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Social Displays of the American Alligator (*Alligator mississippiensis*)[1]

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SYNOPSIS. Adult alligators perform two conspicuous social displays, bellows and headslaps. Both of these behaviors are performed from a "head oblique tail arched" (HOTA) posture. Bellow displays, by both males and females, involve the production of a loud, roaring vocalization. Male alligators also produce a infrasonic signal, termed subaudible vibrations, just prior to the audible bellow. Bellowing occurs throughout the year but is most frequent during the courting season, when alligators bellow daily in choruses. Chorus length appears to be correlated with the size of the adult population. Chorusing is frequently initiated by females but seems to be perpetuated by male alligators. Bellowing may serve to attract alligators of the opposite sex and possibly to space out animals of the same sex.

The headslap display is an assertion display consisting of eight component behavioral acts: the elevated posture, HOTA posture, subaudible vibrations, headslap, jawclap, growl, inflated posture, and tail wag. Each act component is variable in presence and intensity producing a highly variable, graded signal. The alligator typically remains motionless in the HOTA posture for about 16 sec before executing the headslap/jawclap acts. The headslap display involves a rapid clapping shut of the jaws as the undersurface of the head is slapped against the water surface. Headslapping is most common in early morning and afternoon hours. Analysis of 1,050 headslap displays by 91 known individuals indicates that 94.5% of the observed displays were performed by males. Headslap displays are generally performed from typical display sites which the alligator seeks out prior to the display. Responses to headslap displays include headslapping by others, lunges, approaches, and bellow growling. The headslap display functions as a declaration of presence.

A musky odor is commonly detected in association with both of these social displays, suggesting a possibly important, but little understood, pheromonal component of these behaviors.

The displays both involve complex signals including visual, auditory, olfactory and possibly tactile channels of communication. Most of the behaviors described are shared with many other species of crocodilians.

INTRODUCTION

The study of the social behavior of crocodilians is still in its infancy. Although crocodilians are large, conspicuous, and were, at least historically, common components of their aquatic communities, until recently little but anecdotal observations had been made on them. Accounts of encounters with the American alligator (*Alligator mississippiensis*) fill the notes of many early explorers and settlers of the southeastern United States. Most are highly embellished but include many interesting observations of the alligator's behavior and natural history. Records dating from the late 1500s describe the roaring bellows of alligators resounding through the southern swamplands. Bartram's (1791) florid writings include accounts of bellowing, nesting and the aggressive nature of the alligator. Bartram (1791) and Audubon (1827) both comment on the enormous concentrations of alligators in large southern rivers.

Most early scientific studies of the alligator concentrated on descriptions of their morphology and physiology (Clarke, 1891; Reese, 1907, 1915; Coulson and Hernandez, 1964). However, Harper (1930) and McIlhenny (1935) contributed important observations of the natural history of the alligator obtained during years of close association with the animals in the wild.

In the 1960s, detailed studies of the ecology of the Nile crocodile (*Crocodylus niloticus*) began to emerge, providing the first

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systematic observations of the behavior of any crocodilian species (Cott, 1961; Modha, 1967; Pooley, 1969). Interest in the biology of the American alligator grew in the United States (Joanen, 1969; Joanen and McNease, 1970, 1971). As details of these studies emerged, a picture developed of behavior far more complex than that of any other reptile group yet studied.

Detailed observations of crocodilian behavior required study of the animals under captive conditions. Herzog (1974) and Garrick and Lang (1975, 1977*a*, *b*) studied aspects of the social behavior of American alligators in alligator farms in Florida. Their combined efforts (Garrick *et al.*, 1978) provided the most complete description of behavior and communication of any crocodilian species.

In 1981, I began working with a captive alligator population, primarily to gather sufficient data for a detailed analysis of courtship behaviors (Vliet, 1986, 1987). The study allowed comparison, verification, and further quantification of the behaviors described in the earlier works cited above. I used a large number (*ca.* 160) of adult study animals, each individually tagged and of known sex and size. Working at the St. Augustine Alligator Farm (SAAF) in northeastern Florida, I recorded observations of behavior during the courtship season, April through the beginning of June, from 1981 to 1983. Data were collected during more than 850 hr of observation. The study site was a lake of approximately ¼ hectare surface area traversed by a wooden boardwalk from which observations were made. A detailed description of the study site and methods is provided in Vliet (1987). The majority of observations of courtship and other social behaviors were made from distances as close as 3 m and not greater than 25 m. Observations were recorded on audio cassette, 35 mm slide film, 8 mm film, and ½ inch video for analysis.

Alligators commonly perform two conspicuous social displays, bellowing and headslapping, during the courting season as well as at other times of the year. Information from observations of more than 1,200 timed observations of bellowing and 2,000 headslapping displays, performed by individuals of known size and sex, collected during the SAAF study, allowed a more detailed description of these behaviors than had been possible in the past.

BELLOWING

Introduction

Crocodilians are quite vocal relative to other reptile groups and alligators are among the most vocal of the crocodilians (Campbell, 1973; Gans and Maderson, 1973; Herzog and Burghardt, 1977). References to alligator vocalizations, as early as 1564, were among the first recorded observations of alligator behavior (Neill, 1971). Harper (1930) and McIlhenny (1935) both mentioned the loud roaring vocalizations produced by the male alligator during the breeding season. Evans and Quaranta (1949) discussed the highly vocal nature of the alligator. Oliver (1955) also described bellowing by males to attract female alligators.

Detailed analysis of these behaviors has occurred only recently. Garrick *et al.* (1978) defined the terms used in describing bellowing displays. The vocalization is referred to as the "bellow," the associated movements from one bellow to the next as a "bellowing cycle," a number of bellowing cycles produced in series is referred to as a "bout," and the combined bouts of all individuals are called a "chorus."

Both male and female alligators bellow (Garrick and Lang, 1977*a*; Vliet, 1986). During the the alligator's breeding season, bellowing occurs almost daily. The bellowing of one animal stimulates others in the population to bellow, eventually forming a bellowing chorus. When bellowing does begin, the chorus spreads very rapidly through the population. Bellowing spread through the study lake in the SAAF study in less than 30 sec. Alligators often responded to the bellowing of an initiating animal within 15 sec.

