SOCIAL SIGNALS OF ADULT AMERICAN ALLIGATORS

LESLIE D. GARRICK, JEFFREY W. LANG, AND

HAROLD A. HERZOG, JR.

SOCIAL SIGNALS OF ADULT AMERICAN ALLIGATORS

LESLIE D. GARRICK
Center for Field Biology and Conservation
New York Zoological Society, Bronx, New York

JEFFREY W. LANG
Department of Ecology and Behavioral Biology
University of Minnesota, Minneapolis, Minnesota

HAROLD A. HERZOG, JR.
Department of Social and Behavioral Sciences
Mars Hill College, Mars Hill, North Carolina

CONTENTS

ABSTRACT

For the first time the signaling behaviors of adult American alligators (*Alligator mississippiensis* Daudin) are described systematically. Eighteen behaviors are divided into eight visual, six vocal, and four nonvocal acoustic signals, but some signals are a composite of elements from all three modalities. Among these signals, most are discrete rather than graded, and nearly all are given by both sexes.

Among the vocalizations sound energy is concentrated at less than 1 kHz., with most dominant frequencies less than 250 Hz. Communication over long distances is accomplished by acoustic signals, whereas visual signals are chiefly used at shorter distances between alligators. This dichotomy may be the result of selection for acoustic signals in the alligator's vegetated habitat.

Most of the semi-aquatic alligator's social behaviors occur in the water, and the importance of water is illustrated by the many signals that result from the amount of body surface exposed above the water and by the transmission of acoustic signals through the water.

Alligators and other crocodilians share many signal elements, although they may be combined in different ways in order to serve different communication functions. The alligator signaling system also shows complexity similar to that reported in birds and mammals, again demonstrating that some reptiles are *not* behaviorally uncomplicated in spite of their general inferior capacity for sustained metabolic activity.

INTRODUCTION

Investigations of crocodilian behavior and ecology have produced exciting results. The excellent studies of Cott (1961), Modha (1967), and Pooley (1969) on the Nile crocodile (*Crocodylus niloticus*) detailed many aspects of reproductive ecology and associated social behaviors. These investigations formed, until quite recently, the basis of our knowledge about crocodile behavior. On the other hand, the behavior of the endemic American alligator (*A. mississippiensis*) has not been systematically recorded.

Descriptions of American alligator behavior nevertheless appeared in eighteenth-century writings. For example, Bartram (1791) wrote exaggerated and entertaining accounts of encounters with American alligators in Florida. Later, Darwin (1872) quoted Bartram's embellished descriptions of alligator bellowing. In the twentieth century, Reese (1915) reported on alligator nesting, anatomy, and embryology, and McIlhenny (1935) described the life history of this species. Although loosely organized in places and often personal in tone, many of McIlhenny's observations subsequently have been verified. Recently, Neill (1971) presented a useful overview of all crocodilians but treated their behavior poorly, especially that of the American alligator. It appears that in an effort to debunk many of the myths surrounding the American alligator, Neill rejected the observations other investigators made on many potential adaptive behaviors. Recent research on the behavior of the American alligator has uncovered similarities with the behavior of the Nile crocodile (Pooley and Gans, 1976) and interesting parallels with the behavior of birds and mammals. For example, the maternal behavior of the female alligator and her participation in nest opening and hatching (Joanen, 1970; Kushlan, 1973; Herzog, 1975) and the vocality of young and adults (Campbell, 1973; Garrick, 1974; Herzog and Burghardt, 1977) have broadened expectations about alligator communication and provided new and important information relative to their survival. Nevertheless, detailed descriptions of the adult social behaviors of this threatened and endangered species (U.S. Endangered Species Act of 1968 and revisions) are not available.

Hence, the purposes of the present investigation were to describe in detail adult American alligator social behaviors. Herein we have described the various signaling behaviors and

157

their contexts and the temporal pattern of activities associated with them in an effort to understand their communication functions. Descriptions of lengthy sequences of behavior within major functional groupings such as territorial defense, courtship, maintenance of the body, thermoregulation, and nest construction have been recorded, but are not presented. They appear separately (see Garrick, 1975b; Garrick and Lang, 1975, 1977; Lang, 1975a, 1977).

Finally, the present paper represents the combined efforts of L. D. Garrick and J. W. Lang working at an alligator "farm" at Palmdale, Florida, and of H. A. Herzog, Jr., working independently and concurrently (in the spring of 1974) on captive animals at two localities in north Florida. For his complete research report see Herzog (1974). When we became aware of the other's work, it appeared that the parsimonious step was to combine and report the results. However, interpretation is entirely the responsibility of the first author.

ACKNOWLEDGMENTS

STUDY AREAS

Three study areas were utilized. Garrick and Lang worked solely at Gatorama (GAMA), whereas Herzog (Herzog hereafter refers to his unpublished results) observed at two localities—Ross Allen's Reptile Institute (RARI), and Indian Prairie Farm (IPF). Unless otherwise stated, the results reported are those at GAMA. Herzog is identified separately for completeness and comparison.

GATORAMA

Observations were made during spring and late summer of 1974 and in late winter of 1975 at an alligator farm known as "Gatorama" (GAMA) (26°55'N, 81°17.5'W), situated 3 km. SE of Palmdale in south-central Florida, U.S.A. Specifically, from March 22 until April 30, Garrick and Lang were in residence at GAMA except for several days in mid-April. From May 1 until June 16, Lang continued observations; later, Garrick returned to GAMA from August 15 until September 12, 1974 and Lang observed from February 19 until March 5, 1975.

The regional climate is subtropical and is characterized by seasonal fluctuations in precipitation and, to a lesser extent, temperature. Climatological records, which were obtained from Moore Haven (22 km. SE of GAMA) for 1974, are compared to previous records (table 1). Air temperature averaged only 0.2°C./month more than the 1931-1960 means, whereas the mean of rainfall for the study year exceeded

previous years by 18.81 cm. The usual spring rains were sparse, particularly in March, but the summer rainfall was high, especially in June and July.

At Gatorama, the adult alligators were maintained within a 3.2 ha. fenced enclosure (fig. 1) which was divided by a series of canals that had a maximum depth of 2 m. (total water area=0.90 ha.). The low-lying terrain was covered by natural vegetation consisting primarily of cabbage palm (*Sabal palmetto*) and live oak (*Quercus virginiana*). The behavioral arena was a lake at the terminus of two canals and bordered on one side by a walkway. The north shore adjacent to the lake and canal was a favored communal basking site. Also, the alligators were fed from a walkway that formed the eastern perimeter of the lake. Both factors probably contributed to the preponderance of

alligator activity in the lake. Within this area (35% of the available water habitat), several alligators defended territories (fig. 1; also see below).

ROSS ALLEN'S REPTILE INSTITUTE AND INDIAN PRAIRIE FARM

RARI is a commercial animal exhibit in Silver Springs, Florida. Although some alligators and all other crocodilians were housed individually in pens with sufficient land and water area, most alligators were kept in groups of 9, 14, 28, and 12, respectively, in larger pens, occasionally with a representative of another species. Water temperature in these pens was a constant 22°C. The sex of five individually penned adults of total body length 2.3-3.2 m. was known.

TABLE 1
Monthly Air and Water Temperatures and Precipitation at Moore Haven, Florida (26° 50′ N, 81° 05′ W)

| Month | Air Temperature (°C) | | | | Precipitation (cm.) | | Water Temp. (°C) |
	$\bar{x}$.max.	$\bar{x}$.min.	$\bar{x}^c$	$\bar{x}-x_n{}^a$	$\bar{x}$	$\bar{x}-x_n$	$\bar{x}^{b,\,c}$
Jan.	27.9	16.2	22.0	4.3	.36	−4.11	23.5
Feb.	24.5	9.7	17.1	−0.5	3.45	−1.78	20.0
March	28.9	14.3	21.1	1.4	.20	−7.11	24.0
Apr.	29.5	14.4	22.0	−0.5	2.46	−4.32	31.0
May	32.0	18.4	25.2	0.4	7.62	−3.63	30.0
June	31.9	20.5	26.2	−0.4	37.87	17.42	30.0
July	31.8	21.4	26.6	−0.7	47.14	28.96	28.5
Aug.	31.7	22.1	26.9	−0.7	20.29	3.61	29.5
Sept.	32.4	22.7	27.6	0.4	15.01	−4.01	29.0
Oct.	27.7	18.5	23.1	−1.1	3.42	−7.95	25.8
Nov.	25.9	14.8	20.4	−0.1	4.17	1.27	22.9
Dec.	23.5	11.9	17.7	−0.1	4.34	0.46	18.3
				+2.4	146.33	+18.81	

$^a x_n$ = Climatological normals (means) for period 1931-1960.
^{b}Measured once daily at 0800 Caloosahatchee Canal at Moore Haven station #0229200.
^{c}For period 1964-1974, Maximum daily temperature = 32°C. (July 1969).
                    Minimum daily temperature = 9°C. (Jan. 1970).
    Air temperatures, precipitation and normals from U.S. Dept. Commerce, NOAA Environmental Data Service, *Climatological Data*: Florida vol. 78(13). Annual Summary, 1974.
    Water temperatures from U.S. Department of Interior, Geological Survey Water Resources Data for Florida, Part 2: surface water quality records. 1974.
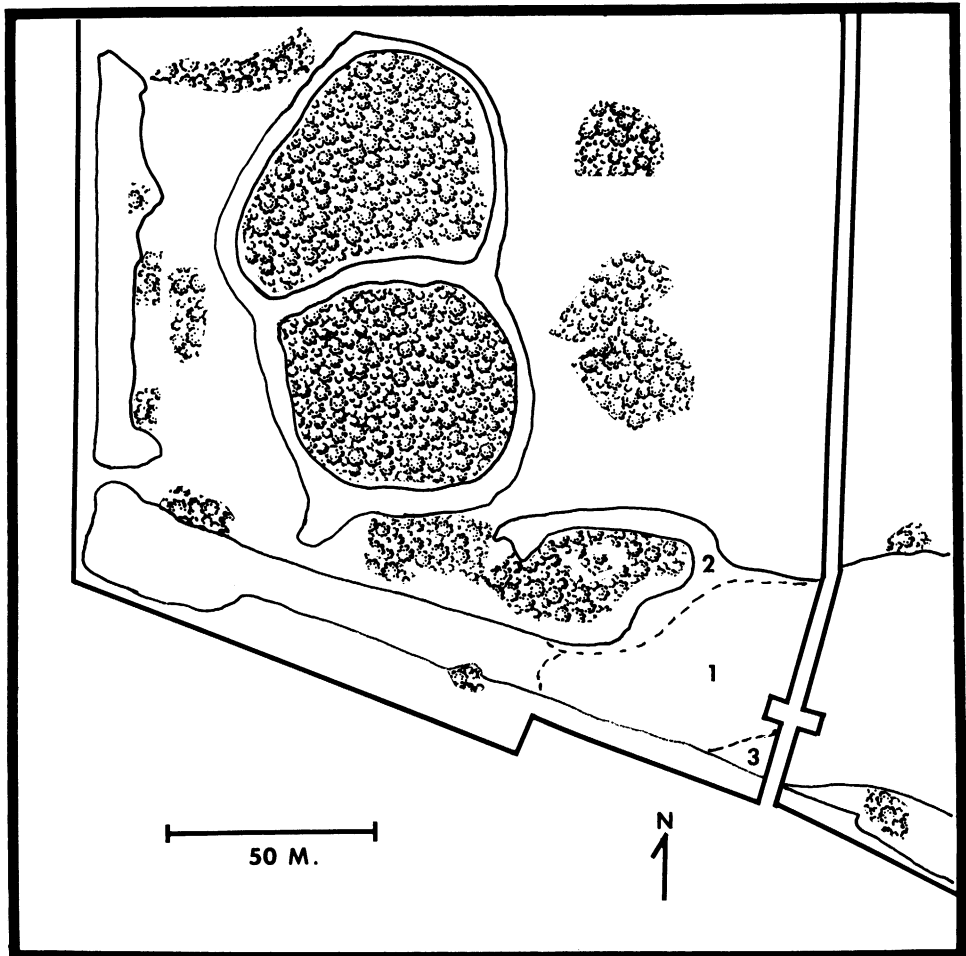
FIG 1. A map of the alligator enclosure at Gatorama illustrating the extent of water area and vegetation (shrubs and trees). Three territories in the lake are separated by dashed markings and are numbered as follows: 1- R♂, 2- O♀, 3- Y♂.

IPF is a 0.2 ha. natural pond enclosed within 0.4 ha. of fenced land employed for the breeding of captive alligators at Anthony, Florida. Water depth in the pond fluctuated with rainfall; its maximum depth was 1.8 m. Eight adults ranging in total body length from 1.8-2.9 m., and approximately 12 young of the year, inhabited the pond.

THE ALLIGATORS

Thirty-five adult American alligators (*Alligator mississippiensis* Daudin) (> 2 m. total body length = tip of snout to tip of the tail) lived within the enclosure at GAMA. They were obtained from diverse sources when the farm was constructed between 1957-1963; thus, their developmental histories were dissimilar. However, each individual within this group probably is familiar with every other, except perhaps for the largest male (R♂) who was reintroduced from an adjoining enclosure during the winter of 1974 after an absence of several years. Alligators associated the presence of humans with the availability of food, but they were not tractable enough to tolerate humans

walking among them while they were basking.

Eleven alligators were recognizable during the study (table 2); three individuals had distinguishing morphological features, and eight others were marked (in early April 1974) with colorful plastic tags attached to the scales of the neck, back, and tail. Hence, the assignment of behaviors to males or females was based on observations of marked and sexed animals and the subsequent comparison of unmarked animals to those of known sex.

Reproduction. Alligators at Gatorama show a definite period of reproduction; courtship begins in April and mating occurs in mid-May (Garrick, 1975b). Similar timing has been reported for populations in Louisiana (Joanen and McNease, 1972, 1976). Apparently, ovulation occurs about 30 days prior to egg deposition (Joanen and McNease, 1972) which is also the time of most matings (Fogarty, 1974; Garrick, 1975b; and see first section of Results and Comparisons below). Females tend to remain near their nests during incubation and may actively chase off potential egg predators (McIlhenny, 1935). Some nesting females unearth the nest at hatching time, possibly in response to the vocalizations of the young within the eggs (Fogarty, 1974; Herzog, 1975; Watanabe, MS). Hatching occurs in late August-early September after an incubation period of about 75 days (Garrick, 1975b). The young remain in the vicinity of the mother for a variable period, sometimes as long as three years (Fogarty, 1974; McIlhenny, 1935).

The density of alligators at GAMA is greater than known densities of breeding alligators in natural conditions. In marsh habitat in Louisiana, males and females form breeding groups of six to eight members in open water areas (Joanen and McNease, 1976). After breeding they separate; females move to nesting areas and males eventually locate overwintering sites away from the females and young (McIlhenny, 1935; Joanen and McNease, 1973). The density of animals can have a profound effect on the structure of dominance systems and the frequency of the expression of aggressive behaviors (Wilson, 1975). Further studies of breeding groups in natural habitats may resolve whether the density of alligators at GAMA did have a significant effect on their behavior.

METHODS

Sampling of Behavior. Because this is the initial systematic study of alligator behavior, *ad libitum* (Altmann, 1974) sampling was mainly employed: Both events and states were described onto magnetic tape. However, recognizable animals (table 2) were often the focus

TABLE 2
Sex, Weight, and Length of 11 Recognizable Alligators

Text symbol	Individual	Sex	Weight (kg.)	Total Length (m.)
Y ♀	yellow tag	f	39	2.2
R ♀	red tag	f	59	2.2
O ♀	orange tag	f	96	2.3
B ♀	blue tag	f	100	2.3
G ♂	green tag	m	68	2.3
Y ♂	yellow tag	m	204	2.7
R ♂	red tag	m	245	3.3
B ♂	blue tag	m	125	2.9
TT ♂	tumor tail	(m)	225	3.3
T ♀	toothy	(f)	100	2.3
FE ♀	flesh eye	(f)	150	2.5

( ) = Sex based on behavioral criteria; weight and length of these three specimens are estimated.

of observations, e.g., the behavior of one or another color-tagged alligator was carefully followed during a particular morning.

