Vocalization in juvenile crocodilians

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With 9 figures

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Abstract

The study is an analysis of the vocalizations of juvenile American alligators (*Alligator mississipiensis*) and three other crocodilian species (*Caiman crocodilus, Crocodylus niloticus,* and *Crocodylus siamensis*). Sonagrams of the calls are presented along with relevant behavioral correlates of the vocalization. The findings are discussed in light of current knowledge of the bioacoustics of other vertebrates.

Introduction

Reptiles are a relatively silent group of vertebrates, but recent studies have demonstrated that some species of crocodilians have a sophisticated repertoire of auditory signals which occur in a variety of contexts (Campbell 1973; Garrick 1975; Herzog 1974). This report presents an analysis of the vocalizations of juvenile American alligators (*Alligator mississipiensis*) and other crocodilians which was undertaken as part of a larger investigation of the acoustic communication systems of crocodilians.

Numerous writers have observed that young American alligators (*Alligator mississipiensis*) begin to grunt while still in the egg. Most observers have ascribed the function of prehatch grunting as an auditory signal releasing nest opening by the female parent (Evans 1961; McIlhenny 1935; Reese 1915). Though some authorities (Neill 1971; Lebuff 1957) have denied the existence of nest opening in alligators, the bulk of evidence indicates that nest opening to aid in the release of hatchlings occurs in at least some ♀♀ (Herzog 1975; Joanen 1969). It is probable that the grunt stimulates nest opening by adults in other crocodilian species including *Crocodylus niloticus* (Pooley 1969, 1974; Pooley and Gans 1976), *Caiman crocodilus* (Alvarez del Toro 1969), *Crocodylus acutus* (Ogden and Singleteary 1973), and *Crocodylus moreletii* (Hunt 1973). It has also been suggested that grunting in the egg may serve to coordinate and synchronize hatching (Lee 1968) though experimental evidence is lacking.

Controversy exists as to the nature and function of the grunt after hatching. NEILL (1971) claimed that the grunt should be distinguished from a juvenile distress call, which has greater volume, higher pitch, and is segmented. He claimed that the distress call had a higher "behavioral threshold" than the grunt, which could be stimulated by various environmental changes such as a moving object, loud noise, or food. The function of the grunt was claimed to be the alerting of nearby adults to the presence of juveniles. NEILL suggested that a distress call is elicited only by seizing the young alligator roughly. Any alligator hearing this call would respond with an attack directed toward whatever was harassing the juvenile. NEILL also claimed that when an alligator reached the length of about four feet it would begin to bellow, cease giving the grunt or distress call, and begin to make the characteristic adult response when encountering the distress call of a younger animal. But MCILHENNY (1935) claimed to have heard grunting in an adult during a fight as it was being held in the jaws of another adult and POPE (1955) also stated that grunts are sometimes made by adults. NEILL concluded that grunts and distress calls are two distinct vocalizations which occur in most species of crocodilians with only minor interspecific differences.

CAMPBELL (1973) used a sound spectrograph to analyse juvenile vocalizations in four species (*Alligator mississipiensis, Caiman crocodilus, Crocodylus acutus,* and *Melanosuchus niger*) and concluded that there is no consistent acoustic difference between the grunt (CAMPBELL's "bark") and the distress call. He suggested that distinctions between the two types of calls were based only on the observer's interpretation of the significance of the sound. The vocalization was given in a variety of contexts and probably functioned to alert groups of young to environmental changes, to maintain group cohesiveness, and to release nest opening by a parent. He reported that there is a greater tendency for spontaneous grunts to be emitted by baby alligators under conditions of reduced visibility (night). Though there were some differences found between species in the readiness to vocalize, sonagrams of the calls of all four species were quite similar. The present study further examines the acoustic properties and behavioral context of vocal signals of juvenile American alligators and other species of crocodilians. Sonagrams representative of the calls are presented.