Behavioral act components

The changes in body posture and associated movement acts in bellowing have been described by many authors

(McIlhenny, 1935; Beach, 1944; Joanen and McNease, 1971; Silverstone, 1972; Fogarty, 1974; Herzog, 1974; and Garrick *et al.*, 1978). A typical sequence of body movements during bellowing by a male alligator is illustrated in Figure 1. Bellowing is composed of four primary body movements.

1. *Inhalation.*—In preparation for bellowing, the alligator raises its head out of the water (Fig. 1A), remains still momentarily, then performs a gulping motion, visibly contracting the laryngeal musculature as if forcing air into its body. The alligator then drops lower in the water (Fig. 1B).
2. *Head oblique tail arched (HOTA) posture.*—Following inhalation, the alligator raises its head to a 30 or 40 degree angle and arches its tail (Fig. 1C) into a posture referred to as the "head oblique tail arched posture" (Garrick *et al.*, 1978).
3. *Subaudible vibrations (SAV).*—In males, the alligator then visibly tenses and produces an infrasonic signal so powerful that water "dances" up around the alligator's torso (Fig. 1D). This signal has been termed "subaudible vibrations" (Garrick and Lang, 1977*a*).
4. *Audible bellow.*—The audible bellow, a deep, roaring vocalization, is produced immediately following the SAV (Fig. 1E). Early authors often claimed that bellows could be heard over distances of a mile or more (Kellogg, 1929; Harper, 1930; McIlhenny, 1935). Although these estimates are extreme, the low frequencies of bellows do carry great distances over open marshes. A sonogram of a 2.86 m male alligator bellow is given in Figure 2. The bellow has a dominant frequency of about 0.1 kHz with harmonics to 0.4 kHz. An artifact of the SAV signal is apparent immediately before each audible bellow.

The bellowing cycle for female alligators differs somewhat from that of males. Female alligators do not produce the SAV signal and the audible bellow of the female is produced as the animal lowers into the water following inflation of the lungs.

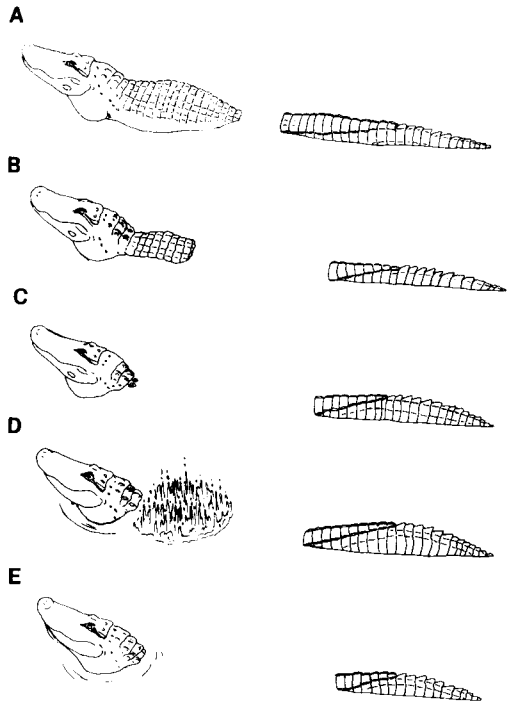

FIG. 1. Body postures and movements associated with the bellowing display in a male American alligator. (A) Inhalation (0.00 sec); (B) lowering (1.33 sec); (C) head oblique tail arched posture (3.78 sec); (D) subaudible vibrations (4.78 sec); and audible bellow (5.40 sec).

Sexual dimorphism in bellowing displays

Characteristics of the bellowing display differ between the sexes. As females do not produce the SAV, the interbellow interval is shorter than that of males and the cadence of female bellowing bouts is more rapid. In the SAAF study, the mean duration of each bellow cycle for female alligators was 5.29 sec (n = 132) as compared to 6.65 sec (n = 352) for males. These values indicate bellowing cycles somewhat longer than those reported by Garrick *et al.* (1978). Females averaged 5.34 bellows per bout (n = 153) while the mean bellows per bout for males was only 4.59 (n = 429). However, the overlap was great enough that the difference is not statistically significant. A frequency distribution of bellows per bout given by alligators at SAAF is shown in Figure 3. On average, an alligator bellows five or six times per bout.

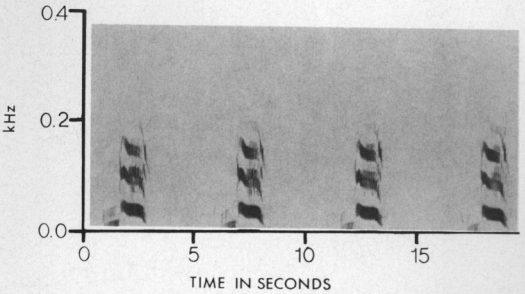

FIG. 2. A sound spectrograph of the bellowing vocalizations of a 2.86 m male American alligator. Artifacts of the "water dance" effect of the subaudible vibrations are visible immediately prior to the audible bellow.

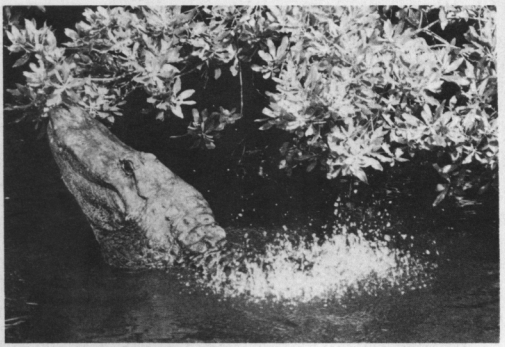

FIG. 4. A photograph of the "water dance," an effect of the subaudible vibrations produced by adult male alligators.