Daily sampling consisted of intensive observations commencing about 0700 and ending at about 1200 hours (EDT, local time). In contrast, observations during the afternoon, evening, and night times varied with the proximity and intensity of activity (see below, the section on Social Contexts). Alligators were observed and cinematography done mainly from the walkway and secondarily from a temporary blind approximately 50 m. west of the walkway along the south shore (fig. 1).

For most of the signals all observed occurrences and the sample sizes for the analyzed signal parameters are reported. Signals given by the 11 recognizable alligators are, of course, better documented. Hence, the number of separate individuals comprising a sample only can be approximated. Nevertheless, quantification of the temporal aspects of a behavior and the frequency of occurrence of behaviors are deemed reliable because there was no turnover of individuals, and because the behavioral arena was always visible to the unaided view of the observers.

At GAMA, behaviors were documented with magnetic tape recordings (Uher, Nagra IVL)

made with directional microphones (Sennheiser, MKH 815 and Electro-voice 644), 35 mm. still cameras, 16 mm. cine cameras at 24 frames/s, and passive night-vision scopes (military, models PVS-1, 2, and 3).

Approximately 250 hours of observations were made at RARI and IPF between April 2 and May 27, 1974. In contrast to GAMA daily hours of observation at RARI rarely continued beyond 1000 h. Herzog made tape recordings (Uher), film records, and sound level measurements (General Radio Corp. meter type 1551-B).

Data Treatment and Analysis. The majority of data were collected from March 24-June 14, 1974. For analysis this time was divided into three periods: March 24 to April 15; April 16 to May 10; and May 11 to June 14. This division is based on the relative intensity of courtship, which peaks in mid-May, and changes in activity related to the changing climatic conditions (which are described below). Data collected in late summer 1974 and late winter 1975 are presented without time divisions. Films were analyzed as single frames utilizing a Photo-Optical Analyzer Model 224-A. Tape recordings were analyzed with a Kay Electric Sound Spectograph 7029A using the wide band pass filter.

RESULTS AND COMPARISONS

SOCIAL CONTEXTS

In order to facilitate the interpretation of the alligator signaling repertoire, the activity patterns and social behaviors, both diurnally and seasonally, are summarized.

At Gatorama during the spring most activity occurred during the day, but at night the aquatic alligators were sedentary. Basking on land, which usually occurred in aggregations, invariably followed early morning courtship, aggressive, and territorial defensive behaviors and persisted into the afternoon (Lang, 1975a, 1977). Basking terminated and the social behaviors resumed in the late afternoon and early evening, especially at sunset when alligators

returned to the water. Because basking had a strong temporal component the activity of the group was regulated by their thermal requirements (Lang, 1977). For example, in March and April basking began later in the morning and was longer in duration (compared to May and June). During the summer, basking was restricted to early morning and late afternoon in contrast to nearly continuous basking throughout the day in late winter (Lang, 1977). In all cases there was increased tolerance among all members of the group during basking (Garrick and Lang, 1977).

Briefly, the seasonal courtship and mating activities were as follows (Garrick, 1975b; Gar-

rick and Lang, 1977; Lang and Garrick, unpubl. observ.): In late March and April males attempted courtship but females were not receptive, i.e., they would not remain stationary when males approached them. In late April agonism and combat increased among the larger males. Dominance was determined by the number of contests won against other males (Lang and Garrick, unpubl. observ.). Initially several males contested for dominance; eventually the largest, R♂, defeated TT♂ and Y♂. R♂ subsequently defended the largest territory. Males defended these mating territories against nonterritorial males and other territorial males but females could move among the males' territories with virtual impunity (Garrick, 1975b; Garrick and Lang, 1977; Lang and Garrick, unpubl. observ.). In contrast, O♀ was the only female to defend a territory during the courtship period; within her territory was her future nest site (fig. 1; Garrick, 1975b).

From mid-May on to June, R♂ defended his territory in which he was usually surrounded by several females. R♂ courted much and probably mated with a majority of the females he encountered. During this period courtship occurred at night and during the day, being most frequent in the late afternoon. In late May and early June, courtship activity decreased in frequency and R♂ tolerated subordinate males within his territory and declined to mate with nearby females (Lang and Garrick, unpubl. observ.).

In mid-August to early September encounters among nesting females and other alligators were the only adult social interactions witnessed (Garrick, unpubl. observ.). During late winter of 1975, there were serveral attempted courtships, and a few agonistic encounters between R♂ and other males (Lang, unpubl. observ.).

THE SOCIAL SIGNALS

The alligator signaling system consists of visual, vocal, and nonvocal acoustic elements that occur mostly in the water. The visual elements include movements, postures, which expose variable amounts of the body above the surface, and vibrations. Vibrations may result from both audible and nonaudible (to the human ear) acoustics. Acoustic and visual elements can be combined to form composite signals.

The description of each signaling behavior includes, when they are available, the following: a description of all relevant temporal and/or spectral parameters of a signal, the stimulus situation(s) during which the signal occurs, responses to the signal by other alligators; and then from the above, the probable function(s) for the signal are postulated.

This descriptive method, which unites the physical description, context and responses of a signal, has been justified by Struhsaker (1967) as useful in distinguishing between discrete and graded vocal systems of communication. The nomenclature of these alligator signals is our own. The signals are named descriptively not functionally, e.g., "headslap" is used not "advertisement display."

VOCAL SIGNALS

Bellowing. The booming roar of alligators has been mythologized and misunderstood since the early explorers (see Neill, 1971 for discussion) and it is only recently that descriptions of this important conspicuous vocalization were accurately reported (Harper, 1930; McIlhenny, 1935; Beach, 1944; Joanen and McNease, 1972; Fogarty, 1974). And yet there were still questions whose answers have appeared in the last several years. It is instructive to attempt to clarify some of these queries for which consensus has been reached before reporting our rather detailed observations.

There is evidence that both males and females bellow (Legge, 1967; Neill, 1971; Silverstone, 1972; Joanen and McNease, 1972; Fogarty, 1974; Herzog; and see below), that bellowing occurs mainly in the water, but also on land (Beach, 1944; Neill, 1971; Silverstone, 1972; Joanen and McNease, 1972; Herzog; and see below), that the mandibular glands may be everted during bellowing (Herzog; and see below) but that no scent is detected (by humans) during bellowing (Beach, 1944; Neill, 1971; Silverstone, 1972; see below), and that the pupil of the eye dilates during bellowing

(Beach, 1944; Neill, 1971) or pupil does not dilate during bellowing (Herzog).

Terminology. Bellowing involves repeated alternation of stereotyped postural attitudes coordinated with inhalation and exhalation. Each vocalization is termed a *bellow*; the events from bellow to bellow are a *bellowing cycle*, a series of bellows by one animal is a *bout*, a group of animals bellowing is a *chorus*, and the duration of the chorus or groups of choruses is a *session*.

Events during typical bellowing cycles are described for a large male (TT♂) and a smaller female alligator. At GAMA, alligators bellowed in shallow water, ranging from nearly 0 to 1.5 m. in depth, and occasionally on land.

Male's bellowing cycle starting from rest:

1. Resting posture: head resting with jaws submerged, eyes and cranial plate and dorsum visible, top of back exposed, tail may be visible or submerged.

2. Inhalation and Inflation: The head rises out of the water, the front limbs are extended and the animal moves forward to begin the inflation; at this time the gular region is expanded outward. Then a large amount of the dorsum becomes exposed as the head-water angle increases (fig. 2A). The tail then arches upward out of the water. At the peak of the inflation the gular region is fully extended; just after this, the jaws open slightly, about 6 cm. in a 3 m. individual, and the alligator gulps [the basihyal valve moves posteriorly to cover the pharyngeal opening (fig. 2B)]. Here the mandibular glands may evert whether or not a female is in contact with the male. Finally, the alligator sinks into the water (fig. 2C).

3. Pre-exhalation: After the gulp, the alligator sinks down into the water and moves slightly backward. The head is slightly oblique to the water and the gular pouch is partially extended. At this time the animal has its lowest profile, the tail is visible but no longer arched and the back is submerged.

4. Exhalation and Vocalization: Next, without delay, the head lifts about 30-40 degrees from the horizontal and the tail arches with the tip touching the water on some occasions. As the exhalation begins, the mouth is opened slightly and the gular pouch is expanded prominently. Then jets of water jump from the back

and subaudible vibrations (SAV) spread outward from the neck and chest in the water (fig.
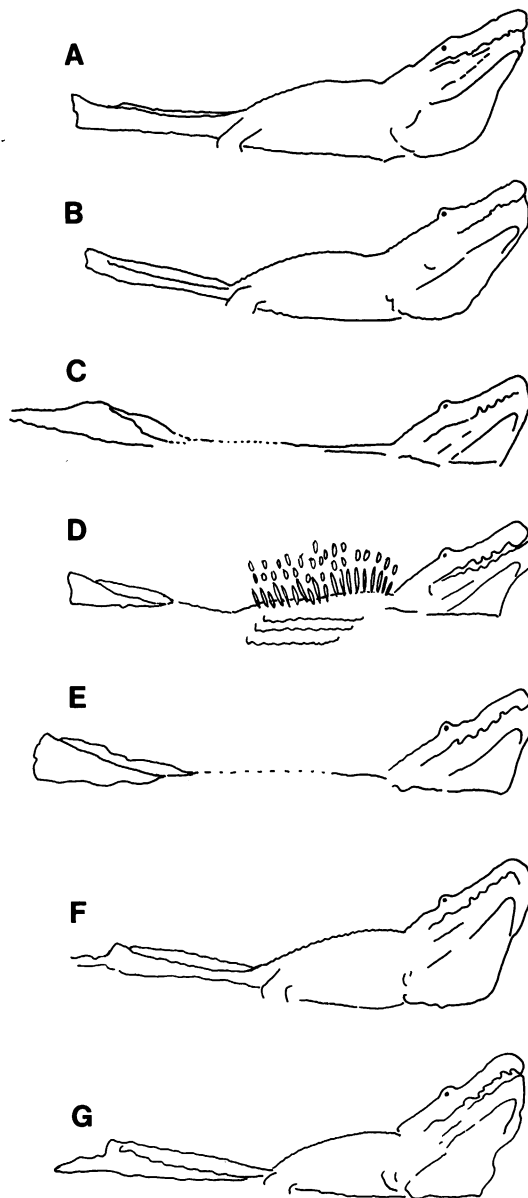

FIG 2. A bellowing cycle of a male alligator. A,B. Inhalation with gulp. C. Pre-exhalation. D. Exhalation and vocalization. E. Post-vocalization. F,G. The next inhalation with gulp. Time between events (in seconds): A-B= 0.62, B-C= 1.71, C-D= 0.79, D-E= 1.50, E-F= 3.71, F-G= 1.33; A-G= 9.66.

2D); within one second an audible low frequency, high volume sound is produced: This is the bellow proper.

5. Post-vocalization: After the bellow the alligator sinks back into the water (fig. 2E) before raising up for the next inflation (fig. 2F, G).

The female's bellowing cycle is similar to the male's except that females appear to adjust their postures in deep water presumably because of less mass. Whether all females or all males follow this pattern has not been determined.

1. Inhalation: The body rises, the head is inclined upward, the back about two-thirds exposed, and the tail raised with tip above the water. She gulps and then sinks down. The gular pouch is extended (fig. 3A, B).

2. Pre-exhalation: The female sinks down, the tail tip hits the water and the head-water angle decreases; almost all of the back is submerged. Then, the tail and head are lifted and the tail tip emerges from the water and the head-water angle increases. The gular region is still expanded (fig. 3C, D).

3. Exhalation and Vocalization: The tail tip drops back into the water as the head rises to a near perpendicular position, exhalation commences, and the vocalization becomes audible. The gular region is expanded during the bellow (fig. 3E, F). Thus, the female's tail is not highly visible, but the head is at its greatest angle with the water (compare fig. 3F with 2E). The dorsal body is submerged; therefore, there are neither visible vibrations nor water bouncing above the dorsum.

4. Post-vocalization: After the bellow, the head moves forward and the tail submerges (fig. 3G); then the female rises up for the next inhalation (fig. 3H, I).

Harper (1930), McIlhenny (1935), and Joanen and McNease (1972) reported tail wagging during bellowing, although this was not observed at GAMA.

Spectral and Temporal Qualities of the Bellow. Most of the sound energy of the bellow, as represented by the darkest portion of the spectrogram, is concentrated between 50 and 250 Hz., although harmonic bands may extend to 750 Hz., and in exceptional high volume recordings, to 1 kHz. (n=48 bellows) (fig. 4).

Bellows possessed three different spectral qualities—unmodulated broad bands throughout (e.g., TT♂), definite modulated components mixed with fused broader bands (e.g., Y♀), and upward and downward modulated bands (e.g., O♀) as shown by the examples in figure 4. The bellows of individual alligators were recognizable to the human ear based on their auditory frequencies (pitch), loudness, and du-
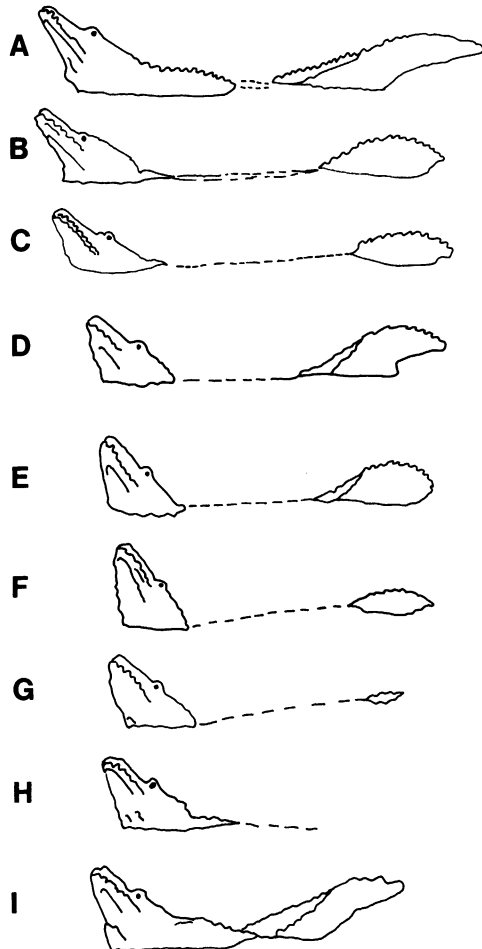
FIG 3. A bellowing cycle of a female alligator. A,B. Inhalation with gulp. C,D. Pre-exhalation. E,F. Exhalation and vocalization. G. Post-vocalization, H,I. The next inhalation with gulp. Time between events (in seconds): A-B= 1.25, B-C= 1.0, C-D= 2.99, D-E= 0.33, E-F= 1.33, F-G= 1.13, G-H= 0.50, H-I= 2.25; A-I= 10.08.