Methods

Subjects and Study Sites

Observations and tape recordings were obtained at the Silver Springs Reptile Institute in Silver Springs, Florida, a commercial animal exhibit that during the study period housed 103 crocodilians representing 17 species. Juveniles of 4 species were tested for the presence of distress vocalizations: *Alligator mississipiensis, Caiman crocodilus, Crocodylus niloticus,* and *Crocodylus siamensis.*

A second study site was a breeding pond for captive alligators owned by Mr. E. Ross ALLEN at Indian Prairie Farms (IPF) in Anthony, Florida. This area was more natural and represented confinement within the species' native environment. The pond was .2 ha in surface area located within a fenced .4 ha heavily vegetated plot. 8 adult alligators (length 1.8 m—2.9 m) inhabited the area as well as at least 12 juveniles which had hatched from a nest at the breeding pond in September 1973.

In addition to observations made at the two primary study sites, observations and recordings were obtained on a group of 5 sibling juvenile alligators housed together in the laboratory from two weeks of age to 7 months. These hatched at the IPF breeding pond in September 1973.

Apparatus

Magnetic tape recordings of vocalizations were recorded using a Nagra IIIB tape recorder (Kudelski Corporation) at a tape speed of 19 cm/s and with either a Dan Gibson E.P.M. parabolic microphone (R.D.S. Systems of Canada Limited) or an Electro-Voice Sound Spot directional microphone Model 644 (Electro-Voice Incorporated). Playbacks were made with the Nagra IIIB tape recorder.

Two instruments were used to analyze the physical parameters of crocodilian vocalizations. Sonagrams of the calls were produced by a Sona-Graph, Model 6061A (Kay Electronic Company). All sonagrams were made using the narrow filter band width (45 Hz) at a frequency range of 80—8,000 Hz. Oscillograms were made with a storage oscilloscope, Model 564 (Tektronix Corporation) and a mounted Polaroid Land Camera.

Procedures

Approximately 250 h of observations were made at the two study sites between April 2, 1974 and May 27, 1974. Manipulative methods of data collection involved eliciting distress calls from animals by physical contact and playing recordings of various vocalizations to crocodilians of the same or different species. Non-manipulative techniques included making recordings, films, and field notes of vocalizations as they spontaneously occurred.

Results

Vocalizations of Juvenile Alligators

Juvenile Grunt: The grunt is a vocalization of brief duration and descending frequency given by immature alligators in a variety of circumstances. A sonagram of two grunts given by one of the group of captive juveniles in response to approach by an observer is presented in Fig. 1. Virtually all of the acoustic energy is below 2000 Hz. In this group, grunting was heard most often when being fed or in response to movement by nearby humans.

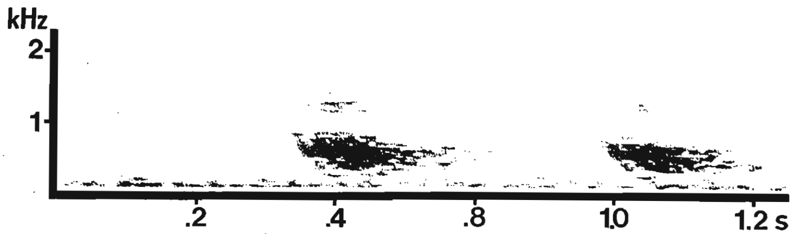

Fig. 1: Sonagram of juvenile grunts made by 7 month old alligator when approached by the observer

A different context pattern for grunting was found during 34 h of observation of young alligators in the breeding pond at IPF. These alligators were approximately the same age as those kept in the laboratory. Most observations were made during the mid-morning and early afternoon when the animals basked along the shoreline in groups. The observer approached the young alligators along the shore to within hearing range of the grunts (usually within 10 m), then sat quietly and recorded the context in which grunting occurred. Grunts tend to occur in bursts, ranging from a single grunt to 6 grunts. However, it frequently proved impossible to accurately count the number of grunts given by an individual due to the proximity of other young alligators. Thus, each group of grunts was counted as a single series. A total of 130 series of grunts was recorded.

8 contexts were identified in which grunting was heard at the breeding pond. These are identified below together with the total number of grunt series occurring in that context.