A primary difference between the sexes is the production of the SAV signal in males. The SAV involves the production of an infrasonic acoustic signal from within the torso causing water droplets to be projected up as much as 25 cm above the water surface (Fig. 4). The signal also causes nearby physical objects to vibrate. Very preliminary measurements suggest that the signal has a frequency of approximately 10 Hz (Vliet, 1986). This signal is strongest prior to the first audible bellow and subsequently becomes weaker and of shorter duration with each subsequent bout. The duration of the initial SAV of a 3.2 m male at SAAF was 1.35 sec while that of the fifth bellowing cycle lasted only 0.55 sec. A signal of this frequency should theoretically travel long distances under water. It is conceivable that the SAV signal in association with the bellowing display allows females to locate males during the courting season (Garrick *et al.*, 1978).

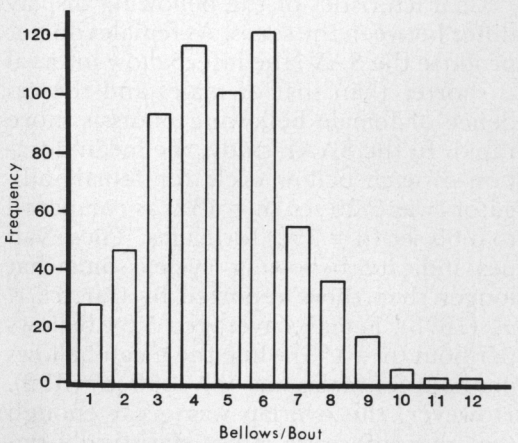

FIG. 3. A frequency distribution of the number of bellows included per bout in bellowing displays of male and female American alligators in April and May 1983 at the St. Augustine Alligator Farm (n = 640).

Vague references to this behavior are scattered throughout the literature of alligator behavior. Bartram's (1791) much maligned descriptions of alligator bellowing included remarks that the bellow was "not only shaking the air and waters, but causing the earth to tremble." Kellogg (1929) noted that the voice of the female was "less tremulous" than that of the male. McIlhenny (1935) included an accurate account of this phenomenon, referring to "tremulous vibrations" during bellowing by a male. His description is the first to clearly mention the "jets" of water "bouncing into the air from the water." Ditmars (1946) also alluded to this behavior and Beach (1944) noted that the "spasmodic jerks" were not produced by a 1.5 m male alligator. More recently, Herzog (1974) clearly referred to this behavior during bellowing, but failed to make note of the sex of the animals. A compilation of behavioral acts by Garrick and Lang (1977*a*) included SAV in bellows by females. In observations of thousands of bouts of bellowing and headslap displays by individually marked animals of known

sex in the SAAF study, females were never observed to produce this signal.

There are very clear examples of sex recognition during bellowing perhaps as a result of perception of the SAV. Alligators of opposite gender often pair up and bellow simultaneously near, or in contact with, one another (Garrick and Lang, 1977*a*; Vliet, 1986, 1987). Females frequently approach bellowing males and twist or wrap their bodies around the head and neck as he continues to bellow. Many of these interactions proceed into courtship encounters (Evans and Qauranta, 1949; Garrick and Lang, 1975), although in captive situations most courtships occur outside of bellowing choruses (Vliet, 1987).

Circannual and circadian patterns

Alligator bellowing may occur at any time of the year although it is a rare occurrence during the coldest months (Garrick *et al.*, 1978). The peak of bellowing activity occurs at the peak of the courting season (Bartram, 1791; McIlhenny, 1935; Joanen and McNease, 1971, 1972, 1975, 1979; Fogarty, 1974; Garrick and Lang, 1977*a*; Garrick *et al.*, 1978; Vliet, 1986). Following the courting season, bellowing choruses continue, but are of shorter duration and are less regular than before (Joanen and McNease, 1971; Herzog, 1974; Garrick *et al.*, 1978).

Sporadic bellowing may be heard at any time of the day or night. However, sustained choruses of bellowing occur only in morning hours (Reese, 1907; Harper, 1930; Herzog, 1974; Garrick *et al.*, 1978; Vliet, 1986). In the breeding season, choruses become a daily occurrence. Periods of bellowing choruses recorded at SAAF in the spring months of 1983 are shown in Figure 5. Through the course of the breeding season, choruses were initiated progressively earlier in the morning (Herzog, 1974; Vliet, 1986). Total length of chorusing per day also increased. In late May, when bellowing activity was at its peak, there were typically two morning choruses; one near dawn, and another later in the morning (Vliet, 1986).

There is evidence that population size

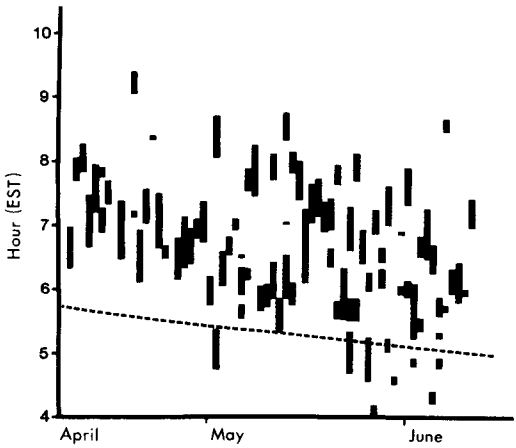

FIG. 5. Temporal distribution of morning bellowing choruses at the St. Augustine Alligator Farm from April through mid-June 1983. Broken line indicates time of sunrise.

may influence the length of bellowing choruses (Vliet, 1986). In a few published records of chorus length, larger populations of captive adult alligators appear to have longer periods of bellowing. Herzog (1974) recorded an average chorus length of 11.3 min for a captive group of 26 adult alligators. Garrick *et al.* (1978) reported that at the peak of bellowing activity for a population of 35 adults, choruses averaged 21.5 min. During the 1983 courting season at SAAF, I found the average length of chorusing per day for a population of more than 350 adult alligators to be 35.4 min ($n = 60$). During the peak period of bellowing, in mid to late May, total chorus lengths averaged more than 55 min per day ($n = 7$).