ration. Spectral analysis verified the individual nature of the bellows and also suggested the likelihood of sex differences (fig. 4 A-D). Moreover, the largest individuals, the males, gave the loudest and deepest bellows and were the most conspicuous during bellowing. Joanen
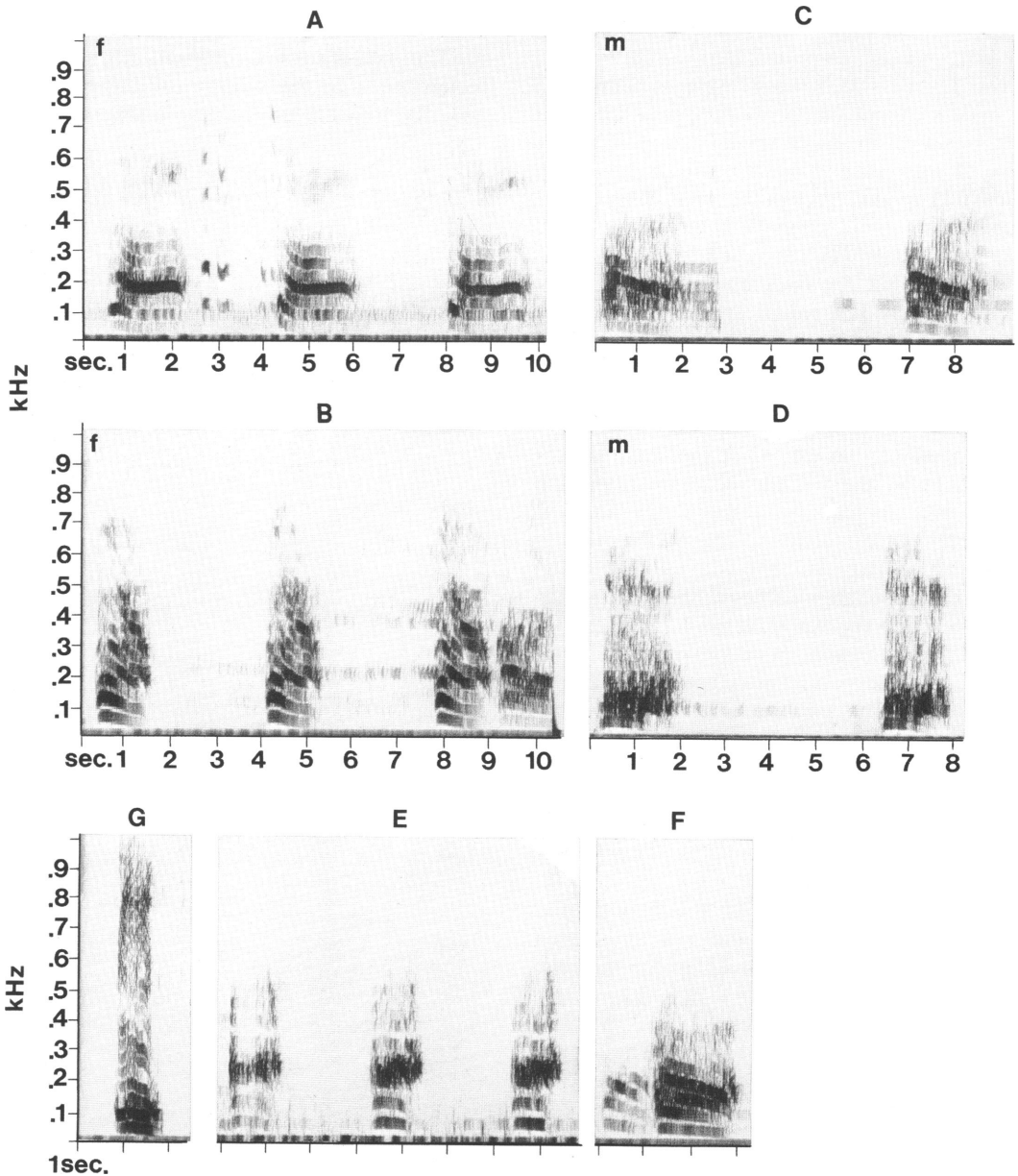
FIG 4. Sound spectrograms of adult alligator vocalizations. A. Bellow, O♀. B. Bellow, B♀. C. Bellow, R♂, D. Bellow, TT♂. E. Bellow growl. F. Bellow growl grading into a bellow, G. Deep grunt (sex unknown). For this and all other sound spectrograms the filter band width = 300 Hz. and each time division equals 1 second.

and McNease (1972) reported bellows of males to be lower pitched than those of females.

Comparison of partial and complete bouts for seven recognizable alligators revealed no difference in the mean duration of a bellow between the sexes (1.83 sec. males versus 1.71 sec. females). However, males had significantly (p< .01) longer interbellow intervals and therefore longer bellowing cycles (table 3). Hence, bouts of five or six bellows (the median of recognizable animals) lasted 20 to 35 seconds depending on the sex of the animal. Herzog determined that the duration of bellowing cycles ranged from 3.97 to 6.57 seconds, which is within the range of the data for Gatorama animals.

Distance Bellows Carry in Air. It is important to gauge the distance bellows carry in air in order to understand long-distance communication. At GAMA the observer easily heard bellowing at a distance of 150 m. However, McIlhenny (1935) reported that bellowing can be heard at a distance of 3 miles, whereas Chabreck (1966) suggested a distance of one-half mile. The discrepancy between our observations and those above would appear to involve more than the conditions obtaining during the various observations. A more standardized value of broadcast range can be approximated by measuring the loudness of the vocalization. Herzog measured the loudness (the sound pressure or SPL) of bellows during the morning chorus at RARI on three days and found that at distances from 3-6 m. when animals faced toward the observer, maximum SPL ranged from 84 to 92 db., and when facing away from the

meter, maximum SPL ranged from 70 to 76 db. For comparison, a SPL of 100 db. is the noise made by a small propeller aircraft at a distance of 5 m. (Tavolga, 1971).

Seasonal Occurrence. During late winter 1975 only two bellowing choruses were heard; they lasted 10 and 40 min. In March 1974, two bellowing sessions greater than 30 minutes duration were observed, and in early April one 41-minute session was observed. The most intense bellowing occurred from April 16 to May 10, during which the duration of 18 sessions ranged from three to 58 minutes with a mean of 21.5 minutes. Herzog found the mean duration of the morning chorus to be 11.3 minutes with a range of 6 to 22 minutes.

From May 11 to June 14 the intensity of bellowing declined; the duration of 19 bellowing sessions ranged from two to 43 minutes with a mean of 12.9 minutes. In contrast, from August 15 to September 12 bellowing was directly observed on four of 29 days and bellowing which was reported to Garrick by the proprietor occurred during three other days. The longest bellowing session during the late summer was 5 minutes.

Harper (1930) and McIlhenny (1935) reported that bellowing occurred from April to June and during August and September. McIlhenny also observed bellowing during warm mornings and nights in the fall, but rarely in the winter. Neill (1971), who also reported bellowing as occurring during the summer but only occasionally in spring and fall, stated that most bellowing occurred *after* courtship and egg deposition. Silverstone

TABLE 3
Comparison of Male and Female Bellowing Cycles

Sex	Bellow	n[a]	Mean Durations (sec.) Interbellow Interval	n	Bellow Cycle	n
Males	1.83±0.05[b] (1.23−2.79)[c]	63	3.94±0.12[d] (2.92−6.70)	40	5.73±0.13[d] (4.58−8.34)	43
Females	1.71±0.07 (1.23−2.67)	29	2.60±0.21 (1.76−4.83)	20	4.27±0.27 (3.45−7.22)	20

[a] n = Number of variates taken from both partial and complete bouts of 4 ♂♂ and 3 ♀♀.
[b] Standard Error of Mean.
[c] ( ) = Range
[d] ♂♂ are significantly greater in duration than ♀♀ (p < .01, t-test).

(1972) observed bellowing from April 19 to September 28 by the male and from April 19 until October 4 by the female. In Louisiana, bellowing, which definitely was associated with courtship, peaked in May and frequently was observed from mid to late April through early June (Joanen and McNease, 1972). Fogarty (1974) noted a May peak for bellowing in the Everglades (Florida).

Thus our observations are corroborated by the above reports and it can be concluded that bellowing is seasonal, coinciding with the warmth of spring and onset of breeding activity; that bellowing occurs simultaneously with courtship activity; that bellowing continues after the eggs are laid; and that some bellowing can be heard in late summer and in early fall, but rarely during the winter.

Times and Onset of Bellowing. Bellowing was clearly an early morning activity. During the 63 days of spring observation (March 24 to June 14) bellowing was observed within 129 hours out of a possible 1512 hrs. (24 by 63). During these 129 hrs., 72 percent of bellowing bouts occurred between 0600 and 1000. The

median hour when most bellowing occurred was between 0800 and 0900 (table 4). From March 24-April 14, 75 percent of bellowing occurred prior to 1000, compared with 100 percent and 93 percent, respectively, for the later two periods.

During the spring observation period, bellowing after dark until 0215 was noted 12 times. Fewer animals than during the light period participated in the shorter choruses (approximately one or two bouts); three was the most bellowers (April 29). On four occasions only a single individual bellowed. The postures appeared to be identical when the vocalization was emitted during the night and day.

After April 15 bellowing started earlier in the day (table 5). Overall, 67 percent of bellowing onsets occurred prior to 0800 during the 59 days when the onset was observed. At RARI prior to May 10, the onset of bellowing commenced after 0815; however, thereafter the onset occurred between 0630 and 0715.

Bellowing Bout. The bout, or the series of bellows emitted by one individual, varied from one to 11. No sex differences in the number/

TABLE 4

Number of Times at Least One Bellowing Bout Occurred Within a Particular Hour of the Morning

Observation Periods	No. Obs. Days	Hours						
		6-7	7-8	8-9	9-10	10-11	11-12	Totals
March 24 - April 15	13	1	3	7	4	3	2	20
April 16 - May 10	22	6	13	19	3	0	0	41
May 11 - June 14	28	9	14	10	4	1	2	40
Totals	63	16	30	36	11	4	4	101

TABLE 5

Onset of Bellowing Within a Particular Hour of the Morning

Observation Periods	No. Obs. Days	Hours					
		6-7	7-8	8-9	9-10	10-11	11-12
March 24 - April 15	12	1	3	4	1	1	1
April 16 - May 10	20	6	9	4	1	0	0
May 11 - June 14	27	9	11	4	2	1	0
Totals	59	16	23	12	4	2	1

bout were observed and thus all 245 bouts were treated together. The mean number of bellows/ bout was 4.6, the median 5, and the mode 3 (fig. 5).

For six marked and recognizable alligators, four males and two females, the median number of bellows/bout was either 5 or 6 (unrelated to the sex of the animal), but for unmarked or unrecognizable alligators the median number of bellows/bout was 3 (table 6). Herzog recorded 82 bouts with a range of 1-12/bout, a mean of 4.7 and a mode and median of 5.

McIlhenny (1935) heard "a dozen or more" bellows given in a series by males. Beach's

(1944) laboratory studies of one animal demonstrated a range of 1-10 bellows/bout with a mean of 7.4, 24 of 30 bouts contained six to eight bellows. Neill (1971) reported five to eight bellows/bout, and Silverstone (1972) observed two animals and determined that the range was 1-11 bellows/bout, the means were 4.7/bout for the male and 5.8/bout for the female.

Thus, there is good agreement that the range of bellows/bout is 1-12, five being the most common number for either sex. However, still to be answered is why unmarked or unrecognizable alligators had a median of three bel-
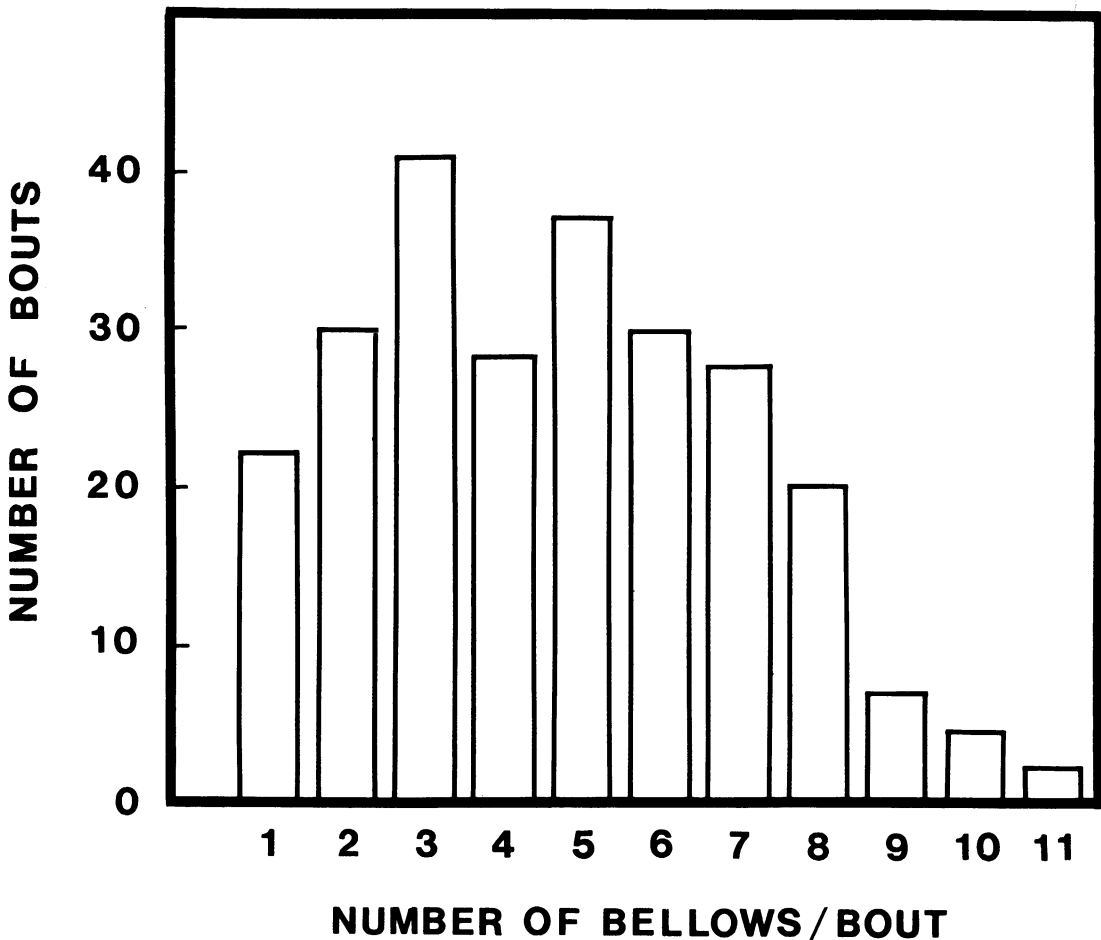

FIG 5. Number of bellows/bout. n= 245 and the median is 5.

lows/bout (table 6). Two possibilities are suggested: that these were less "social" animals or animals excluded from the main body of socially active and conspicuous alligators, or that they could not complete their bouts because more vocal animals interrupted them early in the bout. For instance, R♂, the dominant male, had a mode of three bellows/bout probably because of his frequent interjections into bellowing choruses (Garrick, unpubl. observ.).

Bellowing Chorus. Bellowing is a contagious behavior. That is, once an animal begins to bellow others also may respond in kind. On 19 mornings during the spring observation period a single alligator was observed to initiate a bellowing chorus. Besides being emitted spontaneously, bellows also are prompted by other signals, e.g., headslaps and bellow growls, both of which are discussed below, and nonbiological sounds such as a truck exhaust backfire. Beach (1944) and Evans and Quaranta (1949) found that nonbiological sounds also elicited bellowing.

Responses and Probable Functions. The most frequently observed response to bellowing by one alligator is bellowing by another alligator. Sometime during each of the 58 days of the spring observation period when bellowing was heard it inevitably was followed by further bellowing, although not for each bout.

