other females during the breeding period; within the territory was her future nest site.

Territorial defense of the three species is essentially similar. 1) Territorial males are likely to approach intruders after displaying a *head emergent, tail arched posture* which apparently signifies alertness (Fig. 2d). 2) Exchanges between territorial males and intruder males often take the form of chases, lunges, and mock or real fighting. 3) The *inflated posture* (Fig. 2c), displayed by territorial males, does not function as a "threat" to reduce the frequency of immediate aggressive encounters (aggression used in the sense of behaviors performed with an "intent to injure": Hinde, 1974), but rather follows most chases. 4) Territorial male CN and CA systematically patrol their territories. 5) *Narial geysering* (a spout of water rising from the nares) occurs during a face-off of two male CN (Modha, 1967) and in territorial CA males alone or following headslapping. In AM, narial geysering frequently accompanies *headslaps*, which at times are performed within a territory. 6) Mutual tolerance increased among all members of AM and CA groups during basking.

Differences among the species in territorial defense behaviors also occur. 1) AM males do not patrol their territories. 2) *Snout lifting*, which is a submissive or appeasement behavior (Fig. 2g) is given by intruder CN males when responding to territorial or other dominant males, and by CN females to all males. In CA, intruder males rarely snout lift, but females typically snout lift in the presence of territorial males. Female AM rarely snout lift and theirs differ in form from the snout lifting of CA and CN. 3) Territorial male CA respond to an intruder by *headslapping* (Fig. 2e) 1-3 times accompanied by *tail wagging*. 4) Territorial male CA also *jaw clap* during a chase producing a loud hollow "pop" as the jaws are closed rapidly. Jaw claps are apparently similar to a noise

(a "snap") made by a territorial male CN after it had chased an intruder male out of the water (Modha, 1967). Although rare in AM, jaw claps are also a response to an intruder. 6) Agonistic behaviors such as *mock biting* in male CA, and *open jaw contact* by male CA and CN contrast to the aggressive behaviors of AM.

Shifts in dominance occurred in all three species. Initially in AM, two males contested for dominance. The largest animal, a recent introduction into the lake, became the alpha male. The defeated male and another male were obvious subordinates and held smaller territories adjacent to the alpha male's territory. Similarly, the introduction of a male CA apparently led to changes in the dominance hierarchy. In the fall of 1973, there was a single territorial male. However, following the introduction in April, 1974, three males, but not the introduced one, defended territories.

Courtship behavior between two individuals appears quite "leisurely," lasting from several minutes to nearly one hour (in CN: Cott, 1975). There are several important differences between AM courtship and the courtships of CA and CN: The sequence of precopulatory behaviors is more predictable in CA and CN than in AM (Fig. 3). Also, in AM, the precopulatory behaviors are arranged complexly and are of indeterminate order. Moreover, one rarely observes a complete sequence to copulation in AM, but is more likely to do so in CA. For ease of comparison, typical courtship sequences are divided into three chronological segments. They are: 1) the attraction and advertisement signals, 2) pair formation, and 3) the precopulatory behaviors, which are followed by copulation (Fig. 3).

In AM, the advertisement displays of *bellowing* (Fig. 2b) and *headslapping* (Fig. 2a) by either sex elicit approaches by the opposite sex. Bellowing choruses are frequent during the courtship period, and alligators typically bellow from within their territories. In addition, females and males often bellow in close proximity. In contrast, headslaps, given singly by AM, attract males or females, sometimes from a distance of 50-75 m. The alpha and beta