Female alligators produce a vocalization referred to as a "bellow growl" (Garrick *et al.*, 1978) in response to mostly male activities such as headslapping or approaching for courtship. Bellow growl vocalizations differ from the typical bellows in that the HOTA posture is not assumed before vocalizing (Garrick *et al.*, 1978). At SAAF, I found that bellow growls by female alligators were often the stimulus for bellowing choruses. Frequently females would bellow growl in response to male aggression nearby and then continue to bellow

with the normal movements and cadence of the bellowing display. However, once chorusing had begun, male alligators seemed responsible for perpetuating the bellowing chorus.

Functions of bellowing displays

Numerous reports suggest that bellowing serves as a sexual attractant between alligators of opposite sex (Carr, 1967, 1976; Fogarty, 1974; Garrick, 1975*a*; Vliet, 1986, 1987). Joanen and McNease (1971, 1975) believed bellowing attracts alligators to the open areas of the marsh in which they court. Bellowing may also act as an agonistic signal to alligators of the same sex (Kellogg, 1929; Oliver, 1955). Additionally, bellowing may provide information on the size, sex, location, and possibly social position of the performer (Garrick and Lang, 1977*a*, Garrick *et al.*, 1978). Garrick *et al.* (1978) also speculated that bellowing interactions may serve to synchronize group activity.

Bellowing displays may be instrumental in defining territories or home ranges in the early part of the season. In captive situations, males fight vigorously during bellowing choruses at the beginning of the courtship season (Garrick *et al.*, 1978; Vliet, 1986). Many serious and permanent injuries are sustained in these fights. Males appear to become more tolerant of other bellowing males as the courtship season progresses. There is some evidence that suggests this aggression also occurs in wild populations. Schmidt (1922) reported frequent mutilations of large specimens and suggested this was due to males fighting one another in association with bellowing in the spring. Joanen and McNease (1972) mentioned that there was evidence, in the form of fresh injuries, suggesting that males had recently taken part in combat.

HEADSLAP

Introduction

Alligators of both sexes perform a social display referred to as a headslap (Garrick and Lang, 1977*a*; Garrick *et al.*, 1978). The headslap appears to be a typical reptilian advertisement display, simply indicating the presence and location of the performer (Garrick, 1975*a*; Garrick and Lang, 1977*a*). In its simplest form, the display may involve only an isolated jawclap. In its most intense form, the headslap display includes eight behavioral acts.

Accounts of the headslap display are poorly represented in the older literature. Joanen and McNease (1971) mentioned a "ritualistic biting of the water" by males as a part of courtship. Silverstone (1972) referred to "jaw-smacking" by the male, and rarely by the female, alligators he observed near Fort Pierce, Florida.

BEHAVIORAL ACT COMPONENTS

Garrick and Lang (1977*a*) recognized seven different forms of the headslap display "each resulting from the addition of signal elements." In addition to seven behavioral acts commonly associated with the headslap display, I consider the "elevated posture" to be a good indication that the display will be performed and have thus included it as an additional act component. So, at SAAF, I recognized eight acts commonly associated with the display.

Any of the behavioral act components of the headslap display described below may be included or omitted from a display. Most of these acts are variable in intensity. Consequently, headslap displays are extremely variable, both in content and intensity.

Elevated posture

Alligators preparing to headslap may assume a characteristic body posture here referred to as an "elevated posture." The body is held straight and somewhat elevated so that the entire cranium, nuchal scales, dorsal scalation, pelvis, and much of the dorsal surface of the tail is held above the water surface (Fig. 6A). Alligators may remain in the elevated posture longer than 35 min before performing the display.

Head oblique tail arched posture

A HOTA posture indistinguishable from that of bellowing is assumed in preparation for a headslap display (Fig. 6B). Once positioned, the displayer remains motionless for about 16 sec before rapidly executing the headslap. The body is always held straight during the headslap display.

Rarely, headslap displays are performed from an elevated posture. In intense displays, alligators begin to tail wag before headslapping (Fig. 6C). Garrick *et al.* (1978) state that this posture was assumed in four of the seven cases used in their description of variation of the display. At SAAF, the head oblique tail arched posture was observed in association with more than 99% of the hundreds of headslap displays recorded.

Subaudible vibrations

The SAV display is frequently included with the headslap display (Garrick and Lang, 1977*a*; Vliet, 1986), immediately before or simultaneously with the headslap act itself. As in association with bellowing, the SAV is produced solely by male alligators (Vliet, 1986). It is not included in all male headslap displays performed by adult males. The SAV signal is occasionally presented in series, with as many as eight repetitions before the headslap (Vliet, 1986). Multiple SAVs prior to headslapping were not common at SAAF. In such cases, the first was always the most intense with subsequent SAVs becoming weaker and more rapid, ultimately culminating in a headslap display. Only 12% of the males exhibited multiple SAVs and, of these, none performed them in more than 36% of their observed headslap displays.

Headslap

Generally presented simultaneously with the jawclap, the headslap involves a vigorous and sudden slap of the undersurface of the alligator's head against the water surface (Fig. 6D).

Jawclap

The jawclap consists of a rapid opening and snapping shut of the alligator's jaws, producing a loud (67 db at 4.5 m [Herzog, 1974]) percussive sound (Fig. 6E). The jawclap can be heard at least 200 m through air and probably even farther underwater (Garrick and Lang, 1977*a*).