TABLE 6
Number of Bellows/Bout for Six Recognizable and Marked Alligators and a Combined Group of Unrecognizable Animals

Individual or group	Number of Bellows/Bout			
	Median	Mode	Range	n^a
R ♂	5	3	1-9	53
TT ♂	6	6	1-9	39
B ♂	5	5	1-8	8
Y ♂	5	4	3-11	11
R ♀	5-6	5-6	5-6	2
O ♀	6	5-6	1-11	61
Unrecognized	3	2-3	1-8	52

[a]n is the number of bouts (a series of bellows by one animal).

However, for the consequences of the display the most important response appears to be approach to the bellower, which was observed on 34 of the same 58 days. Other obvious responses are nonspecific movement of alligators, which was recorded on eight of the 58 days, and returning to the water from the land during bellowing, which was recorded on four days.

The results of approach to the bellower are significant for the social structure (Lang and Garrick, unpubl. observ.). If the bellower is a male he may be approached by a male with the possibility of an agonistic encounter resulting in lunging, chasing, and fighting. A female may approach a male and this can lead to courtship. However, when approached by a male, never a female, a female may emit a series of bellow growls (see below) and then swim away, or she may be receptive to the male's courtship attempts. Thus, the two main results of the approaches following bellowing are courtship and aggression, which were observed on 11 and 14 of the 58 observation days, respectively. Herzog (1974) observed increased mounting during bellowing choruses.

Probable functions of bellowing can be postulated. First, bellowing signals the presence and location of the bellower which then may lead to increased contact between individuals. This is of obvious importance in the formation of breeding groups (Joanen and McNease, 1976) and in locating potential mates. Also information about the sex, individual identity, and social position of a bellower may be imparted (see Summary of the Signaling System below). However, from another viewpoint, the bellowing chorus synchronizes group activity and this might ultimately influence the synchrony of reproductive events (Cullen, 1972, p. 102). Bellowing has been suggested to function in territoriality, courtship, and aggression (Evans, 1961; Neill, 1971; Joanen, 1970).

Bellow Growl. Bellow growls are sequential, short, hoarse bellows emitted exclusively by females, during which they assume a posture with the head out of the water and nearly parallel to the surface (fig. 7A). Bellow growls occur during three particular stimulus situations:

(1) Bellow growls were emitted by sexually nonreceptive females when approached by males. They then submerged or swam away rapidly. Several examples from the field notes illustrate this behavior:

> 1057 on March 28—T♀ was approached near the walkway, she turned her head toward the approacher. The approacher's tail, back, and head were visible. As T♀ swam away she bellow-growled.

> 0643 on April 29—O♀ bellow-growled when approached in center lake, then she swam into her territory. She then swam back toward center lake and submerged.

> 1835 on May 19—R♂ approached a female. She held her head out of the water at a slight upward angle, her tail also out of the water. She bellow-growled three times and then moved away.

Forty-one bellow growls were given in response to approaches by males during the spring observation period. They were observed only once from March 24 to April 15, 22 times from April 16 to May 10, and 18 times from May 11 to June 14. None were observed during August and September, but two occurred in late winter 1975.

Bellow growls occurred mainly in the morning and late afternoon, the times when most "courtship" was observed (see above Social Contexts). The median hour was 0800-0900 and the modal hour was 0700-0800 when 13 were observed.

Bellow growls are given in a series or bout. For this first stimulus situation the range was 1-6/bout and two was the median and modal number/bout (n=26).

(2) Bellow growls also were emitted in response to headslaps, after which the female may flee or submerge, or sometimes approach a male. She in turn may be approached. Two excerpts from the field notes illustrate this behavior:

> 1430 on May 23—Y♂ headslapped (with a tail wag), this was followed by a bellow growl near a tree along the south shore.

> 0900 on May 31—R♂ headslapped. Immediately thereafter a female under the tree along the south

shore bellow-growled twice. That female approached R♂, and B♂ approached her.

Ten bellow growl bouts were given after headslaps, all after May 7, and six of these 10 headslaps were given by R♂. The median and modal number/bout was also 2 and the range 1-4/bout. Eight of the 10 bouts occurred between 0700 and 1000.

(3) The third context of bellow-growling was a nearby male-male agonistic encounter. The females did not swim away or submerge after vocalizing. Two examples illustrate this behavior:

> 1620 on May 16—O♀ bellow-growled three times as R♂ chased another male.

> 0042 on May 17—R♂ chased an animal and when he ceased he displayed a tail wag and inflated posture. Two small animals nearby each bellow-growled twice.

Five bouts of bellow-growling were emitted during this stimulus situation. They all occurred after May 15, and four of the five bouts contained two bellow growls; the other one had three bellow growls.

Spectral and Temporal Qualities. There are no apparent correlations of structure and pattern of bellow growls with the three stimulus situations. Sound energy is concentrated at about 200 Hz. and the mean duration of a bellow growl is 0.90 second, with an intercall interval of 2.8 seconds (n=7) (fig. 4E). Overall, the mode and median number of bellow growls/bout was 2, the range was 1-6 (n=71). The loudest bellow growls carried 75 m.

Bellow growls spectrally grade into bellows (fig. 4F), and on two occasions alligators bellowed after bellow-growling.

Responses and Probable Functions. Not every bellow growl elicited an observable overt response. In response to approaches by males bellow growls were emitted 41 times. During 16 of these 41 bouts females moved away from the male, and in the remaining 25 bouts further approaches by the males also were inhibited. However, other responses to bellow growls included bellowing (n=15) and approaches of the bellow growler (n=13). Several examples taken

from the field notes illustrate these responses, e.g.:

> 0830 on May 14—FE♀ headslapped and a female near R♂ bellow-growled one time. Then after a 30-second pause she gave four more and then R♂ began bellowing.

> 0724 on May 23—O♀ was approached by R♂. O♀ bellow-growled two times which set off bellowing along the north shore.

Thus, bellow growls may elicit bellowing from nearby animals or trigger a chorus from alligators some distance away.

There is also movement toward some bellow growls as exemplified by the following excerpt from the field notes:

> 0708 on May 23—R♂ headslapped (with tail wag and inflated posture); this was followed by a bellow growl along south shore. The female who bellow-growled was approached by B♂ and Y♂.

In summary, females that bellow growl in response to a male's approach inhibit mating attempts. Presumably, these females are sexually nonreceptive. But those females that remain after bellow-growling in response to a headslap or nearby male-male encounter (in contexts 2 and 3 above) can be approached and courted, i.e., the vocalization apparently identifies the alligator as a female and thereby prevents attack by the males.

Deep Grunt. A single deep grunt was recorded from an adult alligator as it approached an audio speaker in response to playbacks of tape-recorded juvenile alligator grunts. The vocalization is characterized by a fundamental at 50 Hz. and about eight harmonics (fig. 4G). It is noteworthy that Herzog also reported a single "growl" given by an approaching animal during playbacks of the recorded distress call of juvenile alligators. These circumstances are remarkably similar. It could be suggested that this vocalization is employed by adult alligators in response to the calls of the young. In fact, McIlhenny (1935) described a female calling her young (toward her) with low grunts, and Watanabe (MS) has recently witnessed a mother alligator call her young from the nest to a pond in which she waited.

Low Growls. Low growls apparently are a rather ubiquitous set of vocalizations heard as part of three composite signals viz. headslaps, yawns, and inflated postures. Only one low growl was recorded, this as part of a headslap and is described below (fig. 6C and table 9).

Coughs (chumpfs). Coughlike calls are used by either sex during courtship (Garrick, 1975b; Garrick and Lang, 1975). They are emitted in two forms (< 300 Hz.), each grouped into units of three, and they are employed at very short range (fig. 6B and table 9).

Hiss. The hiss is a prolonged, audible expulsion of air, at the start of which the body is inflated and the mouth is usually open (fig. 7C). This hiss is composed of a broad spectrum of low frequency sound (< 1kHz.) (fig. 6A). Its duration is 1-3 seconds and an initial hiss may be followed by an inhalation and then another hiss (fig. 6A).

This vocalization is commonly given on land in response to an intruder. For example, it is part of female nest defense behavior (fig. 7C; Carr, 1967; Neill, 1971). Herzog (1974) has suggested that louder hisses are given by larger alligators and that loudness is inversely related to the distance of the intruder.

VISUAL SIGNALS

Yawning. Yawning, whose nonsocial functions have been the subject of speculation, is herein treated as a signaling behavior (Hediger, 1955), although it also may be a thermoregulatory behavior (Lang, unpub. observ.).

In its basic form alligator yawning is the parting of the jaws to their widest distance during which the head is raised and usually held at an oblique angle to the anterior-posterior axis. There are at least two variations— one in which the jaws close and then the lower jaw is partially submerged below the water, and another in which the jaws close when the head is oblique to and above the water. The yawn lasts about 20-40 seconds; Silverstone (1972) reported the same durations.

Three times yawns occurred on land, although the majority (n=56) were given in shallow water during basking. Both females and males yawn. Some individuals gave two yawns in succession and several animals yawned si-
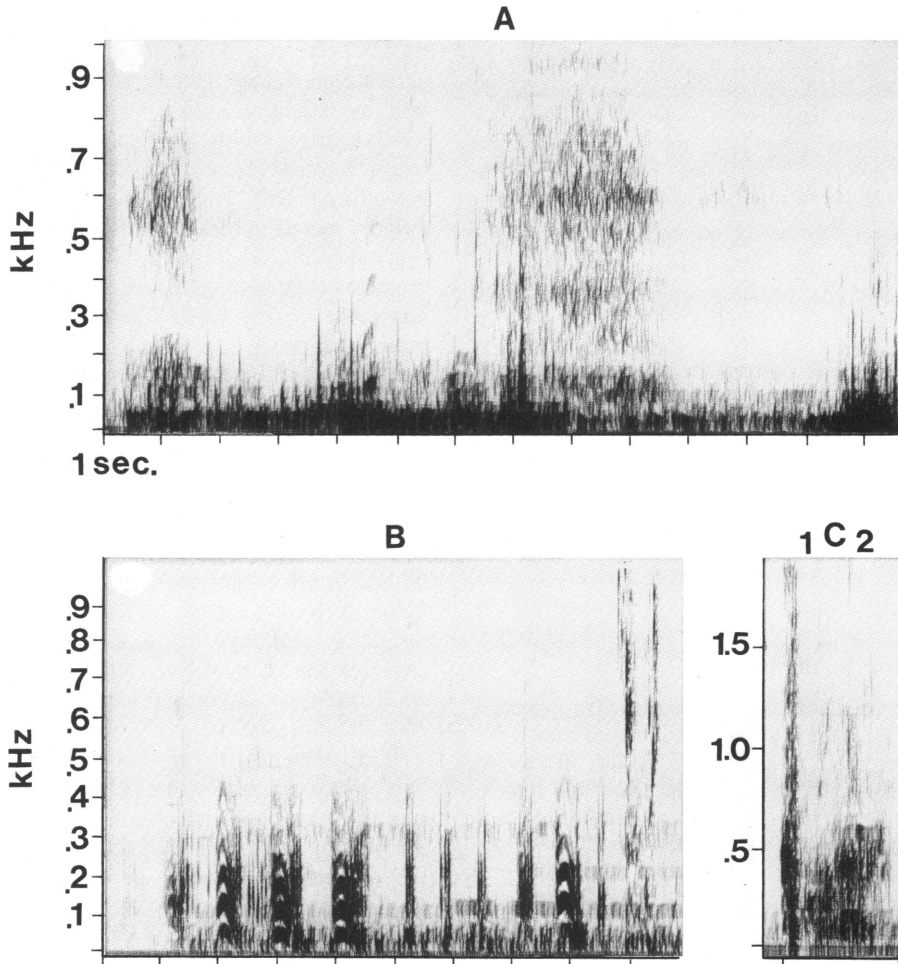
FIG 6. Sound spectrograms of adult alligator vocalizations. A. Hiss. B. Coughs. C-1 Headslap. C-2 Low Growl. Note difference in scale.

multaneously. A growl and a hiss terminated two yawns; the hiss also was reported by Herzog and by Silverstone (1972). Five times the yawn persisted as a gape, i.e., the mouth remained open. One time the yawn started from the bellowing posture (fig. 2); this was also reported by Silverstone (1972).

Times of Yawning. Yawning appeared to be a morning activity whose occurrence was correlated with basking times. Eighty percent of observed yawning occurred from 0700-1200.

The median and modal hour was 0900-1000 during which bellowing and headslapping were diminishing and basking beginning. Yawning during evening basking aggregations was not distinctly noted.

Responses to Yawns and Probable Functions. Responses to yawns were very infrequent and yet there is evidence that yawns may be contagious. Examples from the field notes will illustrate:

At 0938 on March 27 there was one yawn then

another yawn within 30 seconds which made a total of five in the last two minutes.

At 0811 on March 28 an alligator near the n. bank yawned; then a nearby animal on the n. bank that was basking also yawned. Later on the same day an alligator along the n. shore yawned, then an animal 15 m. away yawned. The first animal was approached after the yawn.

Also on March 28 an animal yawned from a posture with elevated tail and entire neck and back visible and then was approached by another individual.

These limited observations suggest that yawning might be contagious and that yawning alligators might attract others.

Narial Geysering. Geysering is a stream (spout) of water about 10 to 20 cm. in height resulting from a release of air from the external nares while the snout is just under the surface of the water (fig. 7B). It occurred rarely (n=8) but was correlated with bellowing and head-slapping. Examples taken from the field notes illustrate its occurrence:

At 0805 on April 16 in the midst of an extended bellowing chorus a small animal assumed the bellowing posture but did not bellow; instead its snout submerged just under the water and it blew air through its external nares creating a stream of water—a geyser. This was followed by bellows by one animal.

Again on April 21 at 0830—in the midst of a bellowing chorus an animal geysered.

Also as part of headslapping at 0812 on May 6— Headslap by an animal in corner near breeding pen. It lifted its head and paused about 20 seconds and then headslapped, geysering as it slapped. Four nearby animals did not respond.

Thus, narial geysering appears after bellows but no response was observed following one. As a component of the headslap narial geysering might be perceived by an alligator close by, but from a distance it probably is masked by the splash. Geysering also has been described as a precopulatory behavior in *Alligator mississippiensis* and two other species (Garrick and Lang, 1975, 1977). A similar behavior, bubbling through the mouth (fig. 9E is an example), also occurs during courtship (Garrick and Lang, 1975, 1977).

Submergence. Submergence removes the individual from view, recognition and contact, thus it is considered an antisocial behavior. The external nares are usually the last part of the body to submerge and from them may emanate an exhalation with a hissing sound. Besides being a component of bellow growls, narial geysering, and bubbling, submergence behaviors occur during courtship, thermoregulation, feeding, aggression, and maintenance of the body (Garrick, 1975b; Lang, 1975a; Garrick and Lang, 1975, 1977; Lang and Garrick, unpubl. observ.).

Slimming Posture. During the slimming posture the snout is partially submerged in the water and the body compressed laterally. Slimming postures were displayed by stationary alligators as others moved toward the basking area, and by some females during encounters with O♀ (Lang and Garrick, unpubl. observ.). Although rarely observed (fewer than five individuals), it may signal "assertiveness" and represent a challenge to a conspecific. Lateral compression in lizards is also a component of challenge-type displays (Greenberg and Noble, 1944; Crews, 1975).

Tail Wagging. Tail wagging occurs as a component of bellowing, inaudible bellowing, headslapping, and the inflated posture, but also alone. For example, tail wagging occurred in the absence of other signal elements during territorial defense and during or following male-male agonistic encounters (n=28). Silverstone (1972) described tail wagging from the "bellowing posture" (no bellows were emitted) in shallow water. The ubiquitous nature of this movement suggests that it is an important signal during agonistic situations and also that it may emphasize or modify another signal with which it occurs.

Head Emergent Tail Arched Posture. In this commonly observed posture the head and tail are emergent above the water (fig. 7D). It is displayed by males and females. For example, it was given by females in the water near their nests when we approached them, and by O♀ at the boundary of her territory (Garrick and Lang, 1977; Lang and Garrick, unpubl. observ.). This posture probably signals "alertness" and means that the alligator is prepared to defend territory or nest.