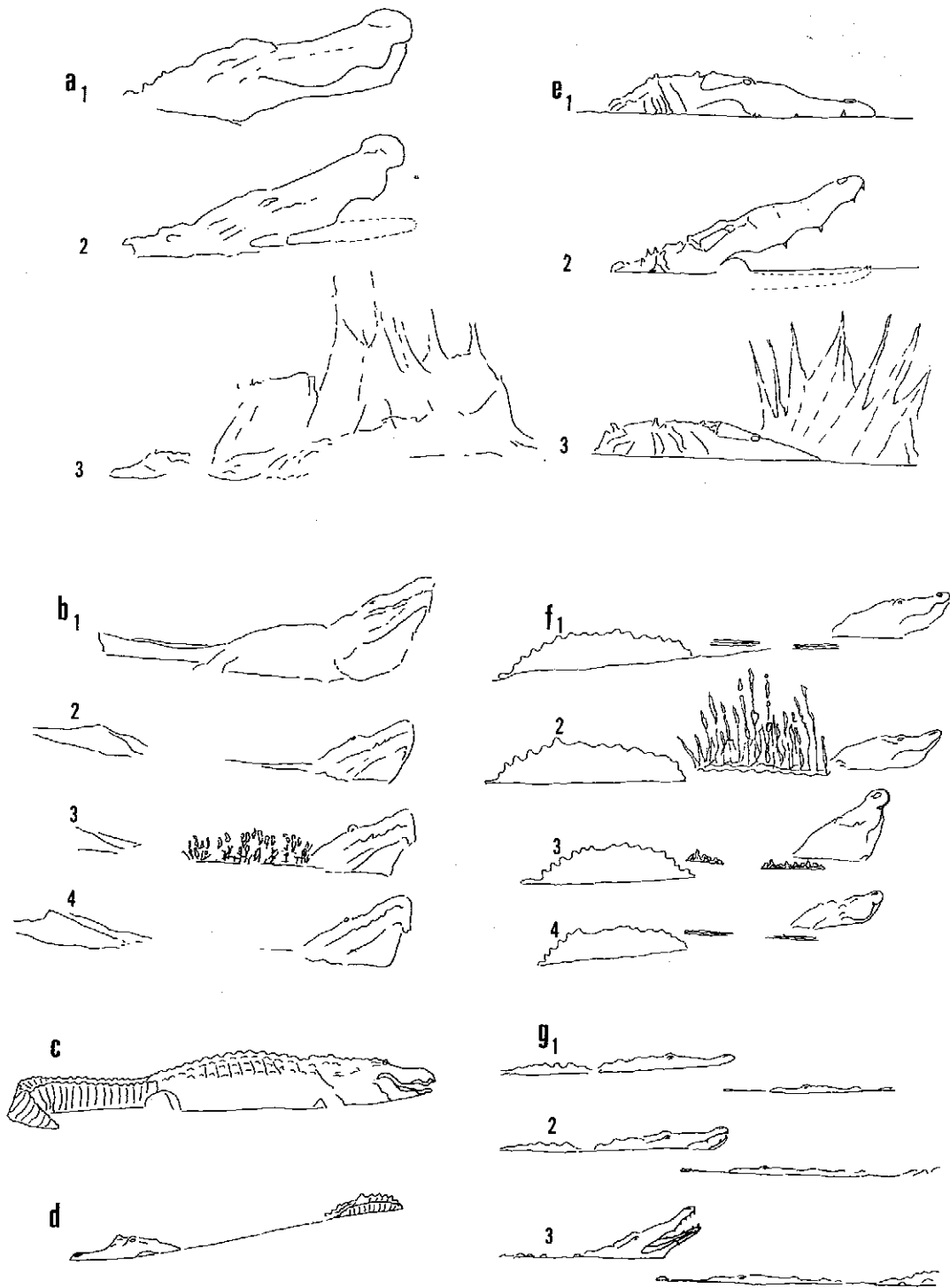


FIG. 2. Selected social signals of *A. mississippiensis* (a-d) and *C. acutus* (e-g) traced from movie and still photographs: (a,e) headslapping, (b) bellowing, (c) inflated posture, (d) head emergent tail arched posture, (f) subaudible vibration, and (g) snout lifting. All the signals figured here occurred in the water; however, certain

of them (bellowing and snout lifting) may also be performed on land. Time (in seconds) elapsed between sequential frames is as follows: a1-a2=0.5, a2-a3=0.2, b1-b2=2.1, b2-b3=1.0, b3-b4=1.5; e1-e2=0.1, e2-e3=0.2; f1-f2=0.6, f2-f3=2.4, f3-f4=2.0; g1-g2=4.2, g2-g3=2.3.