The presentation of the jawclap is highly variable. Very rarely, an animal performs two jawclaps in series separated by only a few seconds (Vliet, 1986). Jawclaps may also

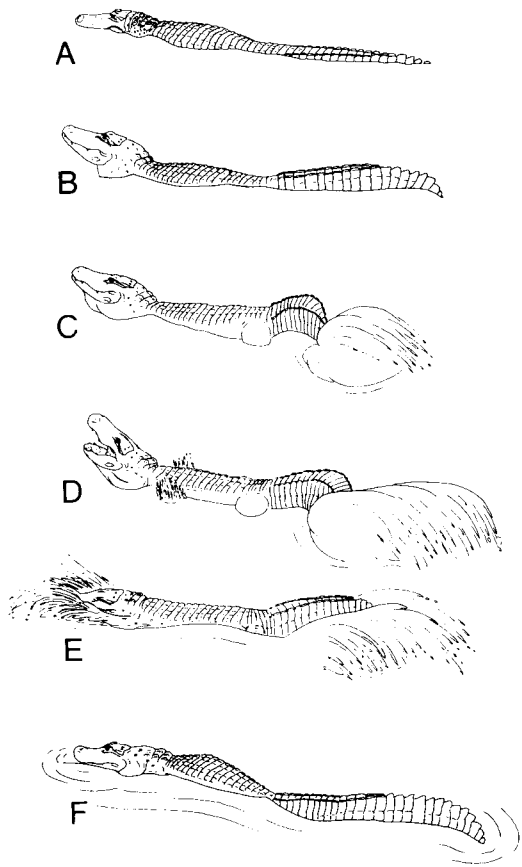

FIG. 6. Body postures and movements associated with the headslap display of a male American alligator. (A) An alligator in the "elevated posture," assumed prior to performance of the headslap display; (B) head oblique tail arched posture (0.00 sec); (C) tail wag begins (17.22 sec); (D) headslap with subaudible vibrations (17.33 sec); (E) jawclap (17.39 sec); and (F) inflated posture (at 33.50 sec).

be presented without an accompanying headslap. Alligators performing jawclap displays on land rarely include the headslap behavioral act in the display. Conversely, headslaps are only very rarely performed without an accompanying jawclap. In a nonsocial context, the jawclap is also used by alligators toward human intruders (Bartram, 1791; Garrick and Lang, 1977*a*).

Growl

Alligators often produce a gutteral growl just before, during, or immediately after the headslap/jawclap. The growl has a fre-

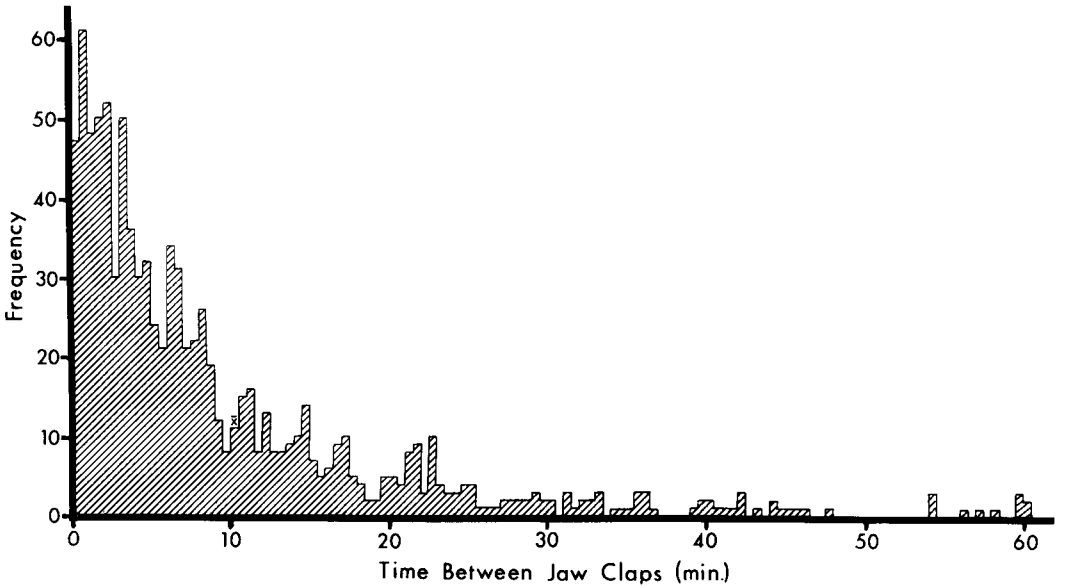

FIG. 7. A frequency histogram of time intervals between more than 900 headslap displays recorded in April 1983 at the St. Augustine Alligator Farm. Several intervals of greater than 60 min are not represented.

quency of approximately 100 Hz (Garrick *et al.*, 1978). It is performed mostly by males. However, a few headslap displays performed by females also include a growl.

Inflated posture

Following the headslap/jawclap display, the alligator typically rises into a conspicuous body posture (Fig. 6F) referred to as an inflated posture (Garrick *et al.*, 1978). The legs are extended fully, the back arched, and the tail is held at or above the water surface. The head may be held either above or below the water level, and the mouth may be open or remain closed.

Tail wag

While in the inflated posture, alligators generally perform a "tail wag" (Silverstone, 1972; Garrick and Lang, 1977*a*; Garrick *et al.*, 1978), undulating the tail vigorously from side to side, and thus violently churn the water. In the most intense displays, tail wagging is initiated before the headslap and intensifies following the display.

BEHAVIORAL ACT CADENCE

The cadence of the headslap display is relatively stereotyped. The length of time the HOTA posture is maintained before execution of the jawclap averaged 16.2 sec (n = 113) in the SAAF study. Garrick *et al.* (1978) reported a maximum pause of 45 sec and Herzog (1974), a maximum of 75 sec. At SAAF, I noted that alligators appeared cautious at this time and often suspended the display momentarily. Following this motionless period, the headslap/jawclap is performed rapidly, within 0.08 and 0.15 sec (Garrick *et al.*, 1978).

Headslapping displays are contagious (Garrick *et al.*, 1978; Vliet, 1986). The headslap of one animal causes others to headslap. However, the response may be more than 15 min after the first display (Vliet, 1986). This very long response time may be the result of alligators selecting a display site before displaying (see below). Once in position, the animal either initiates the display performance, or waits for another animal to headslap. As a result, headslaps are grouped in time; several displays occur within 15 or 20 min and then there are no displays for the next 45 min or an hour. Figure 7 illustrates the time intervals between more than 900 headslap displays recorded in the SAAF study. Although the average interval was more than 10 min, the modal classes are of very

short intervals of less than 1 min, indicating the clumped nature of these displays. Although even large males typically do not headslap more than two or three times in a day, rarely, in the SAAF study, I noted that some males headslapped twice within as little as 6 min.