Inflated Posture. During an inflated posture the back is upwardly arched, the body inflated, the tail wagging, and mouth open (fig. 7F). The posture may be followed by a low growl. It is employed by males and females. Thirty-eight inflated postures were specifically recorded; the duration of the posture varied from approximately 11 seconds to 2 minutes. An alligator in this posture appears quite formidable. This posture terminated many agonistic encounters such as chases, lunges, and even fights (Lang and Garrick, unpubl. observ.). After this threatening display the animal to whom it is directed flees. McIlhenny (1935) also described this posture.

Snout Lifting. Snout lifting is the rapid lifting of the partly opened mouth to an oblique angle above the water's surface during an encounter with another alligator (fig. 7E). It may be combined with rapid swimming away. An example from the field notes illustrates the context for this behavior:

> At 0950 on March 29 a small alligator lifted its snout as it passed by a large individual and moved out of the water onto the bank.

Snout lifting was observed infrequently (n=5).

Snout lifting while in the water appears to be a submissive or conciliatory signal. Two crocodile species (*C. acutus* and *C. niloticus*) employ pronounced, conspicuous snout lifting more frequently than alligators in the same and different contexts (Garrick and Lang, 1977).

NONVOCAL ACOUSTIC SIGNALS

Inaudible Bellow (subaudible vibrations). An inaudible bellow is a "bellow" without sound audible to the human ear. It has the same movements as a bellow (see fig. 2), but may include tail wagging. Only four were observed; no approaches were noted.

At RARI, alligator inaudible bellows were not observed, but a 2.7 m. American crocodile (*C. acutus*) emitted subaudible vibrations from a posture very similar to that observed during alligator bellowing. These subaudible vibrations stimulated bellowing by an American alligator in an adjacent pen but with a common water supply. This observation suggests that alligators may use frequencies below the normal human auditory range (perhaps utilizing the ear), and that these vibrations are transmitted through water.
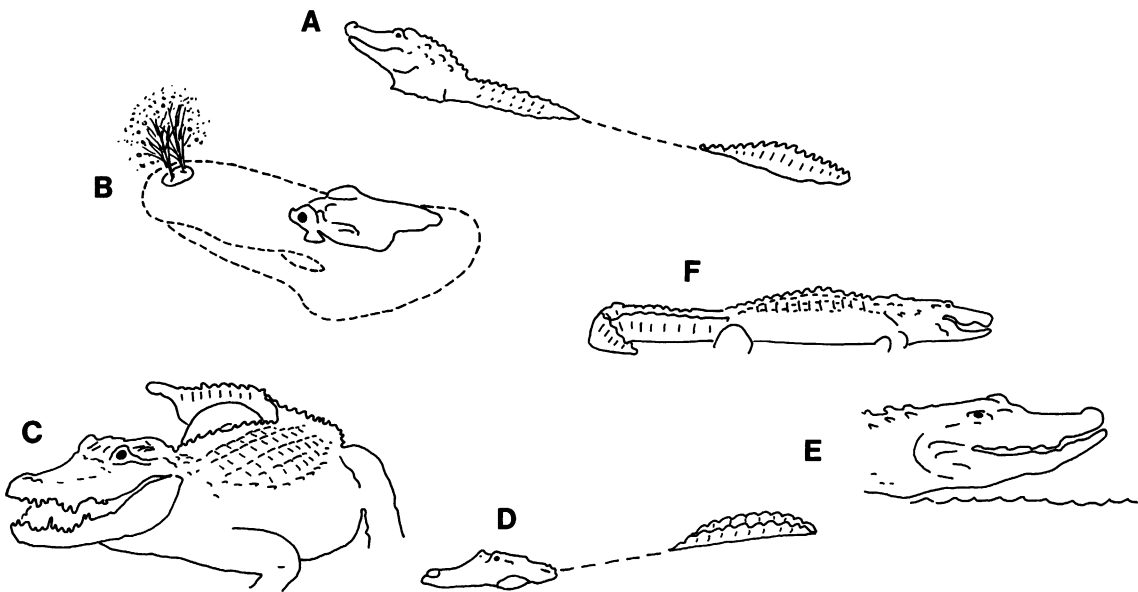

FIG 7. Postures and behaviors of adult alligators. A. Bellow growl posture (♀). B. Narial geysering. C. Hiss posture (♀ at nest). D. Head emergent tail arched posture. E. Snout lifting (♀). F. Inflated posture (♂).

Headslapping. Headslapping is the slapping of the head against the water's surface. There are two forms of this behavior, both of which may be combined with other signal elements. It is given by both males and females. A series of headslaps by the same animal never was observed (n=210). Descriptions, which are derived from the analysis of seven headslaps and associated signal elements, progress from the least complex to the most complex variation.

(1) Beginning from a resting posture, i.e., head and tail nearly submerged, the head is raised so that the lower jaw is partially submerged. Next without pause, the mouth opens and the lower jaw sinks below the surface. Then the head moves downward toward the water creating a loud splash when the upper jaw hits the water and a "pop" when the jaws come together (fig. 8). This sequence from jaws open to splash lasts about 0.5 second or less.

(2) Two modifications of the above were observed. About 0.5 second after the splash copious amounts of bubbles appeared about the head (bubbling). And in another case an inflated posture with tail wagging followed the bubbling.

(3) Four times headslaps commenced from a "bellowing posture," i.e., head oblique to the water's surface and tail arched, but instead of bellowing there was a 15-45 seconds pause (fig. 9). Then, in two instances, the mouth opened and the head moved rapidly toward the water creating the splash. The other two were consummated as described in (1) above. In one case, bubbling followed the headslap.

(4) Twice during headslaps from the "bellowing posture" the splash was preceded by subaudible vibrations, so as the mouth opened, water bounced from the dorsum and flanks. In one instance, bubbling appeared after the splash, and twice the display terminated with an inflated posture.

(5) A low growl may be emitted after the splash (see below). Herzog found that a low growl preceded the splash three times but followed the splash during 34 of 44 headslaps. Narial geysering and tail thrashing are also elements accompanying headslapping. Others have evidenced less variability in the form of the

display: Silverstone (1972) observed "jaw smacking" 14 times by the male and once by the female between April 28 and June 28; all were given from the "bellowing posture," usually out of sight of the other alligator. Herzog
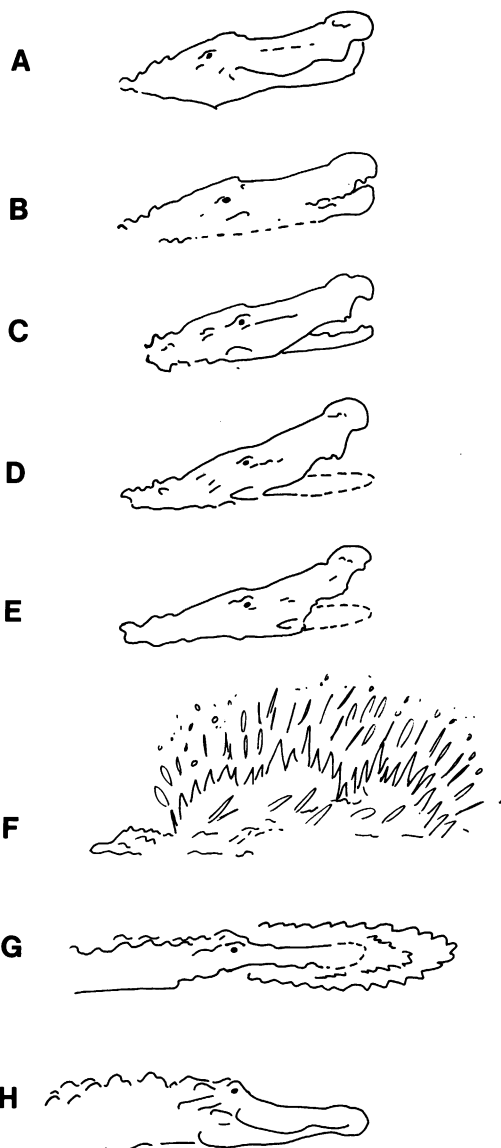

FIG 8. Alligator headslap from the resting posture. Time between events (in seconds): A-B=0.37, B-C=0.04, C-D=0.09, D-E=0.04, E-F=0.16, F-G=0.75, G-H=1.54; A-H=2.99.

also found that headslapping proceeded from the "bellowing posture," and that in five of six sequences tail wagging accompanied headslapping.

Among recognizable alligators, known dominant animals, both males and females headslapped more frequently than the subdominants (table 7). For example, R♂ was the dominant male and TT♂ and Y♂ were two subordinates; O♀, the only territorial female, and FE♀ were "prominent" females, and T♀ somewhat less so (Lang and Garrick, unpubl. observ.). Moreover, the three males headslapped nearly four times as much as the three females (table 7). Twenty-five headslaps were recorded as occurring from within an alligator's territory: R♂ (17), O♀ (4), and Y♂ (4).

Spectral and Temporal Qualities of Headslapping. Four headslaps were tape recorded; one of these also had a low growl immediately after the splash. The splash and pop are not dissociable (fig. 6C) and together they have a duration of between 0.08 and 0.15 second. The headslap with a low growl lasted 0.9 second, of which the low growl was heard for 0.68 second (fig. 6C). Herzog measured the duration of four headslaps with vocalizations as 1.77 seconds, but six headslaps alone had a mean duration of 0.16 second from opening of the jaws to the splash. Most of the sound energy in the splash itself was between 50 and 425 Hz., the majority less than 250 Hz., whereas the low growl showed a fundamental frequency at 100 Hz. with three distinct harmonics (fig. 6C). Herzog found that the sound pressure of four splashes, which were louder than the accompanying vocalization, averaged about 60 db. at a distance of approximately 6 m. Headslaps carry about 200 m. in air, and alligators within 50-75 m. approached the alligator that headslaps.

Seasonal Occurrence. Headslapping was rare from March 24 to April 15, an average of 1.75/day were observed compared to 4.50/day from April 16 to May 10 and fewer (3.52/day) from May 11 to June 14 (table 8). From August 15 to September 12 headslapping was observed on only one day (August 27).

Hourly Onset and Times of Headslapping. Headslapping appears to be a morning activity. During the spring, 61 percent of the 210 head-

TABLE 7
Number of Headslaps Given by Six Recognizable, Marked Alligators and by Those Unrecognizable or Recognized But Not Recorded During Spring Observation Period March 24 - June 14

Individual or group	Number of headslaps
R ♂	47
Y ♂	15
TT ♂	5
O ♀	9
FE ♀	7
T ♀	2
(Subtotal—recognizable, marked)	85
Unrecognizable/Unrecorded	125
Total:	210

slaps occurred between 0600 and 1000 and 81 percent before 1200 (table 8). The remaining 19 percent was nearly equally dispersed from 1200 to 2400, e.g., 4 percent of the headslaps occurred between 2000-2400. The 0800 to 0900 hour was the median and mode for the frequency of occurrence (table 8), and except during April 16 to May 10, headslaps did not occur prior to 0700.

There are certain similarities between the onset and times of headslapping and those of bellowing. Headslaps preceded bellowing on 22 mornings and appeared to "set off" the first bellowing on four of these days. Both are morning activities with a median hour of occurrence from 0800-0900. Here is an instance where a common causality may be sought; in fact, both displays function as courtship advertisements (Garrick, 1975b; Garrick and Lang, 1975, 1977).

Context, Responses and Probable Functions. The variety of elements accompanying headslapping suggests correlations with intrinsic and extrinsic factors. For example, among the seven filmed headslaps noted above, those accompanied by fewer elements occurred twice after agonistic encounters, each time eliciting approaches, and those accompanied by more elements occurred in the course of other ongoing behavior and elicited no approaches. Other
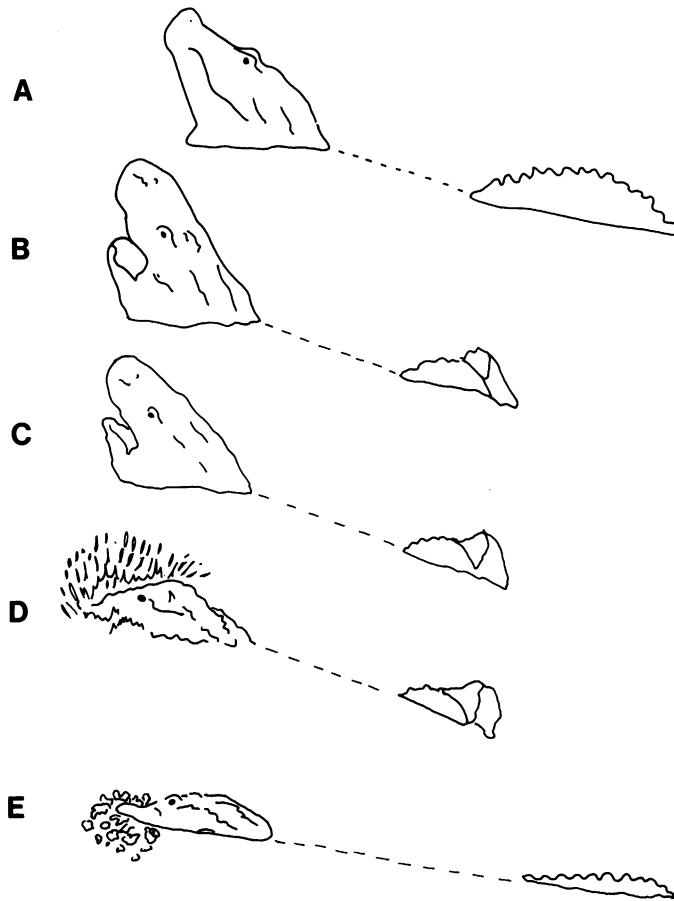
FIG 9. Alligator headslap from head oblique tail arched posture. Time between events (in seconds): A-B= 2.45, B-C=0.09, C-D=0.04, D-E=2.21; A-E=4.79. Bubbling through the mouth is shown in E.

headslaps occurred in the contexts of courtship, chasing, and bellowing.

Responses to headslapping may clarify its signal function. The most prevalent response was approach to the headslapper which occurred during 44 of 90 observations. An example from the field notes illustrates this response:

On May 17 at 0741 R♂ headslapped; two animals are nearby and one bellow-growled twice. R♂ rotated to the east and headslapped again. Two animals then approched R♂ and contacted him, now four alligators are around him.

However, fewer approaches occurred when a headslap display terminated with a tail wag and/or an inflated posture. Specifically, of the 44 approaches only 11 occurred after a headslap with a tail wag and/or inflated posture. Furthermore, 10 approaches led to courtship but only two did following a headslap with a tail wag and/or inflated posture. Thus it appears that this inflated posture, which is indistinguishable in form from that which follows a fight or chase (see above), might signal the aggressive tendencies of the signaler and thereby inhibit approaches.

Headslapping is an explosive disturbance above and underwater that alerted other alligators. For example, two submerged alligators surfaced after a headslap by R♂. Headslaps,

which may be given from within a territory, signal presence and location and promote approach of potential mates to the headslapper.

Jaw Clapping. Jaw clapping is the rapid closing of the open jaws producing a loud, deep pop. It is an element of headslapping (see above). It also occurs during interspecific encounters and as a response to the approach of an intruder in the water (Neill, 1971, p. 44).

Splashing. Splashing is an unusually intense disturbance created by an alligator exclusive of times of fighting and flight employing tail, head, and body movements. Two examples from the field notes illustrate this behavior:

> At 0822 on May 8—animal in NE corner vigorously tail wagging, cleared a lot of water and made much noise then headslapped.