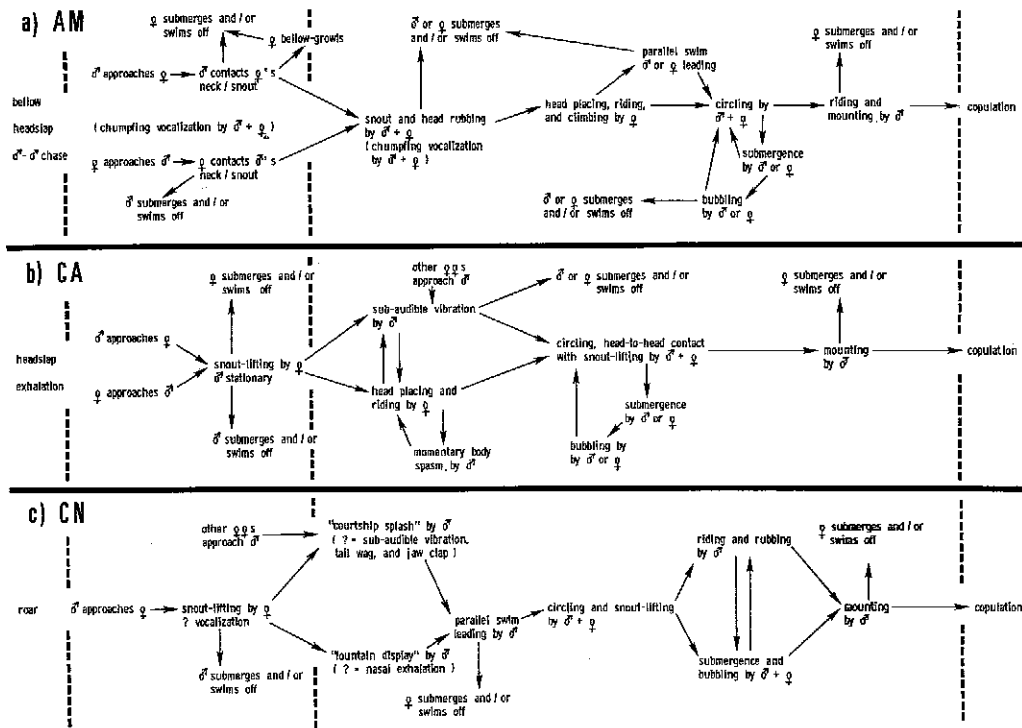


FIG. 3. Sequences of courtship behaviors in AM, CA, and CN. For each species, the vertical dashed lines separate (from left to right): 1) attraction, advertisement, and other signals, 2) initial pair formation, 3) the precopulatory behaviors, and 4) copulation.

males and the territorial female AM headslap often from within their respective territories. These advertisement displays are evidently effective as the alpha and beta males are often surrounded by 2-4 females during the peak of the breeding season.

"Roars" are emitted only by territorial male CN, and apparently function similar to the bellowing of AM in attracting females (Cott, 1961, 1975). An isolated CA has been observed to roar on land (Herzog, 1974), but Lang did not witness this vocalization at Gatorama. In fact, the most dramatic advertisement display of a territorial male CA is a rapid series of one to three headslaps.

The initial approach and interaction between a potentially breeding pair take different forms in the three species (Fig. 3). The most distinctive behavior is that female CA and CN snout lift, while AM females do not. Indeed, AM pair forma-

Descriptions for AM and CA are based on our observations and the CN sequence is synthesized from descriptions by Modha (1967), Cott (1975), Pooley (1976), and Pooley and Gans (1976).

tion occurs without any obvious submissive behavior by either partner: The pair engages in mutual snout contact on specific regions of the head and both sexes produce a cough-like vocalization. These signals may reassure the partner of an alligator's non-aggressive tendencies. At this point courtship may terminate in AM when the female emits a series of *bellow growl* vocalizations and swims away, apparently signalling her disinclination toward further courtship. Male AM may also move away from the female at this time. Female crocodiles may also abandon courtship and leave the male's territory, or the (CA) male may submerge and swim off. If they remain together, the pair engage in precopulatory behavior.

CA and CN males respond to snout lifting females by performing a complex display (Figs. 3 b,c). CN males employ a "courtship splash display" (Modha, 1967) and/or a "fountain display" (Cott,



1975:143) = narial geysering in the present terminology. CA males signal by *sub-audible vibrations (SAV)* radiating from the body (Fig. 2f). In this context, occurrence of *SAV* is a good predictor of further courtship in CA (Fig. 3b).