1. Response to movement or approach by another juvenile (6 series).
2. Response to approach or movement by nearby adult (15 series). Grunting in this context was frequently accompanied by movement away from the adult.
3. Response to approach of human observer (5 series). As in the previous category, grunting was usually accompanied by movement away from the intruder.
4. Prior to movement (6 series). These grunts were followed by "spontaneous" movements, having no identifiable stimulus.
5. During movement (33 series). Most identifiable grunts were heard during "spontaneous" movement, usually swimming towards or away from another hatchling.
6. While stationary (16 series). Grunts given by animals basking on the shoreline or lying motionless in shallow water.
7. During feeding (2 series). Grunts emitted by animals foraging for food along the shoreline.
8. Unknown (47 series). Often, it was not possible to identify the animal or the context in which the sound occurred.

Because of the softness of grunting and the high background noise, satisfactory field recordings were not obtained of grunts emitted by juveniles at the IPF breeding pond.

Juvenile Distress Calls: The distress call of alligators is similar to the grunt in that it is of relatively short duration and declines rapidly in fre-

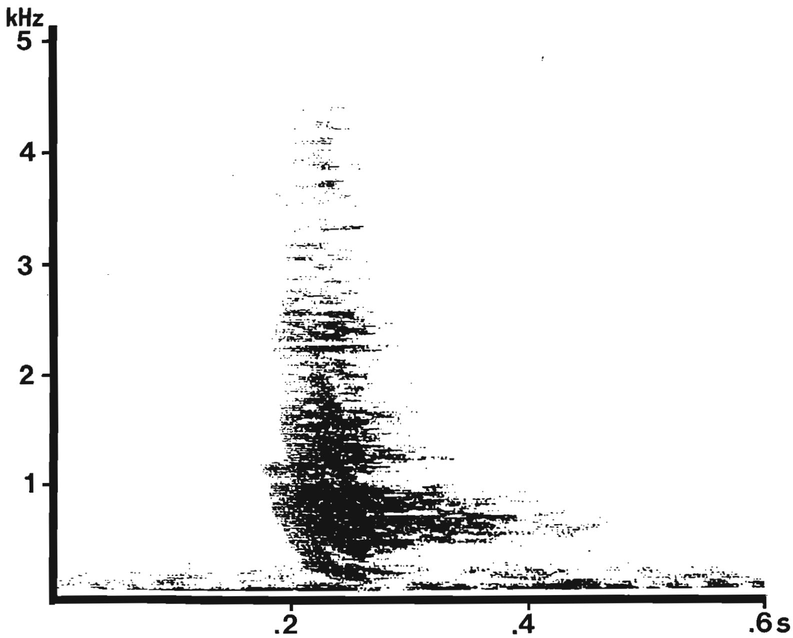

Fig. 2: Sonagram of a distress call of a 7 month old alligator

quency. It has been argued (CAMPBELL 1973) there are no consistent differences between the distress call and the grunt. Evidence is presented here that a distress call may in fact be distinguishable on the basis of context and structure of the signal, though the calls grade into one another.

Recordings of vocalizations made by alligators as they were harrassed by shaking, squeezing the base of the tail, or pinching the webbing of the feet, were obtained from animals 33 cm—106 cm long. This treatment usually resulted in calls similar to the grunt but having greater volume, and in some cases having larger amounts of sound energy at higher frequencies. Distress calls also tended to show greater harmonic structure when graphically portrayed as sonagrams, as in Fig. 2. A comparison of Figs. 1 and 2 shows that the grunts are identical to that portion of the distress call below 1200 Hz. The distress call differs in having significant amounts of energy up to 4500 Hz.

In some of the alligators in which distress calls were elicited, the basic form as presented in Fig. 2 remained constant as the call was repeated. In other alligators, changes occurred in the nature of the signal with continued harrassment. A typical change involving three subtypes of sounds is presented in Figs. 3—5, representing calls produced by a 53 cm alligator as it was pinched on the foot. Fig. 3 presents the initial vocalization as the animal was