Alligators in Florida perform headslapping displays throughout the year. However, there is seasonal variation in the frequency of this behavior. Silverstone (1972) and Garrick *et al.* (1978) indicated that headslapping was most frequent in the breeding season.

Within the breeding season, there is considerable variation throughout the day in the frequency of the display as well. Garrick *et al.* (1978) found headslapping to be primarily a morning activity with 81% of all such displays recorded before noon. At SAAF, the frequency of headslapping through the day (Fig. 8) showed a more complex pattern (Vliet, 1986). Headslapping was a very frequent activity in early morning (*ca.* 4.5/hr) but lessened as most of the animals moved up into basking areas. After basking, animals moved back into the water and the frequency once again increased (*ca.* 6/hr) in early afternoon. A late afternoon basking period caused another drop in the likelihood of the display. This was followed by a final increase near dusk. Headslapping occurs often at night but no quantitative data exist to compare with daytime frequencies.

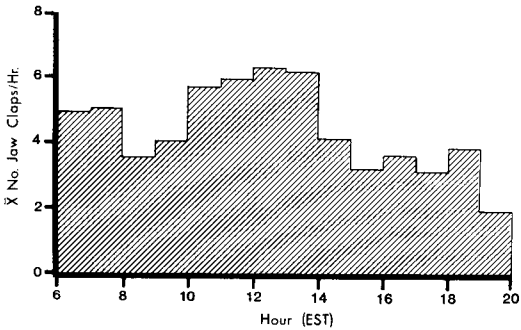

FIG. 8. Average hourly frequency of headslap displays recorded in April 1983 at the St. Augustine Alligator Farm.

SEXUAL DIMORPHISM IN HEADSLAP DISPLAYS

In the SAAF study, during approximately 395 hr of behavioral observation in the 2 mo period from 8 April through 7 June 1983, a total of 2,073 headslap displays were documented. In 1,050 of these, I determined the individual identity of the alligator performing the displays. Male alligators performed headslap displays much more frequently than did females. Most (95.5%) of the males (n = 66) in the study population were observed to headslap while only 43.1% of the females (n = 65) were identified performing displays. These males (n = 63) averaged 15.5 headslap displays per individual during the period of observation while those females that did display (n = 28) averaged only 2.4 observed headslap displays. As a result only 5.5% of the 1,050 headslaps recorded from identified alligators where performed by females. Female displays tend to be less intense, and less complex, than most male displays (Silverstone, 1972; Vliet, 1986). I found no correlation between body size and frequency of headslap displays for either sex. However, Garrick *et al.* (1978) stated that dominant males and females headslapped more often than subordinate animals.

DISPLAY SITE SELECTION

The SAAF study indicated that alligators actively seek out specific display sites from which the headslap display is performed (Vliet, 1986). Animals often position themselves in these display sites for as long as 35 min before they actually perform the display. Frequently used display sites were most often against the shore (87% within 0.6 m). More than one third of the display sites were covered by overhanging vegetation or structures. Secluded locations in backwaters or cuts in the bank were often preferred as headslap display sites. A few displays were performed in open water (*ca.* 1%) or on land (5.5%).

OBSERVED RESPONSES

In addition to stimulating headslapping activity in other alligators, several common responses to headslap behavior have been observed. These include lunges by male alligators, bellow growl vocalizations by females, swimming away from or ap-

proaching the displayer and approaches followed by courtship (Garrick *et al.*, 1978).

Lunges are performed exclusively by male alligators. Immediately following a headslap display, the lunging animal propels itself forward, charging through the water. Lunges are not always directed toward the displaying alligator; they can be directed at an angle to the displayer. Most lunges do not culminate in contact between the animals although attacks and bites do occasionally occur. Lunges may be elicited from animals as much as 15 m from the displaying animal.

As mentioned previously, female alligators, especially small adults, produce a bellow growl vocalization in response to nearby agonistic interactions or when approached by a large male (Garrick and Lang, 1977*a*; Vliet, 1986). This vocalization is also very rarely made by very small (<220 cm) males (Vliet, 1987). Females respond with bellow growls to headslapping displays or fights between males from as much as 15 m away.

Headslap displays frequently elicit the approach of other alligators (Garrick, 1975*a*; Garrick and Lang, 1975; Garrick and Lang, 1977*a*; Vliet, 1986, 1987). Garrick and Lang (1977*a*) reported animals approaching from as far as 50 to 75 m. Displayers are occasionally approached by alligators of the opposite sex. This fact led Garrick *et al.* (1978) to consider headslap displays as courtship advertisement displays. In the SAAF study, approaches following headslaps lead to courtship only rarely (Vliet, 1986, 1987), in less than 1% of the headslap displays observed.

FUNCTION OF HEADSLAP DISPLAY

The function of the headslap display might best be described as a declaration of presence (Garrick *et al.*, 1978). Like other reptilian assertion displays, it seems to serve to advertise the location of an alligator, frequently being presented soon after an alligator has arrived at a new area or just before it leaves an area. The contagious nature of the display suggests that it might play some role in establishment and maintenance of dominance or hierarchical relationships. In the captive population studied by Garrick *et al.* (1978), the majority of headslaps were performed by the most dominant males and females. However, in the SAAF study, the frequency of headslapping by an individual was not correlated with size or other behaviors that might indicate dominance, such as lunging or courtship activity. The fact that headslap displays do occasionally lead to courtship suggests a small sexual component to the display.

DISCUSSION

These two social displays, bellowing and headslapping, form an integral part of the social communication of adult American alligators. Ontogenetically, these displays are first performed while the alligators are still subadults. I have seen alligators at 1.1 m total length perform headslap displays and alligators slightly smaller attempting to bellow.

The displays are complex, involving stimuli to several sensory apparati, including visual, auditory, olfactory, and probably tactile cues. The aquatic environment in which these signals are transmitted and received undoubtedly enhances the alligator's ability to perform these complex social displays, allowing easy mobility and rapid transmission of signals as well as emphasizing visual signals at the water surface.