> At 0824 on May 14—bellowing stopped several minutes ago. Headslap and tail thrashing by Y♂ in NE corner of lake.

There were no obvious responses to these headslaps, splashes, and thrashings.

Silverstone (1972) described splashing as a "violent thrashing of the body and tail in the water, usually while submerged," which occurred after headslapping, bellowing, and assuming the bellowing posture, and which was followed by rapid swimming. Splashing seems to be used to emphasize presence.

SUMMARY AND CHARACTERIZATION OF THE ALLIGATOR SIGNALING SYSTEM

The eighteen alligator signaling behaviors described above are not homogenous in their frequency of occurrence, conspicuousness, and complexity. Some signals are "displays" (see Beer, 1977, for a discussion of the term) while other signals are postural changes and movements, or what Hinde (1974) has called "low-keyed" signals. But classification is not our major concern; rather we will summarize the signals by exploring the structural affinities among the signals. This approach may be instructive for future behavioral studies of alligators and other crocodilians.

Arrangement of the postural aspects of the signals from the least complex (fewer elements) to the most complex (greater number of elements) demonstrates the degree of structural similarity (fig. 10). Commencing from the resting posture in the water, the least complex act appears to be raising the head out of the water—at an oblique angle as in snout lifting, and jaw clapping, or positioning the head above the water's surface as in bellow growls. The head emergent tail arched posture easily can be transformed into the head oblique tail arched (bellow) posture, apparently necessitating only a downward arching of the spine. This latter posture is common to bellowing, inaudible bellowing, headslapping, yawning, narial geysering, splashing, and tail wagging. And yet these seven signaling behaviors are of grossly different complexity.

Also it is apparent (fig. 10) that a resting posture can be simply transformed into an inflated posture (on land, the inflated posture is accompanied by a prolonged hiss).

In spite of their structural similarity these postural signaling elements are components of,

TABLE 8

Number of Headslaps Occurring Within a Particular Hour of the Morning Compared With the Total During the Entire Day

Times of Observation	No. Days[a]	6-7	7-8	8-9	9-10	10-11	11-12	6-12 Total	Daily Total
					Hours				
March 24 - April 15	8	0	1	6	3	2	1	13	14
April 16 - May 10	21	6	20	28	7	8	5	74	94
May 11 - June 14	29	0	26	20	10	16	12	84	102
Totals	58	6	47	54	20	26	18	171	210

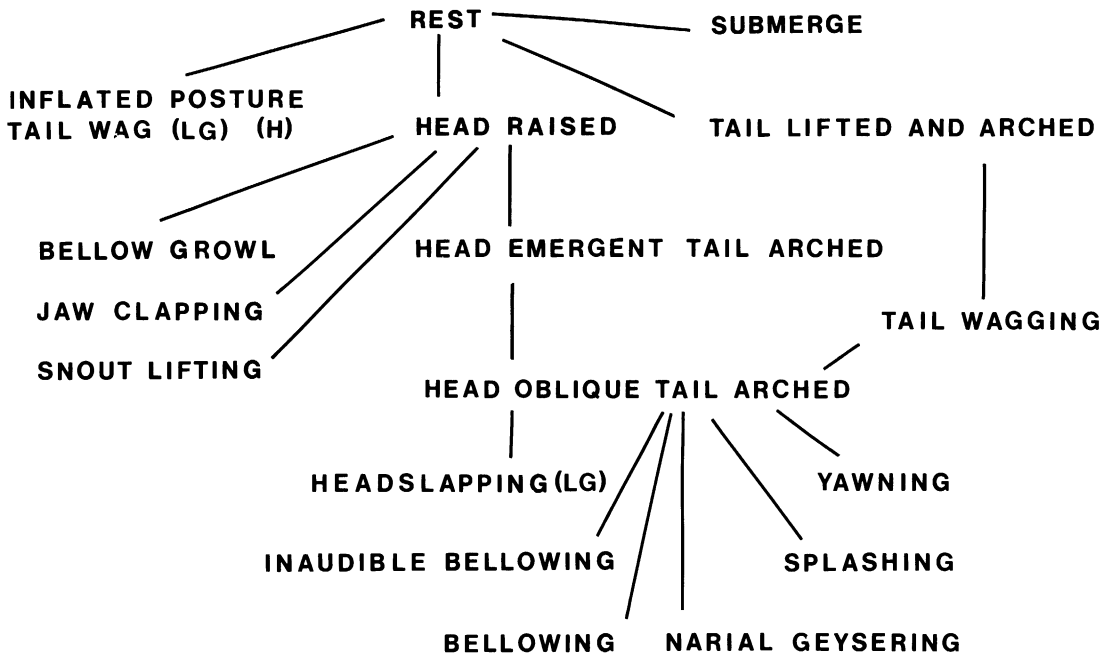[a] Number of days when headslaps were observed in each period.

FIG 10. Interrelations of postural elements of alligator signaling behaviors. Vocalizations are in parentheses: LG=low growl, H=hiss.

or are themselves, discrete, nonoverlapping signals, some of which are combined to form composite signals.

Adult alligator vocal signals consist of six low frequency sounds in air, at least five of which are given in particular stimulus situations (figs. 4 and 6; table 9). The six vocalizations are, in order of their spectral affinities—bellow, bellow growl, deep grunt, low growl, cough (chumpf), and hiss (table 9). Although some vocalizations appear structurally graded, only bellows and bellow growls show any functional grading, i.e., females have been observed to follow bellow growls with several bellows. Other similarities between bellow growls and bellows are that each is given in a series or bout, and that both are used in long and moderately long distance signaling. However, bellows have longer durations than bellow growls (table 9). In summary, the vocalizations show the following characteristics (table 9): sound energy is less than 1 kHz. with most dominant frequencies less than 250 Hz.; four vocalizations contain repeating units, most transmit less than

about 10 m., and only one, bellow growls, is sex specific.

In general, reptiles have been considered behaviorally uncomplicated because they lack the capacity for sustained metabolic activity characteristic of many birds and mammals. It is true that most reptiles cannot successfully compete with endotherms, although the varanid lizards may be an exception (Bennett, 1972; Regal, in press). Nonetheless, reliance on ectothermy apparently has not constrained the evolution of complexity within reptilian social behavior, as evidenced in two recent reviews (Greenberg and McLean, in press; Greenberg et al., 1977). And now we have shown above that the alligator communication system is much richer and demonstrates a greater signaling capacity than previously suggested in the reviews of Bogert (1960), Blair (1968), Thorpe (1972), Gans and Maderson (1973), and Brattstrom (1974).

In addition to the general properties such as the number of different signal types, we can identify similar characteristics in the alligator signaling system and the communication sys-

TABLE 9
Summary of Alligator Vocal Elements

Vocalization	Median & range of no. units	Sex	Mean & (range) call duration (seconds)	Median & range of duration(s) of intercall intervals	Fundamental or dominant frequency Hz.	Estimated distance vocalization carries in air (m.)
Bellow	(1-11) 5/bout	M	1.83(1.23-2.79)	3.94 (2.92-6.70)	50-250	150
Bellow Growl	(1-6) 2/bout	F F	1.71(1.23-2.67) 0.91(0.36-1.43)	2.60 (1.76-4.83) 2.86 (1.76-5.38)	125-200	75
Deep Grunt	1	unknown	1.04	—	50 with harmonics	~5
Low Growl	1	M,F	0.68	—	100 with harmonics	<10
Coughs = Chumpfs	3 2 forms	M,F	0.20 0.29	1.0	75 with harmonics	<5
Hiss	1 or 2	M,F	1-30	3-5	50-250 and 550-650	~5

Vocalization	Stimulus Situation	Post-vocal Responses	Probable Functions
Bellow	*External* Bellow Headslap Bellow Growl Nonbiological sounds *Internal* "Spontaneous"	Bellowing Approach of Bellower Nonspecific movement	Signals presence and location Synchronize group activity Individual recognition Attract conspecifics for breeding
Bellow-Growl	Approach by male Nearby male-male agonistic encounter	Female swims off, submerges or leaves water Female remains	Inhibits mating attempt by male Identifies vocalizer as a female; inhibits attack
Deep Grunt	Playbacks of juvenile grunts		Signal to young; recognition
Low Growl	During headslapping, yawning and inflated posture	Females bellow-growl	Signal modification
Coughs = Chumpfs	Initial phase of courtship	More courtship, usually	Initial identification; facilitates further contact
Hiss	"Defensive display" to an intruder on land	Retreat or attack	Display inhibits further approach

tems of birds and mammals. These qualities of the alligator signaling system would appear to be essential for the maintenance of the alligator's social organization. Ultimately, comparisons among species of major taxa are useful for what they may reveal about the similarity in the functional organization, and perhaps even messages, of signals (Smith, 1969). In this light the following brief analysis examines three characteristics of the alligator signaling system.

1. The same signal can be used in many contexts. For instance, bellows are given during and after the breeding season, within and without a bellowing chorus, near a member of the opposite sex, and in different regions of the habitat. For some of these contexts of bellowing the message appeared to be "here I am" to which approach was often an appropriate response. Moreover, the sex, size, and social rank of sender and receiver can be additional determinants of the context of the bellow: In other words, the meaning to a recipient may be more than the message transmitted by the sender (Smith, 1968; Hinde, 1974). For example, bellowing by a large male outside of the breeding season may have a different meaning to a conspecific of either sex than it does during the breeding season (Campbell, 1973). As evidence of this possibility, Petrinovich et al. (1976) found that the responses of male and female white-crowned sparrows to songs of territorial males varied with the reproductive condition of the responders. And in a study suggesting the use of one signal in many contexts, Beer (1976) described how the "long-call" of laughing gulls occurred in many social situations.

2. Signal elements may be combined in different order around a basic signal creating a complex display. For instance headslapping has two basic forms and may be combined with seven elements. Evidence was presented above that the usual response to the headslap was modified by the addition of different signal elements, i.e., the incidence of approaches to the headslapper was reduced when a tail wag and/ or an inflated posture terminated the display. Perhaps by employing these elements the animal signals its preference for reduced social

contact or its intolerance of the proximity of other alligators. Hence, for this combination of signal elements specific information about the behavioral tendencies of the signaler may be available to conspecifics.

To give one example of a similar display among other vertebrates: Schaller (1963) found that Mountain Gorillas frequently interchanged and combined the nine different acts or elements of the "chest beating display." Silverbacked males usually gave a complete display, whereas use of various combinations of elements depended on the gorilla's sex, the intensity of the display, and "individual" variation.

3. Signals may serve to identify individuals. Alligator bellowing potentially contains clues for individual recognition in the duration of the interbellow interval, length of the bellowing cycle, loudness, and frequency configuration of the bellow, as well as other unanalyzed parameters such as amplitude modulation (Beer, 1976). We noted above that several bellowers in table 5 could be identified by us without visual confirmation, and that spectral analysis (e.g., fig. 4) corroborated these observations. The adaptive significance of individual recognition by voice among adult alligators may be recognition of conspecifics from a distance which may aid in locating mates and establishing breeding units. Within a breeding group, though, individual recognition by voice in conjunction with other cues might facilitate choice of mates and foreclose potentially chaotic and energy wasting encounters. In this later regard the low density of alligator breeding groups (Joanen and McNease, 1976) implies that individual recognition is likely (Brown, 1975).

Individuality is evident in the vocalizations of birds (Thorpe, 1968; Beer, 1970a, 1976) and of chimpanzees (Marler and Hobbett, 1975) to name just two of many possible examples. Use of individual information within a voice only has been demonstrated by playbacks of the vocalization of offspring to their mothers who then showed a preferential response to their own rather than alien young (gulls: Beer, 1970a; reindeer: Espmark, 1971; elephant seal: Petrinovich, 1974), and by playbacks of parent's calls to gull chicks who oriented toward

them but not to the sounds of other adults (Beer, 1970b). Parent-young vocal recognition also may exist among crocodilians in which parental attention is common (Garrick and Lang, 1977).

SIGNALING BEHAVIORS OF *ALLIGATOR MISSISSIPPIENSIS* AND OTHER CROCODILIANS

At this point in the study of crocodilians it is appropriate to compare and contrast the signalling behaviors of *Alligator mississippiensis* with those of other crocodilians. This discussion includes vocal, nonvocal acoustic, and visual signals.

Vocalizations are the commonest signals that have been ascribed to crocodilians in captivity or in the wild throughout their life. Even prior to hatching while in the nest and within the closed egg, the late embryo vocalizes (for *C. porosus*, Deraniyagala, 1939; *Paleosuchus palpebrosus*, Medem, 1972; *C. acutus* and *A. mississippiensis*, Garrick, unpubl. observ.). And Cott (1961) and Pooley (1969) have reported the vocalizations of unhatched *Crocodylus niloticus*. In response to vocalizations from within the nest one or another of the parents excavates the nest (for *C. niloticus* ♀, Pooley, 1969, 1976; *C. moreleti* ♀, Hunt, 1975; *Caiman crocodilus* ♂, Alvarez del Toro, 1969, 1974; *A. mississippiensis* ♀, Reese, 1915, p. 25, McIlhenny, 1935, p. 110, Herzog, 1975; Watanabe, MS). Using its mouth, the parent cracks open the unhatched eggs (for *C. acutus* ♀, Ogden and Singletary, 1973; *C. niloticus* ♀, ♂, Pooley and Gans, 1976; *C. crocodilus* ♂, Alvarez del Toro, 1969), carries the young to the water, and releases them (Ogden and Singletary, 1973; Hunt, 1975; Pooley, 1974, 1976). However, Alvarez del Toro (1969) noted that the female *Caiman* remained in a pool and vocalized, presumably grunting; then all 25 young liberated by the male entered the pool and approached her. And Pooley (1974) demonstrated that a female *C. niloticus* responded to the vocalizations of hatchlings by approaching and picking them up and then carrying 19 of them in her mouth. Similar observations were made for *C. moreleti* by Hunt (1975).

Young of all crocodilian species emit distress calls when they are held, grabbed abruptly, or when their limbs, tail, or body are squeezed (Campbell, 1973; Herzog, 1974; Herzog and Burghardt, 1977; L. Garrick and R. Garrick, 1978). These calls elicited approach of adults (*A. mississippiensis*, Kushlan, 1973; Garrick, unpubl. observ.; *Caiman crocodilus*, Alvarez del Toro, 1969; *C. palustris*, Whitaker, 1974; *C. novaeguineae*, Neill, 1946; *C. moreleti*, Hunt, 1975), and thus this response might be considered as parental defense of the young.

In addition to their communication with parents, the young grunt in response to each other's grunts (Pooley, 1974; Deraniyagala, 1939; Campbell, 1973; Herzog, 1974; Herzog and Burghardt, 1977).

As the crocodilian grows it continues to emit distress and grunt vocalizations. At about three or four years of age juvenile alligators attempt to bellow, but even though they assume the "correct" posture the sound is weak (Garrick, unpubl. observ.; Herzog, 1974). Several years later they will bellow adequately. However, a 0.75 m. alligator emitted a high-pitched "bellow" in response to a tone from a signal generator (W. King, personal commun.). The ontogeny of this vocalization presents some intriguing research possibilities.

Many adults of the 21 extant crocodilian species (Brazaitis, 1974) have been heard to roar or bellow in zoos, breeding farms, or in the wild. Alligators vocalize readily in captivity and thus have been relatively well-studied. For example, Beach's (1944) study of the American alligator and Garrick's (1975a) report of the roars of the Chinese alligators (*Alligator sinensis*) provided detailed information unattainable at the time from other sources. To begin the discussion of adult vocalizations, the roars, bellows, and other vocal signals of these two alligators are compared.