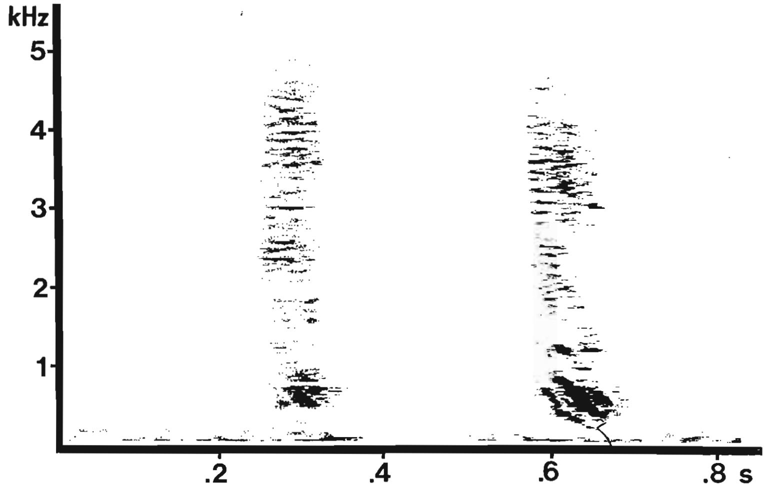

Fig. 3: Sonagram of distress calls made at the beginning of the series by a 53 cm alligator as the rear foot was pinched

pinched. The vocalization is basically the same as Fig. 2, having short duration and frequency ranging up to about 5000 Hz. In this series occurred about 70 calls having this basic form. Gradually, however, the calls became longer, having a more definite downward frequency change, giving the signal a moan-like quality. The first sound on Fig. 4 represents such a moan. The duration has increased from about .1 s to about .3 s. The harmonic structure is more evident, showing a decrease in dominant frequency from 1000 Hz to less than 200 Hz. A number of harmonics are present, the first beginning at about 2000 Hz.

About 50 of these moans were made when a third type of vocalization began to appear. This vocalization is pictured as the second vocalization in Fig. 4. The structure is similar to the moan, though the frequency range is

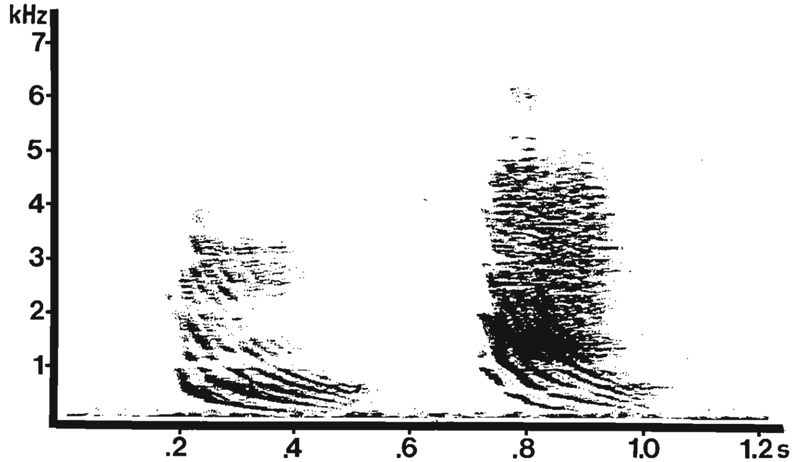

Fig. 4: Sonagram of the distress calls of a 53 cm alligator showing moan and screech components

greater. This vocalization has a harsh, screech-like quality, and sounds clearly different from the moan. Fig. 5 presents a sonagram of three closely spaced vocalizations recorded during the same series as Figs. 3 and 4. The first vocalization is a moan followed by the screech, which develops into a second moan. In this example, the frequency of the screech extends past the 8000 Hz limit of the sonagraph. Unlike the regular distress call and the moan, which are produced with the gular fold closed, the fold was open whenever the screech was produced. This suggests that the mechanisms of production of the moan and screech are the same, but that the tone of the moan is somewhat dampened as the sound passes through the gular fold. CAMPBELL (1973) observed a similar gradation of vocalizations in *Crocodylus acutus*. This sequence did not appear in the majority of alligators tested. Table 1 shows the relative