Many authors have noted an association between bellowing activity and reproductive activity in crocodilians. In addition to repeated references to this for *Alligator mississippiensis* (Schmidt, 1922; Beach, 1944; Fogarty, 1974; Garrick and Lang, 1975, 1977*a*; Joanen and McNease, 1975; Garrick *et al.*, 1978), it has also been reported in the spectacled caiman, *Caiman crocodilus* (Alvarez del Toro, 1969), the American crocodile, *Crocodylus acutus* (Alvarez del Toro, 1974), the Nile crocodile, *Crocodylus niloticus* (Cott, 1961), and the saltwater crocodile, *Crocodylus porosus* (Deraniyagala, 1939).

Garrick and Lang (1977*a*) and Garrick *et al.* (1978) suggested that the highly vocal nature of the alligator might be an adaptation to the marsh habitats in which they

live, which are dense and thus restrict the importance of visual signals in social communication.

The headslap display appears to have evolved to maximize several cues well suited for the water surface environment in which the alligator lives. The display has a number of components that function to make the alligator conspicuous. Visual components include the HOTA posture, the inflated posture following the headslap, and possibly the "water dance" visual effect of the SAV. The HOTA and the inflated postures are held for a period of time sufficient for other alligators to recognize the location, and possibly the size or identity, of the displaying alligator. Auditory components of the display, consisting of the jawclap and the growl, draw the attention of nearby animals. Additionally, the headslap act provides an underwater, percussive signal. The tail wag possibly adds a tactile component to the display by producing surface waves which may be felt by alligators some distance away. Males also incorporate the SAV, a gender-specific signal that might be perceived underwater throughout the lake. Interestingly, despite the conspicuous nature of the headslap display, alligators choose secluded display sites from which to perform the display.

The use of olfactory cues in alligator social communication has not been clearly demonstrated. Alligators of both sexes have two pairs of scent or musk glands, one just medial to the mandible on the underside of the jaw and another in the lateral walls of the cloaca (Bell, 1827; Reese, 1921). Many authors observe that the mandibular glands are everted and musky fluid is ejected during bellowing (Schmidt, 1922; Kellogg, 1929; LeBuff, 1957). Others (Beach, 1944; Silverstone, 1972; and Garrick *et al.*, 1978) say there is no detectable scent during bellowing. McIlhenny (1935) thought musk could be smelled but saw no ejected liquids. Neill (1971) stated that glands were not everted in bellowing and no scent was noticeable.

During the course of the SAAF study, I detected musk at some point during most bellowing choruses (Vliet, 1986). Mandibular glands are occasionally everted during bellowing although this is unusual. In air, musk remains concentrated in trails, and is not easily detected unless one moves through a trail. The wooden boardwalk at SAAF allowed easy movement around the study lake and through these trails of musk.

In many headslap displays and aggressive encounters, I also have noted areas of oily sheen on the water, usually near the cloaca of the animal. Musk is most easily detected when near the animal, especially at water level. Perhaps the primary mode of transmission of alligator musk is on the water surface and not through the atmosphere.

The importance of the SAV signal in crocodilian social communication has not been explicitly stated. References to similar behavior in other species of crocodilians include the Nile crocodile, *Crocodylus niloticus* (Modha, 1967), the American crocodile, *Crocodylus acutus* (Garrick and Lang, 1977*a*), the New Guinea crocodile, *Crocodylus novaeguineae* (Lang, 1980), the Chinese alligator, *Alligator sinensis* (Garrick, 1975*b*) and the spectacled caiman, *Caiman crocodilus* (Herzog, 1974). I have also observed the SAV in a male of the Orinoco crocodile, *Crocodylus intermedius.* It seems likely that most, if not all, species of crocodilians use this signal in social communication.

The density of the study population at SAAF was much higher than that of other captive alligator populations in which behavior was previously studied (Herzog, 1974; Garrick *et al.*, 1978). More than 150 adult alligators were kept in the 0.25 ha lake at SAAF while only 35 adults were enclosed in the 0.9 ha lake studied by Garrick and Lang (Garrick *et al.*, 1978). In spite of the very high density, the social behaviors observed at SAAF (Vliet, 1986, 1987) differ little from those described by Garrick *et al.* (1978). The most striking differences arise in the frequency of displays performed by subordinate alligators. Garrick *et al.* (1978) reported that dominant male and female alligators performed the majority of courtship and headslap displays. Although courtship activity was correlated with size at SAAF (Vliet, 1987), the

frequency of headslapping was not clearly associated with dominance. In very high captive alligator densities, dominant/subordinate social structures may break down. Although very large males were still clearly dominant in agonistic encounters, smaller, subordinate alligators did perform many social displays.

The behavioral act components of social displays for all crocodilian species are remarkably similar. Most of the signals described above are also reported from other crocodilian species, although bellows are sufficiently distinct from the roaring vocalizations of other crocodilians to be considered unique (Garrick and Lang, 1977*a*; Garrick *et al.*, 1978). Species differences arise not in the types of behaviors utilized but in the order and combination of which acts are performed. The living species of crocodilians are relicts of a once more diversified group of reptiles (Romer, 1966). The few species that have survived to modern times are relatively conservative in their morphology. These remnant species seem to have been conservative in the evolution of their social displays as well.

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REFERENCES

Alvarez del Toro, M. 1969. Breeding the spectacled caiman, *Caiman crocodilus* at Tuxtla Gutierrez Zoo. Int. Zoo Yrbk. 9:35–36.

Alvarez del Toro, M. 1974. *Los Crocodylia de Mexico.* Inst. Mexicano de Recursos Naturales Renovables.

Audubon, J. J. 1827. Observations on the natural history of the alligator. Edinburgh New Philos. J. 2:270–280.

Bartram, W. 1791. *Travels through North and South Carolina, Georgia, east and west Florida.* James and Johnson, Philadelphia.

Beach, F. 1944. Responses of captive alligators to auditory stimulation. Amer. Nat. 78:481–505.

Bell, T. 1827. On the structure and use of the submaxillary odiferous gland in the genus *Crocodilus.* Phil. Trans. Royal Soc. London 117:132–138.

Campbell, H. H. 1973. Observations on the acoustic behavior of crocodilians. Zoologica 58:1–11.