AM of both sexes perform precopulatory behaviors, consisting of cough-like vocalizations, as well as tactile, visual, and possibly olfactory signalling behaviors; these behaviors may be shifted about in sequence. CA precopulatory behaviors differ from AM in that there is no distinct vocalization, they are more determined in their order, and are sex-specific (Fig. 3). The determined order is illustrated in Figure 3b; if a pair begins *circling* behavior, *mounting* and *copulation* predictably follow. In addition, female CA lift their snout high and arch the tail out of the water; no such behavior occurs in AM. Apparently the behavior signals an invitation of further courtship to the males, and apparently this signal is similar to the "prenuptial display" of CN females (Cott, 1975: 144). Both sexes of all species engage in precopulatory behaviors such as *circling*, *bubbling* and *submergence*, *mutual head contact* (Lang, 1976a; cover photo), and *riding*. Few of the courtship sequences we observed ended in copulation.

In AM, the peak of courtship activity and copulation coincides with ovulation, which in turn precedes egg laying by about one month (Joanen and McNease, 1976). The timing may be similar in CA and CN (Fig. 1). It is not known whether fertilization results only from insemination during this time, or if sperm is retained from prior reproductive seasons. Copulation takes place in shallow water and lasts 2-4 minutes or longer (in AM: McIlhenny, 1935; Legge, 1967; Joanen and McNease, 1972; in CN: Modha, 1967).

#### *Nesting and incubation*

Various agonistic encounters occur with conspecifics during nest site selection and preparation, and also during the subsequent defense of the site and the nest against conspecifics and potential predators (references in Table 1).

Nest defense is common to all three species. However, interactions with humans provide the best data, especially for AM.

We have witnessed the behaviors employed for nest defense by AM and CA. On land, a female alligator attacks a human intruder transgressing to within about seven meters of her nest (Garrick *et al.*, 1977; Neill, 1971). This aggression takes the form of an *open-mouthed lunge* with a loud sustained vocal *hiss*. Occasionally, when the nest is between the female and the intruder, she will climb upon the nest (AM) and confront the intruder with the same display. On land, female CA resort to *open-mouthed hissing* and *jaw clapping* directed toward an intruder. When in the water near their nests, AM and CA females assume the *head emergent tail arched posture* (Fig. 2d) in response to human intruders.

Nile crocodiles defend their nests nearly constantly against predators such as Nile monitors and marabou stork (Cott, 1961, 1975); but in response to humans, most females leave the nest and enter the nearby water. However, Pooley (1969) reported that one female stood her ground and "growled" when irritated, and that a female responded to humans near her nest by "splashing water with her tail," and another chased an 18-foot boat as it neared her nest.

In areas where they are not harassed, females of all three species probably remain near the nest for a majority of the incubation period (references in Table 1).

#### *Hatching and post hatching*

As incubation of the eggs nears completion the young begin to vocalize a bark or "eeau" sound even prior to pipping (Pooley, 1969). In response to vibrations or sounds on or near the nest surface (Pooley, 1962, 1969), the hatchlings call collectively, each one apparently reinforcing the others. Possibly cued by this sound, the female exhumes the young and unhatched eggs from the nest. Partially hatched eggs are picked up in her mouth and gently cracked open, and then the young are

transported in her mouth to the water (references in Table 1).

The young remain with the female for various lengths of time (Table 1). CN defends young against natural predators, but the evidence for AM is still equivocal and is based on responses to humans (Table 1). Although parent-young contact may be of long duration (Table 1), we know relatively little about their social interactions.

In AM, vocal signalling between mother and young, and among the young likely aids maternal care and promotes group cohesiveness (McIlhenny, 1935; Campbell, 1973). In all three species, a loud, repetitive *distress call* is emitted by young when they are grasped. Adults are attracted reliably to the location of such calls (e.g., Kushlan, 1973; Pooley, 1974; Modha, 1967).

#### COMPARISON OF SIGNALS AND SIGNALLING SYSTEMS

In order to further characterize each signalling repertoire and clarify the similarities and differences in the communication systems, we compare the functions of ten signals during three social contexts among the three species (Table 2). Nearly all of these signals are described above, and selected examples are illustrated in Figure 2.