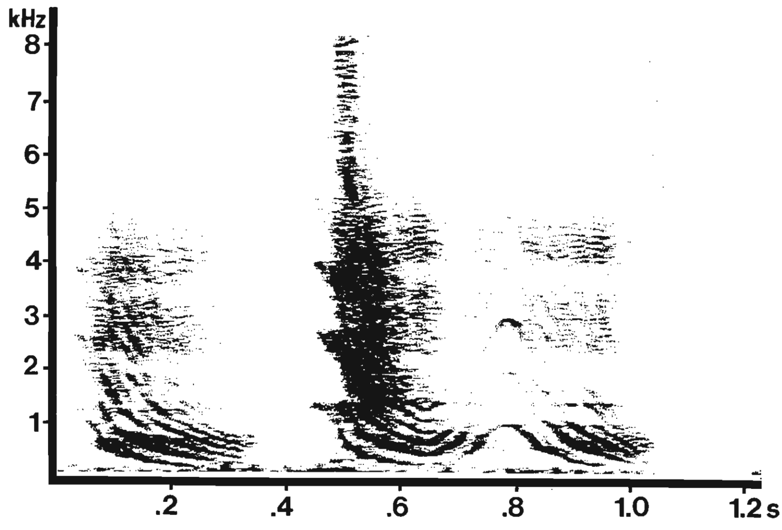

Fig. 5: Sonagram of distress calls of a 53 cm alligator showing closely spaced moan and screech series

numbers of responses of each category occurring in 8 alligators in response to pinching of the webbing of the feet.

Table 1: The duration of every fifth distress call made by 8 juvenile alligators and the relative frequency of screech and moan components

Subject	Size (cm)	No. of Distress Calls	% "Normal" Distress Call	% "Moan"	% "Screech"	X Duration (s)	S
1	122	21	85	5	10	.29	.02
2	53	223	44	42	14	.30	.01
3	33	33	100	0	0	.17	.02
4	38	37	100	0	0	.12	.02
5	39	28	100	0	0	.13	.01
6	43	29	100	0	0	.13	.02
7	51	69	84	16	0	.15	.01
8	57	150	49	44	7	.25	.12

Distress Calls in Other Species of Crocodilians

It was not possible to obtain recordings of grunts in other species of crocodilians because of the lack of groups of conspecific juveniles. The distress calls of small crocodilians of various species were obtained by pinching the hind feet, though size differences may account for some of the variation in the sonagrams. Recordings of distress calls of three species were of adequate quality for sonagrams to be made, and are presented below. Fig. 6 shows the sonagram of the distress call of a 1.1 m Nile crocodile (*Crocodylus niloticus*). The call differs from distress calls of alligators in having an increase in frequency and a subsequent decrease. The frequency of the call ranged up to 5000 Hz, and at least four well defined harmonics are present. The mean duration of a series of 10 calls as measured with the storage oscilloscope was .37 s (S = .12).

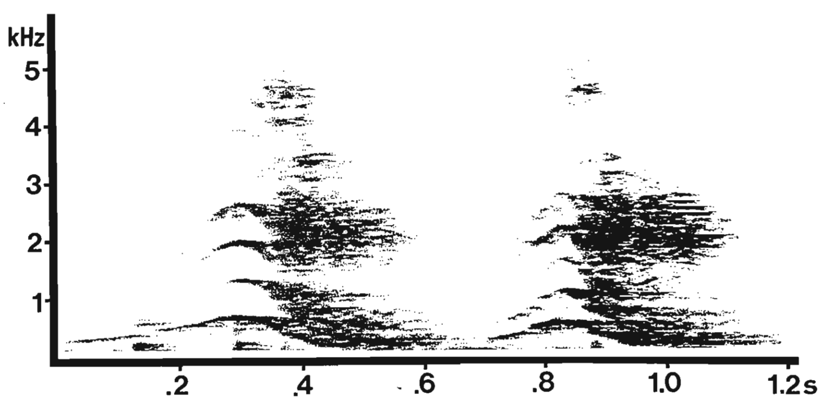

Fig. 6: Sonagram of distress calls of a 1.1 m *C. niloticus*

The distress calls of an 80 cm spectacled caiman (*Caiman crocodilus*), Figs. 7 and 8, were similar to some alligator distress calls in having both a screech component in which the gular fold was opened and a moan component in which the fold was closed. Comparison of these sonagrams with those of the distress call of the alligator in Fig. 4 and 5 show the similarity in the