Carr, A. F. 1967. Alligators: Dragons in distress. Nat. Geogr. 131(1):133–149.

Carr, A. F. 1976. Excerpts from the life of an alligator: A reappraisal of "The alligator's life history." *In* E. A. McIlhenny, *The alligator's life history,* pp. v–x. Facsimile reprint. Society for the Study of Amphibians and Reptiles Misc. Publ.

Clarke, S. F. 1891. The habits and embryology of the American alligator. J. Morph. 5:181–206.

Cott, H. 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 29:211–356.

Coulson, R. A. and T. Hernandez. 1964. *Biochemistry of the Alligator. A study of metabolism in slow motion.* Louisiana State University Press, Baton Rouge.

Deraniyagala, P. E. P. 1939. *The tetrapod reptiles of Ceylon.* Vol. 1. *Testudinates and crocodilians.* Colombo.

Ditmars, R. L. 1946. *The reptiles of North America.* Doubleday, New York.

Evans, L. T. and J. Quaranta. 1949. Vocality, a factor in the ecology of the alligator. Anat. Rec. 105: 581–582.

Fogarty, M. J. 1974. The ecology of the Everglades alligator. *In* P. J. Gleason (ed.), *Environments of South Florida: Past and present,* pp. 367–373. Mem. Miami Geol. Survey No. 2.

Gans, C. and P. Maderson. 1973. Sound production mechanisms in Recent reptiles: Review with comments. Amer. Zool. 13:1195–1203.

Garrick, L. D. 1975*a*. Love among the alligators. Anim. Kingdom 79(2):2–8.

Garrick, L. D. 1975*b*. Structure and pattern of the roars of Chinese alligators (*Alligator sinensis* Fauvel). Herpetologica 31:26–31.

Garrick, L. D. and J. W. Lang. 1975. Alligator courtship. Amer. Zool. 15(3):813.

Garrick, L. D. and J. W. Lang. 1977*a*. Social signals and behavior of adult alligators and crocodiles. Amer. Zool. 17:225–239.

Garrick, L. D. and J. W. Lang. 1977*b*. The alligator revealed. Natural History June/July:54–60.

Garrick, L. D., J. W. Lang, and H. A. Herzog, Jr. 1978. Social signals of adult American alligators. Bull. Am. Mus. Nat. Hist. 160(3):153–192.

Harper, F. 1930. Alligators of the Okefenokee. Sci. Monthly 31:51–67.

Herzog, H. A. 1974. The vocal communication system and related behaviors of the American alligator (*Alligator mississippiensis*) and other crocodilians. Master's Thesis, University of Tennessee, Knoxville.

Herzog, H. A. and G. M. Burghardt. 1977. Vocalization in juvenile crocodilians. Z. f. Tierpsychol. 44(3):294–304.

Joanen, T. 1969. Nesting ecology of alligators in Louisiana. Proc. 23rd Ann. Conf. Southeast. Assoc. Game Fish Comm. 1969:141–151.

Joanen, T. and L. McNease. 1970. A telemetric study of nesting female alligators in Rockefeller Refuge, Louisiana. Proc. 24th Ann. Conf. Southeast. Assoc. Game Fish Comm. 1970:175–193.

Joanen, T. and L. McNease. 1971. Propagation of the American alligator in captivity. Proc. 25th Ann. Conf. Southeast. Assoc. Game Fish Comm. 1971:106–116.

Joanen, T. and L. McNease. 1972. A telemetric study of adult male alligators on Rockefeller Refuge, Louisiana. Proc. 26th Ann. Conf. Southeast. Assoc. Game Fish Comm. 1972:252–275.

Joanen, T. and L. McNease. 1975. Notes on the reproductive biology and captive propagation of the American alligator. Proc. 29th Ann. Conf. Southeast. Assoc. Game Fish Comm. 1975:407–415.

Joanen, T. and L. McNease. 1979. Culture of the American alligator. Int. Zoo Yybk. 19:61–66.

Kellogg, R. 1929. The habits and economic importance of alligators. U.S. Dept. Agric. Tech. Bull., no. 147:1–36.

Lang, J. W. 1980. Reproductive behaviors of New Guinea and saltwater crocodiles. Abstract, SSAR-HL meeting, 6–10 August, Milwaukee, Wisconsin.

LeBuff, C. R. 1957. Observations on captive and wild North American crocodilians. Herpetologica 13(1):25–28.

McIlhenny, E. A. 1935. *The alligator's life history.* Christopher Publishing House, Boston.

Modha, M. L. 1967. The ecology of the Nile crocodile (*Crocodylus niloticus* Laurenti) on Central Island, Lake Rudolf. E. Afr. Wildl. J. 5:74–95.

Neill, W. T. 1971. *The last of the ruling reptiles: Alligators, crocodiles, and their kin.* Columbia University Press, New York. 486 pp.

Oliver, J. A. 1955. *The natural history of North American amphibians and reptiles.* Van Nostrand, Princeton, N.J.

Pooley, A. C. 1969. Preliminary studies on the breeding of the Nile crocodile *Crocodylus niloticus* in Zululand. Lammergeyer 10:22–44.

Reese, A. M. 1907. The breeding habits of the Florida alligator. Smithsonian Misc. Coll. Quart. Issue 3:381–387.

Reese, A. M. 1915. *The alligator and its allies.* Putnam's, New York.

Reese, A. M. 1921. The structure and development of the integumental glands of the Crocodilia. J. Morph. 35(3):581–611.

Romer, A. S. 1966. *Vertebrate Paleontology,* 3rd ed. Univ. Chicago Press, Chicago.

Schmidt, K. P. 1922. The American alligator. Field Mus. Nat. Hist. leaflet #3:25–38.

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. Unpubl. report.

Vliet, K. A. 1986. Social behavior of the American alligator. In *Crocodiles,* pp. 203–211, IUCN Publ., new ser., Caracas.

Vliet, K. A. 1987. A quantitative analysis of the courtship behavior of the American alligator (*Alligator mississippiensis*). Ph.D. Diss., University of Florida, Gainesville.