Signals and signal elements are very similar among the three species, but differ slightly. The essential similarities and differences in eight signal categories are as follows: 1) All three species *growl*, *grunt*, *cough*, and *hiss* in nearly all social contexts. 2) All three species produce *subaudible vibrations (SAV)* passing through the water during courtship (Fig. 2f, 3). In AM, however, *SAV* may occur as a component of bellowing (Fig. 2b), and in AM and CA, the *SAV* are performed immediately prior to some headslaps. 3) *Narial geysering* occurs during headslaps in CA and AM, as an advertisement signal by male CA and CN, and as an event during male-male encounters in CN. 4) *Snout lifting* is an appeasement signal of CA and CN females and CN subdominant males and a courtship signal

employed by both male and female CA and CN (Fig. 2g). In AM, snout lifting is observed rarely. 5) Males of all three species *jaw clap* in agonistic situations. 6) Male CA and CN and male and female AM *tail wag* either during signals, such as bellowing, headslapping, and inflated postures (Fig. 2c), or alone from the head emergent tail arched posture (Fig. 2d). 7) Both sexes of AM and CA display the *head emergent tail arched posture* (Fig. 2d). 8) AM males and females, and CA males display an *inflated posture* with mouth open and accompanying low growl and tail wag (in the water), oriented toward a conspecific (Fig. 2c).

Table 2 also demonstrates some definite discontinuities requiring further comment. No "roars" or bellows are reported for CA during social contexts, and *headslaps* have not definitely been reported in CN, but these may be matters necessitating further study. Furthermore, CA appears relatively mute during courtship while AM and CN vocalize.

In summary, the signals compared above (Table 2) include vocalizations, non-vocal sounds, movements, and postures. Thus, it is apparent that these semi-aquatic reptiles have evolved visual and acoustic signals which are transmitted through air or water, and in some cases, e.g. headslapping, through both media.

All three signalling systems are similarly complex. Each species' repertoire appears to contain discrete signals, including certain vocalizations, graded signals, e.g., some postures, and complex or composite displays. Examples of this latter group include the "courtship splash display" (Modha, 1967) of CN males which appears to contain the following signal elements: *SAV*, jaw clap, tail wag, and splashing, and the headslap of AM, which has been observed in at least seven different forms each resulting from the addition of signal elements before and after the headslap (Garrick *et al.*, 1977).

Despite strong similarities in signal elements and complexity among the species, their signalling systems differ in the temporal organization of the behavior and the relative frequency in which certain func-

TABLE 2. Comparison of selected social signals in three social contexts.

Social context	Acoustic signals						Visual signals			
	Vocal		Non-vocal acoustic				Movements		Postures	
	Bellow, roar	Hiss, cough growl, grunt	SAV <sup>f</sup>	Narial geyser	Head slap	Jaw clap	Snout lift	Tail wag	HeTa <sup>f</sup>	IP <sup>f</sup>
AM Defense of territory		♂♀		♂ <sup>a</sup> ♀ <sup>a</sup>	♂♀	♂ <sup>a</sup> ♀ <sup>a</sup>		♂ <sup>a</sup> ♀ <sup>a</sup>	♂♀	♂♀
AM Courtship	♂♀	♂♀	♂ <sup>a</sup> , ♀ <sup>b</sup>	♂♀	♂♀	♂ <sup>a</sup> ♀ <sup>a</sup>				
AM Defense of nest/young		♀				♀		♀	♀	
AM Other contexts						♂♀	♀			
CA Defense of territory		♂	♂ <sup>a</sup>	♂ <sup>a</sup>	♂	♂	♀	♂	♂	♂
CA Courtship			♂	♂	♂		♂♀	♂		
CA Defense of nest/young		♀				♀			♀	
CA Other contexts	X <sup>d,e</sup>					♂♀				
CN Defense of territory	♂	♂			♂		♂	♂ <sup>c</sup> ♀ <sup>c</sup>		♂ <sup>e</sup>
CN Courtship	♂	♀	♂	♂	♂ <sup>a</sup>	♂ <sup>e</sup>	♂♀	♂		
CN Defense of nest/young		♀				♀				
CN Other contexts	X <sup>d</sup>									

<sup>a</sup> May occur with headslap.

