

- DOLE, J. W., AND P. DURANT. 1974. Courtship behavior in *Colostethus collaris* (Dendrobatidae). *Copeia* 1974:988-990.
- DUKELMAN, W. E. 1966. Aggressive behavior in dendrobatid frogs. *Herpetologica* 22:217-221.
- GOODMAN, D. E. 1971. Territorial behavior in a neotropical frog, *Dendrobates granuliferus*. *Copeia* 1971:365-370.
- SEXTON, O. J. 1960. Some aspects of the behavior and of the territory of a dendrobatid frog, *Prostheraps trinitatis*. *Ecology* 41:107-115.

TEST, F. E. 1954. Social aggressiveness in an amphibian. *Science* 120:140-141.

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STRUCTURE AND PATTERN OF THE ROARS OF CHINESE ALLIGATORS (*ALLIGATOR SINENSIS* FAUVEL)

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ABSTRACT: Roars of three captive Chinese alligators *Alligator sinensis* (two ♂♂ and one ♀) were tape recorded, and analyzed with a sound spectrograph. Differences in durations of roars, roaring bouts, and inter-roar intervals as well as spectral qualities and the number of roars/roaring bout suggest that roar structure and pattern contain potential information about the vocalizing animal's sex and individual identity. These possibilities are discussed in terms of adaptations to their natural environment.

As an initial step in the understanding of the biology of the Chinese alligator (*Alligator sinensis*), an endangered species and one which may be extinct in the wild (R. Honegger, pers. comm.), observations and magnetic tape recordings were made of captive animals as they roared. Although previous investigators have described the vocalizations of captive American alligators (*A. mississippiensis*), which were stimulated to roar by artificial means and taped playbacks (Beach, 1944), and analyzed calls of juvenile crocodylians (Campbell, 1973), this is the first report containing analysis of a vocalization of an adult crocodylian.

Quantitative data were collected to determine whether roar structure and pattern contained information about the sender's sex and/or individual identity.

MATERIALS AND METHODS

A pair of adult Chinese alligators (♂ - 560502 = NYZP ♂, and ♀ - 610527 = NYZP

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♀) were housed together in the reptile house of the New York Zoological Park in an area with a pool and basking place under natural daylight conditions for Bronx, New York. The history of these animals and details of shelter construction can be found in the report of Brazaitis (1968). They are fed on horse ribs, liver, and fish supplemented with multivitamins. Another male, U.S. National Zoological Park R00133 = NZ ♂, was also observed.

Six times during September and November 1973 roars were elicited either by a repetitive 32 Hz tone of no more than six pulses, each about 0.5 s duration (Fig. 1c), or by playing back one of NYZP ♂'s five-roar bouts. A roaring bout is a grouped sequence of roars. Both were amplified and presented to the animals by means of the public address system in the reptile house. NZ ♂ roared in response to the filling of its pool with water.

Roars were recorded on 10 September



FIG. 1.—Sound spectrograms (sonograms) of an inhalation and roars of Chinese alligators, and a typical 32-Hz tone. Note the different settings. (a) inhalation, (b) one roar of NYZP ♂, (c) one roar of NZ ♀, and (d) one roar of NZ ♀; (e) 32-Hz tone pulses; (f) three-roar bout of NYZP ♀, (g) three-roar bout of NZ ♀, (h) three-roar bout of NYZP ♂, (i) five-roar bout of NYZP ♂, (j) five-roar bout of NZ ♂. Frequency scale (vertical) is marked in 500 Hz intervals; for the time scale (horizontal) each black bar below the base line = 1 second.

TABLE 1.—Number of times a roaring bout contained a given number of roars.

Animal	No. of bouts	Number of roars/bout						
		2	3	4	5	6	7	8
NYZP ♂	25	0	7	6	11	0	0	1
NYZP ♀	33	7	24	1	1	0	0	0
NZ ♂	4	0	4	0	0	0	0	0

1973 for the NYZP animals, and on 23 May 1974 for the NZ animal at 3% inches per second on a Nagra IVL tape recorder using a Sennheiser condenser microphone (MKH 815). Analysis was conducted with a Kay Electric Sound Spectrograph 7029A using the wide-band pass filter.

In the analysis several different settings were required to form the composite description. The following parameters were considered: (1) instances of recorded respiratory activity associated with roaring, (2) the duration of the roaring bout, (3) the duration of each roar within a bout and the average duration of a roar, (4) the duration of inter-roar intervals, and (5) the dominant or fundamental frequencies; wherein the second harmonic is considered twice the fundamental.