Chinese alligators emit from two to eight explosive roars of about 0.70 second duration with males having more roars/bout than females. Spectral analysis revealed dominant frequencies below 500 Hz. but also sound energy above 1 kHz. (fig. 11A). Compared to the "roars" of Chinese alligators, American alligator bellows are of longer duration, and there are more in each bout and no difference in the number per bout between sexes. The bellow growl of female American alligators (fig. 4), while not so explosive, is similar in sound and duration to the *A. sinensis* roar. Chinese alligators also emit guttural coughs during courtship (Brazaitis, 1968) and a hiss during interspecific encounters (Garrick, unpubl. observ.).

The bellows and roars of the two species of alligator are structurally and perhaps functionally different (figs. 4 and 11A). However, factors responsible for the difference cannot be suggested because virtually nothing is known about the socio-ecology of *A. sinensis*. Both vocalizations could have changed over time because these two extant species have not shared a common ancestor since before the beginning of the Miocene (Mook, 1923, 1925; White, 1942).

Reports of vocal behavior in other adult alligatorids are limited to the mention of "roaring" by *Caiman crocodilus* (Alvarez del Toro, 1969; Herzog, 1974).

Within the family Crocodylidae there are few reports of vocalizations for adults of the genus *Crocodylus*, the 11 species of true crocodiles. Still there are similarities within the group and to *Alligator*. The American crocodile *Crocodylus acutus* bellows on land (Herzog, 1974) and in the water with conspecifics (Neill, 1971, p. 341). According to Neill (1971), the *C. acutus* bellow is a "roar-like hiss." *Crocodylus acutus* also emits shrill, prolonged "groans" when confronted by the more aggressive Cuban crocodile (Varona, 1966), and "growls" during intraspecific encounters (Lang, 1975b).

Neill (1971, p. 353) also described the roars of the Cuban crocodile, *C. rhombifer*, as 10 "roar-like hisses," while a male on land gave a single low volume bellow (Herzog, 1974). Varona (1966) reported that the vocalizations of a male consisted of "*un mugido sordo*" (perhaps translated as a muffled moo), "snorts," and "guttural grunts."

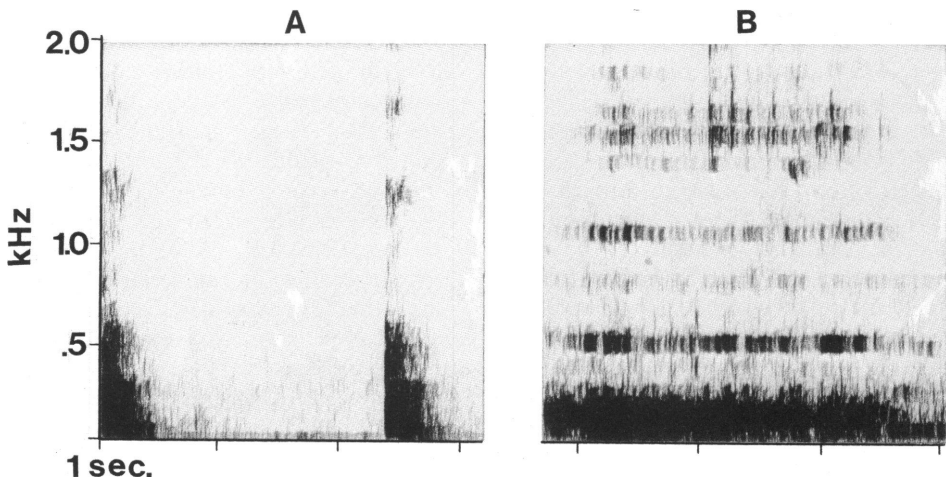Vocalizations also have been reported among the Old World members of the genus in

FIG 11. Sound spectrograms of the roars of two adult crocodilians: A. *Alligator sinensis* (♂) and B. *Crocodylus cataphractus* (♂).

Asia and Africa. Battye (1944) reported that a 12 ft. 4 inch *C. palustris* "bellowed" two or three times and then hauled out to bask. He knew its precise length because he shot it. The Ceylonese marsh crocodile *C. palustris kimbula* emits a "loud croaking grunt" audible at 200 m. (Deraniyagala, 1939). Another inhabitant of Ceylon, the estuarine or saltwater crocodile, *C. porosus*, "grunts" all night during the mating season (Deraniyagala, 1939, p. 362).

Both African *Crocodylus* species vocalize. The roaring of the African slender-snouted crocodile *C. cataphractus* at the New York Zoological Park sounded similar to a series of truck exhaust backfires. Acoustic energy of a roar was distributed at 100-200, most strongly at 500, and 1000 and 1500 Hz., and a roar lasted 2.1 seconds (fig. 11B) (Garrick, unpubl. observ.). Also for this species, Herzog (1974) found 1.83 second as the mean duration of calls in a five-roar bout and 6.51 seconds its mean inter-roar interval, but for a bout of eight roars, the mean roar duration was 0.98 second and the inter-roar interval was 3.79 seconds. These data are within the range of the American alligator bellows for duration and number per bout. In addition, Pooley (personal commun., 1975) suggested that roars of *C. cataphractus* and *C. niloticus* sounded very similar.

Cott (1961, 1975) reported that adult Nile crocodiles use six vocalizations: 1) a "hiss" as part of the threat display; 2) a "low growl" given by a female surprised guarding her nest, and by trapped animals; 3) A "bellow" of pain when wounded; 4) a deep, loud, abrupt "bark" or "cough" emitted by basking males during the breeding season; 5) a protracted "roar" that probably functions in advertisement, attracting others to the caller; and 6) a "creaking or groaning sound" given by the female during courtship. Thus this species apparently has about the same number of vocal signals as the American alligator, and many are similar in function.

Modha's (1967) study at Central Island, Lake Rudolf, Kenya, extended previous observations and provided a social context for the signals of the Nile crocodile. Modha observed that territorial males often chased smaller male intruders out onto the shore and at the end of the chase the dominant "roared" in the direction of the vanquished animal. Modha also observed "growling" during fights and "guttural sounds" by females during courtship.

In contrast to vocalizations, nonvocal acoustic and visual signals are poorly documented, therefore they will be treated together. Modha (1967) observed "narial geysering" by two *C. niloticus* males in an agonistic face-off and "snout lifting" by subdominants in response to a territorial male. Large males approached presumed females and engaged in the following behavior (called the "courtship splash display" by Modha because it was a prelude to courtship): With his head above the water's surface and tail arched so that its tip touched the water he emitted subaudible vibrations ending with the body submerged. The tail was then lashed sideways while the jaws were simultaneously opened and closed one to five times creating much froth near the snout and tail. This composite display contains the following elements which appear similar to those described for the American alligator: subaudible vibrations, jaw clapping, and tail wagging combined with splashing. Recently, a photograph has shown a male *C. niloticus* headslapping (Gore, 1978, p. 100).

The nonvocal acoustic and visual signals of captive *C. acutus* are similar to those of *C. niloticus*. Lang (1975b, 1976) described a signal similar to the courtship splash display—subaudible vibrations with tail wag, which was part of courtship. Lang also reported headslaps given in a series of one to three, inflated posture and tail wagging during male-male aggressive encounters, and snout lifting by females in the presence of a territorial male.

Overall, vocal, nonvocal acoustic, and visual signals are common among crocodilians. These signals are similar in physical quality and are performed with similar intensity. However, within a species, signaling elements may be combined in different ways in order to serve different communicatory functions, and among species major differences appear in the organization of the signaling systems (Garrick and Lang, 1977). Why these particular signal-

ing elements evolved bears on the kinds of selective pressures operating on these semi-aquatic reptiles.

FACTORS INFLUENCING THE SELECTION OF CROCODILIAN SIGNALS

The three families of living crocodilians are essentially unchanged morphologically since the Eocene (Sill, 1968). Therefore, similarity of signaling elements may reflect the evolutionary conservatism of these families or the gross similarity of selection pressures on their signals. We do not have the data at hand to decide which is the more likely alternative. However, it is possible (and important for future research) to speculate on the factors shaping the structure and function of crocodilian signals and to suggest why species differences and similarities exist. As a point of departure we will consider long-distance vocal signals.

First, we can ask whether there are environmental requirements for efficient aerial communication which, given the constraints of the vocal apparatus, influence the structure of long-distance vocalizations. Habitat structure, for instance, may be an important source of selection. Morton (1975) found that, between 200 and 400 Hz. sound attenuation was independent of habitat type but that frequencies in the 0.5 to 1.5 kHz. range showed reduced attenuation in forest compared with forest edge and were strongly attenuated in grassland. Thus, crocodilians can avoid significant signal attenuation either by evolving vocal frequencies less than 400 Hz. or frequencies which are matched to particular habitat requirements. Resolution of these alternatives is difficult. Although harmonics are present near 1.5 kHz., energy in the roars and bellows for three "grassland" species falls into the following ranges: *A. mississippiensis*, 50 to 250 Hz.; *A. sinensis*, 25 to 500 Hz.; and *C. cataphractus*, 100 and 500 Hz., suggesting that these species may avoid this source of attenuation. On the other hand, vocal data from the small forest species, the dwarf crocodile (*Osteolaemus*) and the two small smooth-fronted caimans of the genus *Paleosuchus* would be important in resolving the question of vocal adaptation to particular habitat types because they could exploit frequencies between 0.5 and 1.5 kHz.

Possibly another factor influencing the selection of the characteristics of roars or bellows is the locatability of the signal. In this case the design of the auditory apparatus suggests where selection may operate. Marler (1969) pointed out that vertebrates potentially use three clues to localize a sound source, viz. difference in loudness, direction, and time of arrival at the two ears. Although high frequencies provide the best clues about intensity and loudness, low frequencies and long wave lengths (provided they are greater than the distance between the ears) are better suited for determining phase differences; they also do not attenuate as rapidly over long distances. Repeated units are more easily located independent of frequency. For the alligator bellow at three frequencies—100, 500, and 1000 Hz.—the respective wavelengths in air are 3.44 m., 0.68 m., and 0.34 m. The distance between the ears of a large alligator is between 0.15 and 0.3 m. (Dodson, 1975). Therefore, 1 kHz. approaches the upper limit for efficient binaural locatability. Thus the alligator bellow conforms to prediction; they contain frequencies below 1 kHz. and are repetitive.

Intraspecific vocalizations must be heard; therefore we can expect that the frequency characteristics of alligator audition, for example, are similar to the vocal frequencies. The available evidence shows that adult American alligators respond to free-living adult alligators vocalizing, to playbacks of their own bellows, and to playbacks of juvenile vocalizations which are in the range of 100 to 1500 Hz. (Garrick, unpubl. observ.; Herzog, 1974). There is no data on the physiology of adult hearing but the best sensitivity of the juvenile alligator ear is between 100 and 1000 Hz. (Wever, 1971). Presumably, the aerial sounds are received by the ear; however, underwater sound reception also occurs.

Crocodilians possess signals that are transmitted through water. This is obviously advantageous for crocodilians that submerge, for example, during courtship (Garrick and Lang, 1975, 1977), thermoregulation, feeding, and escape and which can remain underwater for as

long as two hours (Johnson, 1973; Smith, 1975). Here they are concealed and can receive signals through the water. Therefore, it is not surprising that many signals are transmitted through both air and water. For example, submerged alligators surfaced in response to headslaps and bellows (Garrick and Lang, unpubl. observ.). In addition, the nonvocal acoustic signals send pressure waves out through the water which creates other communication possibilities. The physical advantages of communicating through the water are that sound waves travel about four times faster and the sound pressures are 60 times greater in water than in air (Brandt, 1963). Exploiting aquatic communication might compensate in some degree for "deficits" in sound pressure in air at the middle ear of crocodilians compared to birds and mammals reported by Manley (1973). So far all of the examples are of signaling by alligators on the surface to other alligators on the surface or to submerged alligators. As yet there is neither evidence for nor against underwater signaling between two or more totally submerged crocodilians.

Habitat requirements may also influence the selection of visual versus acoustic signals. For example, when long-distance signals containing acoustic and visual elements are compared (for instance bellows and headslaps), alligator signals appear to be more acoustically than visually conspicuous. This may have resulted because sound, provided it is not attenuated, is more easily discerned in their vegetated habitat in which the background would cause difficulty in discriminating visual elements (Marler, 1968). Purely visual signals, such as snout lifting, inflated posture, and head emergent tail arched posture, and some vocalizations (table 9), are used during close range social contact. These same habitat requirements may explain species differences in signaling system organization. For example, compared to *C. acutus* and *C. niloticus*, alligators are more vocal (Garrick and Lang, 1977). This difference may have resulted from the different signaling requirements in a vegetated (alligator) habitat compared to the more open habitats in which these two crocodiles are found (Garrick and Lang, 1977).

SUMMARY

We describe 18 adult American alligator signaling behaviors based on observations of captive animals in natural settings. Our analysis focuses on communication function, hence, lengthy descriptions of sequences of social behaviors are excluded; they appear elsewhere (Garrick, 1975b; Garrick and Lang, 1975, 1977). For each signal we report, when they are available, all relevant temporal and/or spectral parameters, stimulus context, and responses by other alligators, and then we propose a probable function(s) for the signal.

The signaling behaviors are grouped into postulated sensory modes for their reception: eight visual, six vocal, and four nonvocal acoustic signals are recognized. This is simplistic, however, since some signals actually are composed of elements from all three modalities. Nearly all signals are given by both sexes. The alligator signaling repertoire mainly is composed of discrete signals, although there appears to be limited functional grading among

vocal signals. However, structural grading among postures and vocalizations is more prevalent. In fact, a postural element—head oblique tail arched posture—is the basis for seven different signals.

Among the vocalizations sound energy is concentrated at less than 1 kHz., with most dominant frequencies less than 250 Hz. Four of the six vocalizations contain repeating units. Except for bellowing and bellow growls, most vocalizations transmit less than 10 m. in air, and except for bellow growls (a female anticopulatory vocalization) none are sex-specific.

Long-distance signaling is accomplished by two behaviors—bellowing and headslapping; they are capable of carrying at least 150 m. In this instance bellowing presumably functions to signal conspecifics during the formation of breeding groups, while headslapping and bellowing are both advertisements for courtship once the breeding group is formed. Thus, alligator long-distance signals are more acous-

tically than visually conspicuous. Perhaps this dichotomy arose because in the alligator's vegetated habitat visual signals could be difficult to discern. On the other hand, visual signals and some vocalizations are employed nearby other alligators during courtship and agonism.

Alligators are semi-aquatic reptiles and the majority of these signals occur in the water. For example, postures are modified by increasing or decreasing surface area (e.g., inflated posture) but more importantly they are adjusted by the amount of body surface exposed above the water (e.g., head emergent tail arched posture). In the acoustic realm, some signals transmit simultaneously through both air and water (e.g., bellowing and headslapping). One advantage of communication through and below water is that submerged alligators can wait in relative safety and obscurity for signals.

A review of crocodilian signaling systems reveals similarities in vocal, nonvocal acoustic, and visual elements between alligators and other species. However, within a species signal elements may be combined in different ways in order to serve different communicatory functions, and major differences appear in the organization of crocodilian signaling systems (Garrick and Lang, 1977).

Notions that reptiles are behaviorally uncomplicated because they lack the metabolic capacity for activity are rejected. Recent reviews of reptilian social behavior and the results presented above evidence that alligators and other reptiles share with birds and mammals characteristics of complex signaling systems, as well as social organizations necessitating such complexity.