<sup>b</sup> As a component of bellowing.

<sup>c</sup> Appeasement or conciliatory signal; ♀♀ are non-territorial.

<sup>d</sup> Sex of performer not determined.

<sup>e</sup> Tentative assignment on basis of description in literature.

<sup>f</sup> SAV = sub-audible vibration; HeTa = head emergent tail arched (see Fig. 2d); IP = Inflated posture.

tional groups of signals occur or in which signals occur in a particular sensory mode. These major differences are as follows:

1. In AM, vocal signals are more varied and used more commonly than in CA or CN (Table 2).

2. In AM, both sexes perform the same signals; these include advertisement, precopulatory, and agonistic behaviors. In contrast, many CA and CN signals are sex-specific (Table 2).

3. In CA (and apparently CN) courtship sequences appear more ordered and predictable than in AM (Fig. 3).

4. CA and CN display more appeasement behavior in submissive-dominant animal interactions than AM, and in CA

and CN, but not in AM, some precopulatory behaviors incorporate an appeasement signal (snout lifting).

5. In CA (and possibly CN) approach of males and females during courtship is more tentative (cautious) in comparison to AM (Fig. 3).

Therefore, we conclude that the signaling systems of CA and CN are more similar in both structure and function to each other than either is to the signalling system of AM.

#### DISCUSSION

We can now speculate about factors which might account for the differences

between these signalling systems. First we consider two examples—AM vocality, and snout lifting in CA and CN—and correlate their structure and function with habitat type.

During the early spring the bellowing of AM probably functions in long distance intra- and intersexual communication in a marsh habitat where visibility of conspecifics is reduced. Bellowing may also facilitate the congregation of breeding adults to the open waters of a marsh (Joanen and McNease, 1971, 1973). Later, when the breeding group is formed, bellowing, which peaks in frequency of occurrence simultaneously with the peak of courtship activity (Garrick *et al.*, 1977; Joanen and McNease, 1976), probably conveys information about an alligator's location, sex, size, and identity, all of which may determine its mating partner(s).

The prevalence of vocalizations in the AM repertoire (Garrick, 1974; Garrick *et al.*, 1977) also appears to be an adaptation to marsh type habitat. Certainly, vocal signals are less ambiguous (Marler, 1968) than visual signals when given by a black alligator in a poorly illuminated, heavily vegetated marsh or swamp.

Visual signals might be more effective even at moderately long distances in the lakes, bays, and broader rivers inhabited by CN and CA. Snout lifting, for example, may be adaptive in open water environments without vegetation where, at a distance, the form and color of the head contrasts with the aquatic environment. However, the environmental requirements for signalling do not alone explain the major differences among the signalling systems of these three species, and we must consider other factors.

The difference in form of male courtship displays between CA and CN could have originated as reproductive isolating mechanisms. On the other hand the signalling systems may have simply changed over time. Similarities between CA and CN signals, *e.g.*, the frequent use of snout lifting and the temporally ordered precopulatory behaviors suggest a strong phylogenetic affinity and/or evolutionary convergence in response to common

ecological and environmental factors. Because the evidence is lacking, it is difficult to assess the phylogenetic affinity of CA and CN (Sill, 1968).

Among alligatorids however, vocality may have originated in species which evolved in habitats similar to those inhabited by present day forms. There is some evidence bearing on this supposition: An extant species, the Chinese alligator (*A. sinensis*), which does not share a recent common ancestor with AM (Mook, 1923, 1925), inhabits lowland rivers and streams (Brazaitis, 1974) and is also very vocal (Garrick, 1975a). And a fossil alligator (*Albertochampsia langstoni*) from the late Cretaceous of Canada (Erickson, 1972a), may have lived in dimly lit swamp waters (Erickson, 1972b) in which vocal signals were likely advantageous. Unfortunately, there is no morphological structure identified with vocality in extant alligators which could be used as evidence for vocality in fossil forms.