RESULTS

Postures and Respiration.—Roars were emitted in and out of the water and the posture in both cases was head-up with a deep curve in the neck similar to that described for *A. mississippiensis* by McIlhenny (1935) and Beach (1944). Relaxation of the posture occurred between roars coincident with the termination of the roar. Next the head was lifted again and an audible inhalation of about 0.5 s duration preceded the subsequent roar by about 1 s. At exhalation an explosive roar was emitted. The jaws remained closed during the inhalation and roaring. The spectral distribution of sound energy is similar during inhalation (air moving into the lungs via the larynx) and upon expulsion (Fig. 1a and b).

Sound and Pattern.—The word "T₀" from the Chinese, when emphatically pro-

nounced, carefully enunciated and slightly drawn-out, represents the sound of the roar (Brazaitis, 1968); it can also be imitated by striking the closed end of a standard size metal garbage pail. An individual's roars were audibly distinctive, e.g. the roars of NYZP ♀ appeared longer in duration and of different pitch compared to NYZP ♂ and NZ ♂.

Roars occurred in groups or bouts, each bout contained from two to eight roars. The number of roars/bout was characteristically three, four or five for NYZP ♂; two and three for NYZP ♀; and three for NZ ♂ (Table 1).

Durations.—Three parameters of duration were considered in the analysis and the results presented in Tables 2 and 3. Mean duration of a roar within a three-roar bout was greatest for NZ ♂ (1.20 s), followed by NYZP ♀ (0.71 s) and then NYZP ♂ (0.56 s). The duration of the roars was probably influenced by the echoic properties of the crocodilian solarium at the National Zoo. The mean duration of an entire five-roar bout for NYZP ♂ was significantly greater ($P < .01$ and $P < .05$, respectively) than the mean durations when he roared four and three times. Furthermore, the mean duration of a three-roar bout was significantly longer ($P = .05$ and $P < .01$, respectively) for NYZP ♀ (8.76 s) compared to NZ ♂ (7.86 s) and NYZP ♂ (6.37 s) (Table 2 and Fig. 1f, g, and h).

Moreover, the duration of a roaring bout can also be analyzed by considering the inter-roar interval. For the three-roar bouts in particular, the mean inter-roar interval of NYZP ♀ significantly ($P = .02$ and $P < .002$, respectively) exceeded NYZP ♂ and NZ ♂ by more than one second in each instance (Table 3).

Thus, inter-roar intervals, and roaring bouts with three roars of NYZP ♀ were longer than those of NYZP ♂ and NZ ♂.

Spectral Qualities.—Most of the sound energy of these roars occurred in a broad band between 25 and 500 Hz with other bands at higher frequencies depending upon

TABLE 2.—Mean durations of roars and roaring bouts. $N =$ no. of roaring bouts analyzed. Probabilities based on Wilcoxon two-sample test and Student's- t for comparison e .

No. roars/bout	N	Roar number and duration (s)					Mean roar duration (s)	Mean duration of roaring bout (s)	
		1	2	3	4	5			
NYZP ♂	5	8	0.65	0.70	0.60	0.02	0.59	0.63 ^a	11.71
	4	1	0.68	0.68	0.61	0.65	0.66 ^b	8.84	
	3	1	0.53	0.60	0.53	0.56 ^c	6.37	
NZ ♂	3	2	1.47	1.19	0.96	1.20	7.86 ^d
	NYZP ♀	3	8	0.72	0.72	0.68	0.71
2		1	0.95	0.60	0.78	5.98

^a NYZP ♂ (5) differs from NYZP ♂ (3), ($P < .05$, $t_s = 2.02$).
^b NYZP ♂ (5) differs from NYZP ♂ (4), ($P < .01$, $t_s = 3.25$).
^c NYZP ♂ (3) differs from NYZP ♀ (3), ($P < .05$, $t_s = 2.86$).
^d NYZP ♀ (3) differs from NZ ♂ (3), ($P < .05$, $t_s = 16$).
^e NYZP ♀ (3) differs from NYZP ♂ (3), ($P < .01$, $t_s = 4.345$).