LITERATURE CITED

Altmann, Jeanne
  1974. Observational study of behavior: sampling methods. Behavior, vol. 49, pp. 227-267.
Alvarez del Toro, Miguel
  1969. Breeding the spectacled caiman (*Caiman crocodilus*) at Tuxtla Gutierrez Zoo. Internatl. Zoo Yearbook, vol. 9, pp. 35-36.
  1974. Los crocodylia de Mexico. Instituto Mexicano de Recursos Naturales Renovables, A.C., Mexico, D.F. pp. 1-70.
Bartram, William
  1791. Travels through North and South Carolina, Georgia, east and west Florida etc. Philadelphia, James and Johnson, pp. 1-522.
Battye, R. K. M.
  1944. Crocodiles bellowing. Jour. Bombay Nat. Hist. Soc., vol. 45, pp. 93-94.
Beach, Frank A.
  1944. Responses of captive alligators to auditory stimulation. American Naturalist, vol. 128, pp. 481-505.
Beer, C. G.
  1970a. Individual recognition of voice in the social behavior of birds. *In* Lehrman, Daniel S., Robert A. Hinde, and Evelyn Shaw (eds.), Advances in the study of animal behavior, no. 3, pp. 27-74.
  1970b. On the responses of laughing gull chicks (*Larus artricilla*) to the calls of adults. I. Recognition of the voices of the parents. Anim. Behav., vol. 18, pp. 652-660.
  1976. Some complexities in the communication

behaviour of gulls. *In* Harnad, Steven R., Horst D. Steklis, and Jane Lancaster (eds.), Origins and evolution of language and speech. Annals New York Acad. Sci., vol. 280, pp. 413-432.
  1977. What is a display? Amer. Zool., vol. 17, pp. 155-165.
Bennett, Albert F.
  1972. The effect of activity on oxygen consumption, oxygen debt, and heart rate in the lizards *Varanus gouldii* and *Sauromalus hispidus*. Jour. Comp. Phys., vol. 79, pp. 259-280.
Blair, W. Frank
  1968. Amphibians and reptiles. *In* Sebeok, Thomas (ed.), Animal communication. Bloomington, Indiana Univ. Press, pp. 289-310.
Bogert, Charles M.
  1960. The influence of sound on the behavior of amphibians and reptiles. *In* Lanyon, W. E., and W. N. Tavolga (eds.), Animal sounds and communication. Amer. Inst. Biol. Sci., publ. no. 7, pp. 137-320.
Brandt, O.
  1963. Principles of underwater acoustics. *In* Guy-Busnell, Rene (ed.), Acoustic Behavior of animals. New York, Elsevier, pp. 48-53.
Brattstrom, Bayard H.
  1974. The evolution of reptilian social behavior. Amer. Zool., vol. 14, pp. 35-49.

Brazaitis, Peter
1968. T'o. Animal Kingdom, New York Zool. Soc., vol. 41, pp. 24-27.
1974. The identification of living crocodilians. Zoologica, New York Zool. Soc., vol. 58, pp. 59-101.

Brown, Jerram L.
1975. The evolution of behavior. New York, W.W. Norton, pp. 1-761.

Campbell, Howard W.
1973. Observations on the acoustic behavior of crocodilians. Zoologica, New York Zool. Soc., vol. 58, pp. 1-11.

Carr, Archie
1967. Alligators, dragons in distress. National Geographic, vol. 131, pp. 133-148 (January).

Chabreck, Robert H.
1966. The movement of alligators in Louisiana. Proc. SEast. Assoc. Game and Fish Commissioners, 19th Annual Conference, 1965, pp. 102-110.

Cott, Hugh B.
1961. Scientific results of an inquiry into the ecology and economic status of the Nile crocodile (Crocodilus niloticus) in Uganda and Northern Rhodesia. Trans. Zool. Soc. London, vol. 29, pp. 211-356.
1975. Looking at animals: a zoologist in Africa. New York, Scribner's and Sons, pp. 135-152 (the Nile crocodile).

Crews, David P.
1975. Inter- and intra- individual variation in display patterns in the lizard, Anolis carolinensis. Herpetologica, vol. 31, pp. 37-47.

Cullen, J. M.
1972. Principles of animal communication. In Hinde, Robert A. (ed.), Non-verbal communication. Cambridge, the Univ. Press, pp. 101-125.

Darwin, Charles
1872. The expression of the emotions in man and the animals. London, J. Murray. (available through the Univ. Chicago Press, 1965).

Deraniyagala, P. E. P.
1939. The tetrapod reptiles of Ceylon. vol. 1, Testudinates and Crocodilians. Colombo Mus. Nat. Hist. Ser., pp. 307-391.

Dodson, Peter
1975. Functional and ecological significance of relative growth in Alligator. Jour. Zool. (London), vol. 175, pp. 315-355.

Espmark, Yngve
1971. Individual recognition by voice in Rein-

deer mother-young relationship. Field observations and playback experiments. Behaviour, vol. 40, pp. 295-301.

Evans, L. T.
1961. Structure as related to behavior in the organization of population in reptiles. In Blair, W. Frank (ed.), Vertebrate speciation. Austin, Univ. Texas Press, pp. 148-178.

Evans, L. T., and J. Quaranta
1949. Vocality, a factor in the ecology of the alligator. Anat. Record, vol. 105, pp. 581-582.

Fogarty, Michael J.
1974. The ecology of the Everglades alligator. In Gleason, P. J. (ed.), Environments of south Florida: present and past memoirs of Miami Geological Survey, no. 2, pp. 367-373.

Gans, Carl, and Paul F. A. Maderson
1973. Sound producing mechanisms in Recent reptiles: review and comment. Amer. Zool. vol. 13, pp. 1195-1203.

Garrick, Leslie D.
1974. Vocalizations of adult American alligators. Amer. Zool., vol. 14, 1278 (Abstract).
1975a. Structure and pattern of the roars of Chinese alligators (Alligator sinensis Fauvel). Herpetologica, vol. 31, pp. 26-31.
1975b. Love among the alligators. Animal Kingdom, New York Zool. Soc., vol. 78, pp. 2-8.

Garrick, Leslie D., and Jeffrey W. Lang
1975. Alligator courtship. Amer. Zool., vol. 15, p. 813 (Abstract).
1977. Social signals and behaviors of adult alligators and crocodiles. Ibid., vol. 17, pp. 225-239.

Garrick, Leslie D., and Rita Anne Garrick
1978. Temperature influences on hatchling Caiman crocodilus distress calls. Phys. Zool., vol. 51, pp. 105-113.

Gore, Rick
1978. A bad time to be a crocodile. National Geographic, vol. 153, pp. 90-115.

Greenberg, B., and G. K. Noble
1944. Social behavior of the American chameleon (Anolis carolinensis). Phys. Zool., vol. 17, pp. 392-439.

Greenberg, Neil B., et al.
1977. Papers presented at a Symposium—Communications and display behavior in reptiles. New Orleans, Louisiana, 2 June, 1976, Amer. Zool., vol. 17, pp. 153-286.

Greenberg, Neil B., and Paul McLean (eds.)
[In Press] The behavior and neurology of lizards.

Dept. Health, Educ., and Welfare, Washington, D.C.

Harper, Francis
1930. Alligators of the Okefinokee. Sci. Monthly, vol. 33, pp. 51-67 (July).

Hediger, H.
1955. Studies on the psychology and behavior of captive animals in zoos and circuses. (Translated by G. Simon.) New York, Criterion Books.

Herzog, Harold A., Jr.
1974. The vocal communication system and related behaviors of the American alligator (*Alligator mississippiensis*) and other crocodilians. Master of Science Thesis, Univ. Tenn., Knoxville, pp. 1-83.
1975. An observation of nest opening by an American alligator *Alligator mississippiensis*. Herpetologica, vol. 31, pp. 446-447.

Herzog, Harold A., and Gordon M. Burghardt
1977. Vocalization in juvenile crocodilians. Zeitschr. für Tierpsychologie, vol. 44, pp. 294-304.

Hinde, Robert A.
1974. Biological bases of human social behaviour. New York, McGraw-Hill, pp. 1-462.

Hunt, R. Howard
1975. Maternal behavior in the Morelet's crocodile, *Crocodylus moreleti*. Copeia, 1975, pp. 763-764.

Joanen, Ted
1970. Nesting ecology of alligators in Louisiana. Proc. SEast. Assoc. Game and Fish Comm., 23rd Annual Conf. 1969, pp. 141-151.

Joanen, Ted, and Larry McNease
1971. A telemetric study of nesting female alligators on Rockefeller Refuge, Louisiana. Proc. SEast. Assoc. Game and Fish Comm., 24th Annual Conf., 1970, pp. 175-193.
1972. Propagation of the American alligator in captivity. Proc. SEast. Assoc. Game and Fish Comm., 25th Ann. Conf., 1971, pp. 106-116.
1973. A telemetric study of adult male alligators on Rockefeller Refuge, Louisiana. Proc. SEast. Assoc. Game and Fish Comm., 26th Ann. Conf., 1972, pp. 252-275.
1976. Notes on the reproductive biology and captive propagation of the American alligator. Proc. SEast. Assoc. Game and Fish Comm., 29th Ann. Conf., 1975, pp. 407-415.

Johnson, Clifford Ray
1973. Behaviour of the Australian crocodiles, *Crocodylus johnstoni* and *C. porosus*. Zool. Jour. Linnean Soc., vol. 52, pp. 315-336.

Kushlan, James A.
1973. Observations on maternal behavior in the American alligator, *Alligator mississippiensis*. Herpetologica, vol. 29, pp. 256-257.

Lang, Jeffrey W.
1975a. Thermoregulatory behavior of adult American alligators. Amer. Zool., vol. 15, p. 797 (Abstract).
1975b. The Florida crocodile: will it survive? Chicago (Field) Mus. Nat. Hist. Bull., vol. 46, pp. 4-9.
1976. American crocodile courtship. Amer. Zool., vol. 16, p. 197 (Abstract).
1977. Studies on crocodilian thermal behavior. Ph.D. Thesis, Univ. Minnesota, Minneapolis.

Legge, R. E.
1967. Mating behavior of American alligators (*Alligator mississippiensis*) at Manchester Zoo. Internatl. Zoo Yearbook, vol. 7, pp. 179-180.

Manley, Geoffrey A.
1973. A review of some current concepts of the functional evolution of the ear in terrestrial vertebrates. Evolution, vol. 26, pp. 608-621.

Marler, Peter
1968. Visual signals. *In* Sebeok, Thomas (ed.), Animal Communication. Bloomington, Indiana Univ. Press, pp. 103-126.
1969. Animals and man: communication and its development. *In* Roslansky, J. D. (ed.), Communication. Amsterdam, North Holland Publ. Co., pp. 25-62.

Marler, Peter, and Linda Hobbett
1975. Individuality in a long-range vocalization of wild chimpanzees. Zeitschr. für Tierpsychologie, vol. 38, pp. 97-109.

McIlhenny, E. A.
1935. The Alligator's life history. Boston, The Christopher Publ. House, pp. 1-117 (reprinted by the Society Study of Amphibians and Reptiles, 1976).

Medem, Federico
1972. El primer nacimiento de *Paleosuchus palpebrosus*. Academia colombiana de ciencias exactas fisicas y naturales, vol. 14, pp. 33-36.

Modha, M. L.
1967. The ecology of the Nile crocodile (*Croco-dylus niloticus* Laurenti) on Central Island, Lake Rudolf. East African Wildlife Jour., vol. 5, pp. 74-95.

Mook, Charles C.
1923. Skull characters of *Alligator sinense* Fauvel. Bull. Amer. Mus. Nat. Hist., vol. 48, pp. 553-562.
1925. The ancestry of alligators. Natural History Magazine, vol. 25, pp. 407-408.

Morton, Eugene
1975. Ecological sources of selection on avian sounds. Amer. Nat., vol. 108, pp. 17-34.

Neill, Wilfred T.
1946. Notes on *Crocodylus novae-guinea*. Copeia, 1946, pp. 17-20.
1971. The last of the ruling reptiles—alligators, crocodiles and their kin. New York, Columbia Univ. Press, pp. 1-486.

Ogden, John, and Caulion Singletary
1973. Night of the crocodile. Audubon Magazine, vol. 75, pp. 32-37 (May).

Petrinovich, Lewis
1974. Individual recognition of pup vocalization by northern Elephant Seal mothers. Zeitschr. für Tierpsychologie, vol. 34, pp. 308-312.

Petrinovich, Lewis, Thomas Patterson, and Harmon V. S. Peeke
1976. Reproductive condition and the response of white-crowned sparrows (*Zonotrichia leucophrys nuttali*) to song. Science, vol. 191, pp. 206-207.

Pooley, A. C.
1969. Preliminary studies on the breeding of the Nile crocodile *Crocodylus niloticus* in Zululand. Lammergeyer, vol. 10, pp. 22-44.
1974. Parental care in the Nile crocodile: a preliminary report on behavior of a captive female. *Ibid.*, vol. 21, pp. 43-45.
1976. Mother's day in the crocodile pool. Animal Kingdom, New York Zoological Society, vol. 79, pp. 7-13.

Pooley, Anthony C., and Carl Gans
1976. The Nile crocodile. Sci. Amer., vol. 234, pp. 114-124 (April).

Reese, Albert M.
1915. The alligator and its allies. New York, G. P. Putnam's Sons, pp. 1-358.

Regal, Philip J.
[In Press]. Behavioral differences between reptiles and mammals: an eco-evolutionary analy-sis. *In* Greenberg, Neil B. and Paul McLean (eds.), The behavior and neurology of lizards. Dept. Health, Educ., and Welfare. Washington, DC.

Schaller, George B.
1963. The mountain gorilla: ecology and behavior. Chicago, Univ. Chicago Press, pp. 1-431.

Sill, William D.
1968. The zoogeography of the Crocodilia. Copeia, 1968, pp. 76-88.

Silverstone, P. A.
1972. Final report of a study of the behavior of the American alligator (*Alligator mississippiensis*) at the Fort Pierce, Florida Bureau of the Smithsonian Institution. Unpublished report, pp. 1-55 (available from the Smithsonian Inst., Washington, D.C.).

Smith, E. N.
1975. Thermoregulation of the American alligator, *Alligator mississippiensis*. Phys. Zool., vol. 48, pp. 177-194.

Smith, W. John
1968. Message-meaning analyses. *In* Sebeok, Thomas A. (ed.), Animal communication. Bloomington, Univ. Indiana Press, pp. 44-60.
1969. Messages of vertebrate communication. Science, vol. 165, pp. 145-150.

Struhsaker, Thomas T.
1967. Auditory communication among vervet monkeys (*Cercopithecus aethiops*). *In* Altmann, Stuart A. (ed.), Social communication among primates. Chicago, Univ. Chicago Press, pp. 281-324.

Tavolga, William N.
1971. Sound production and detection. *In* Hoar, W. S. and D. J. Randall (eds.), Fish physiology, vol. V. New York, Academic Press, pp. 135-205.

Thorpe, W. H.
1968. Perceptual basis for group organization in social vertebrates, especially birds. Nature, vol. 220, pp. 124-128.
1972. The lower vertebrates and invertebrates. *In* Hinde, Robert A. (ed.), Non-verbal communication. Cambridge, the Univ. Press, pp. 127-151.

Varona, Luis
1966. Notas sobre los crocodilidos de Cuba y descripcion de una nueva especie del Pleistoceno. Poeyana, Instituto de Biologia Cuba, Serie A, no. 16, pp. 1-34.

Watanabe, Myrna E.
  [MS]. Nest opening by an American alligator.
Wever, Ernest Glen
  1971. Hearing in the crocodilia. Proc. Natl. Acad. Sci. USA, vol. 68, pp. 1498-1500.
Whitaker, R.
  1974. Notes on behavior, ecology, and present status of the marsh crocodile (Crocodylus palustris) in south India. Mimeographed report, pp. 1-22 (available from Madras Snake Park Trust, Guindy Deer Sanctuary, Madras 600 022 India).
White, Theodore E.
  1942. A new alligator from the Miocene of Florida. Copeia, 1942, pp. 3-7.
Wilson, Edward O.
  1975. Sociobiology. The new synthesis. Cambridge, the Belknap Press of Harvard Univ. Press, pp. 1-697.