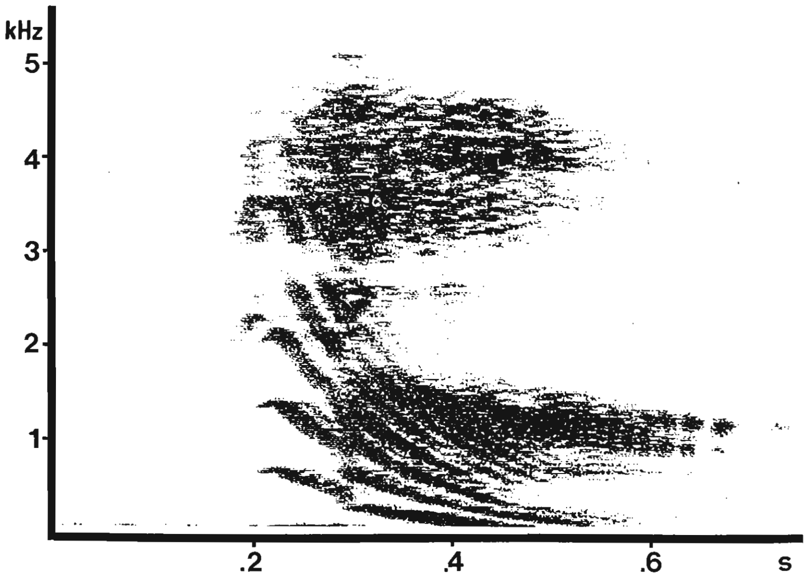

Fig. 7: Sonagram of the screech component of the distress call of an 80 cm *C. crocodilus*

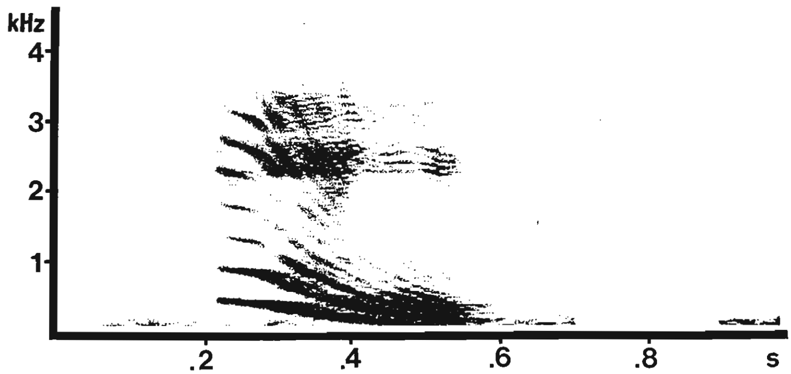

Fig. 8: Sonagram of the distress call of an 80 cm *C. crocodilus* moan component

calls. Few differences exist in the harmonic structure of the sounds, although the fundamental frequency begins at a lower frequency (about 400 Hz) and descends less rapidly than in the alligator distress call. The mean call duration of a series of 12 distress calls was .37 s (S = .08).

The most unique crocodilian distress call encountered during the course of study was given by a 49 cm Siamese crocodile (*Crocodylus siamensis*). When the crocodile was grasped, it issued two series of very closely spaced calls, with a rapid decrease in frequency, which gave the sound a siren like quality (Fig. 9). The mean duration of the separate calls in the series was .10 s (S = .01). The frequency decreases from over 1000 Hz to below 100 Hz in less than .05 s. Of the two series of calls voiced by the animal, one contained 5 separate calls and the other contained 8 calls. We also recorded and analyzed distress calls of the black caiman (*Melanosuchus niger*) with results identical to that reported by CAMPBELL (1973).