In order to speculate further on the evolution of crocodylian signalling systems we need descriptions of the behaviors of other species. These being lacking, we will suggest ecological problems for which these signalling systems appear to be solutions. As a point of departure we focus on the social organization of these three species in order to explain the adaptive significance of the differences among their signalling systems.

Basically, the pattern of social organization for these three species is sequentially: a breeding group of low (AM) to high density (CA, CN) with individuals interacting within a system of males' territories. After courtship in AM, but not in CA and CN, the group disperses and males remain separate from females and their nests (references in Table 1). In further contrast, male CN may inhabit areas close to the female and young (references in Table 1). Thus, continuous temporal and spatial postcopulatory contact between individuals is characteristic of CN (and possibly CA) compared to AM. Hence, the crocodile's social organization appears to require a signalling system adapted for communication at higher population den-

sity than that of AM.

Many of the major differences in the signalling systems of CA and CN vs. AM appear to be adaptations to high-density activity. Particularly, sex-specific behaviors would be adaptive in minimizing signalling ambiguity during breeding. Vocal communication might be reduced in a crowd because of the potential for ambiguity, *i.e.*, there would be more noise than signal. Frequent appeasement signals and more tentative approaches might serve to reduce aggression and avoid the potential loss of gametes and zygotes.

The ordered courtship sequence appears adapted for a mating system in which a limited number of territorial males copulate with many females. It can be suggested that at high densities there are more females attempting to mate with a dominant male, and consequently there is more competition among males. Under these conditions a prolonged, uninterrupted courtship sequence would provide more information for the female about her choice of a male. Thus, female sexual selection could be the mechanism responsible for the temporally ordered courtship. The territorial male's responsibilities are even more extensive because the presence of many nearby subdominant males requires systematic patrolling of his territory. Therefore, a brief, ordered courtship might also be an adaptation to the temporal constraints of territorial defense upon the male.

Furthermore, postcopulatory contact among crocodiles probably necessitates the frequent use of appeasement signals in order to reduce aggression which might injure gravid females or females tending nests or young and as a result endanger the year's reproductive effort.

Ratios of 1:5 (Modha, 1967) and 1:3 (Cott, 1975) of territorial males to nesting females suggests that competition for mates may be severe. Moreover, competition for mates may be exacerbated if some mated females do not lay or if certain males are preferred.

Although it is premature to attribute certain features of crocodilian social organization to particular ecological factors,

as has been done with birds and primates (Crook, 1965, 1970), we can propose the types of questions that can be asked.

One of the most obvious dichotomies between the species is colonial vs solitary nesting (Table 1). In CN inhabiting large rivers and lakes, we can identify characteristics of social organization that are correlated with colonial nesting: the higher density of females, the presence of territorial males at the nesting grounds from breeding through hatching, and the presence of the male near the young. On the other hand, we know less about the social organization of CA in nature. It is known, however, that the species nests colonially in one lake habitat (Garrick, unpubl. obs.) and solitarily in riverine and coastal situations. In a river setting, Alvarez del Toro (1974) noted two females nesting within a male's territory, but it is still unknown whether the male is present at hatching or with the young. In contrast to the crocodiles, AM nests individually and males and females disperse after breeding. In addition, the female alligator departs the open water for nesting and the male apparently wanders until the fall (Joanen and McNease, 1973).

Thus a proper question would be: What resources ultimately favor a colonial vs. a solitary nesting strategy? Answers to this question should make it possible to determine whether there is indeed a causal relationship between nesting strategy and social organization.

In species such as AM that occupy several different habitat types (*e.g.*, marsh or lake), but which appear to be conservative in nesting strategy, we might ask whether differences in habitat generate differences in social organization, and if, among populations in different habitats, signalling systems are organized differently. Answers to these questions would provide powerful tools for understanding the ecological causes of selection on crocodilian signalling systems.

Undoubtedly, meaningful crocodilian research aimed at answering these questions can be pursued in natural settings. Caution is necessary however, because many wild populations have been disturbed and decimated. For example, Cott

(1961, 1975) reports that historically CN nested in colonies, but that today colonial nesting is incompatible with human disturbance. Nevertheless, additional studies on other species would be exceedingly valuable. They should contribute to our understanding of the causes of selection in crocodylian populations and, therefore, ultimately advance our comprehension of the ecology and management of these forms.

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