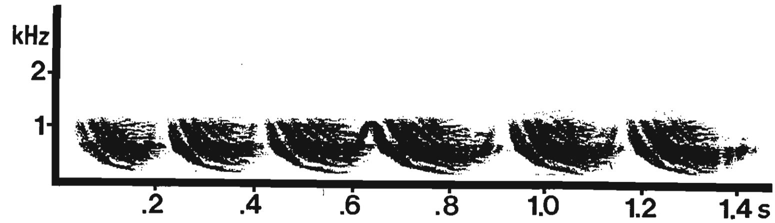

Fig. 9: Sonagram of a series of distress calls of a 49 cm *Crocodylus siamensis*

Discussion

In examining the communication system of a species it is hardly possible to avoid consideration of the message content, function, and meaning of the different signals. The meaning of a particular vocalization may be suggested by the context in which the sender vocalizes and by changes in the behavior of the animal receiving the message. The signal structure of a particular vocalization may also offer clues as to its information content (MARLER 1957). Thus calls which have the characteristics of repetitiveness (segmented calls) and changing frequency are most easily located in space by the receiver because of the structure of the vertebrate ear (MARLER 1955, 1961). Sounds classified as distress calls or contact calls frequently have these characteristics.

COLLIAS (1960) has made the most extensive functional-ecological classification of animal sounds. Using the sound signals of the domestic fowl as a basis, COLLIAS suggested that vocalizations in certain functional categories have similar characteristics over a wide variety of vertebrate species. Acoustic signals with long, low pitched, harsh notes were said to be characteristic of threat signals. Distress calls are characterized by short segmented notes with downwardly changing pitch, while short repeated calls with upwardly changing pitch signify "pleasure call." Alarm calls tend to be harsh, loud, and high pitched. How do the vocalizations of juvenile crocodilians fit this perspective?

The juvenile grunt and distress call in alligators appear to be examples of what are termed graded calls or continuously variable signals (MARLER 1961). The alligator grunts as it flees from a predator but, if seized, the distress call may emerge from the grunt. There are no discrete differences between the two types of calls; the grunt develops into the distress call in certain circumstances (seizure) and in at least some alligators, the nature of the distress call may undergo modification if the animal continues to be harassed (moan, screech). MARLER (1961) suggests several circumstances favoring graded calls, including the conveyance of information regarding the motivational state of the signaller and environmental information of a continuously variable nature. The grunting-distress call continuum probably conveys information primarily of the first type.

CAMPBELL's (1973) suggestion that the grunt may serve as a "contact call" between hatchlings is plausible, and this hypothesis is congruent with our finding that grunts were frequently associated with movement by the juveniles. In some situations, however, the grunt may serve as a warning signal such as when grunting is concurrent with fleeing from an adult alligator or a human. The relationship between adults and juvenile alligators is not clear. Immediately after hatching, the young are defended, at least in some cases, by adults. However, the 7 month old juveniles at the IPF breeding pond normally fled from approaching adults. Adults sometimes stalked babies and one instance of successful predation of a baby by an adult was observed. On the other hand, adults respond to the juvenile distress call by approach to the sound source, and would presumably attack whatever has seized the juvenile making the call.

It may be that the context of the call is important in determining the response of adults to these vocalizations. Observations at IPF indicated that nearby adults clearly within hearing distance generally ignored grunts associated with movement, feeding, etc. and adults did not respond to playbacks of grunts made of feeding captive juveniles (HERZOG 1974). Perhaps the volume of the sound or the presence of a potential threatening stimulus coupled with the volume of the call determines the response to playbacks. More sophisticated playback experiments are needed to clarify the nature of the adult response to juvenile calls. Though the vocalizations of the alligator as described in the present paper are consistent with what is known of the general bioacoustics of vertebrates, many questions remain.

Summary

Evidence is presented that the grunts and distress calls of juvenile alligators (*Alligator mississipiensis*) are examples of graded calls, which are given in different form depending largely on context. Representative sonagrams of the distress calls of three other species of crocodilians (*Caiman crocodilus, Crocodylus niloticus,* and *Crocodylus siamensis*) are presented and compared with sonagrams of alligator distress calls. These findings are discussed in light of current knowledge of the bioacoustics of other vertebrates.

Zusammenfassung

Grunz- und Klagelaute junger Alligatoren können fließend ineinander übergehen. Das Grunzen auf der Flucht vor einem Raubfeind wird zum Klagen, sobald das Tier ergriffen wird. Welcher Laut auftritt, entscheidet weitgehend die jeweilige Situation. Zum Vergleich werden Sonagramme des Klagelautes vom Kaiman, Nilkrokodil und Siamkrokodil vorgeführt. Die biologische Bedeutung der Laute wird besprochen.

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