the individual (Fig. 1). Finer analysis at different settings revealed that the sound energy for the initial part of a roar, independent of the number of roars/bout, was distributed differently among the three animals. For NYZP ♂ modal frequencies were as follows: 125, 250, 1,250-1,300, 1,700-1,750, and 2,500 Hz (Fig. 1b and h); while not exact multiples of 125 the bands were probably harmonics and therefore 125 Hz was believed to be the fundamental frequency. NYZP ♀ roars showed modal frequencies at 125, 320-325, and 1,300-1,350 Hz (Fig. 1c and f); designation of a fundamental frequency was thus more difficult, but 125 Hz was common to both NYZP animals. Moreover, NZ ♂ displayed a possible fundamental at 100 Hz with multiples of 300, 1,000, and 1,300 Hz (Fig. 1d and g).

Other qualities of the roars of these alli-

gators included the deletion of some harmonics and the downward modulation of the fundamental during the middle and final portions of a roar (Fig. 1).

Intensity and Stereotypy.—An attribute of the roaring bouts that is not always obvious from the sonogram is the decrease in sound pressure (loudness) in the last one or two roars of a bout. This was observed for both NYZP animals.

Although the roars are temporally stereotyped, one observation suggests that they are modifiable during their presentation; NYZP ♂ was in the pool midway through a roaring bout in response to the 32 Hz tones when NYZP ♀ entered the water between roars two and three. Measurements showed that the durations of the roars were unchanged but that the inter-roar intervals between three and four, and four and five

TABLE 3.—Mean duration of inter-roar intervals. $N =$ number of roaring bouts analyzed. Probabilities based on Wilcoxon two-sample test.

No. seconds between	Roar number and duration (s)					Mean inter-roar interval/bout (s)	N
	1 and 2	2 and 3	3 and 4	4 and 5		
NYZP ♂	2.10	2.02	2.08	2.26	2.14 ^a	8
	1.97	2.01	2.11	2.04	
	2.38	2.14	2.26 ^b	
NZ ♂	1.99	2.25	2.12 ^c	2
	3.29	3.33	3.31	
NYZP ♀	4.48	8
	

^a NYZP ♂ (5) differs from NYZP ♂ (4), ($P < .01$, $t_s = 2.78$).
^b NYZP ♀ (3) differs from NYZP ♂ (3), ($P < .02$, $t_s = 32$).
^c NYZP ♀ (3) differs from NZ ♂ (3), ($P < .002$, $t_s = 64$).

were extended. Consequently, this roaring bout had the longest duration (12.41 s) of all five-roar bouts given by NYZP ♂.

DISCUSSION

Based on a small sample, analysis of the roars of these Chinese alligators suggests that roar structure and pattern contain potential information about the vocalizing animal's sex and individual identity.

However, first it is important to consider the evidence for communication in the NYZP pair. During playback experiments, it was observed that female roaring (in response to playbacks of the male roars) prompted the male to roar, and roars by the male may have in one instance attracted the female into the water from which he was calling. Thus guided by a definition that communication is at the very least stimulation of a response in another animal (Scott, 1968), these two alligators were communicating.

The next questions then concern the possible kinds of information transmitted by these roars in captive animals and, by inference, in alligators in their natural habitat. Of course, as Marler (1961) points out, information content can only be inferred from the nature of the response to the signal; here very few observations were available and thus speculation runs high. However, as a point of departure four areas of descriptive information (Marler, 1961) are considered.

Species-specific information requires that normally only conspecifics can elicit the vocalization. Evidence in this area is equivocal; NYZP ♀ responded to playbacks of NYZP ♂; NYZP ♂ never responded to his own roars and neither NYZP animal responded to playbacks of the roars of an adult male American alligator. But Brazaitis (1968) and Neill (1971:298) describe roars by the American species stimulating the Chinese alligator to roar. It is of interest that the sound and structure of bellows or roars of the American alligator differ from those of these Chinese alligators (Garrick, unpubl. data). Except for occasional habi-

tat overlap of American alligators and American crocodiles, neither alligator species is presently syntopic with another crocodylian species; perhaps some divergence in roar structure was advantageous during the evolution of the genus.

Roars may also contain information about the reproductive state or sex of the sender. Roaring of both sexes is more common during spring than during winter (Brazaitis, 1968); perhaps there is some cue about reproductive condition in the roars of spring, the time of courtship in the NYZP animals. Another possibility that gains support from the analysis of the roars is that the sex of the individual determines the roar structure and its pattern. In the present investigation the NYZP pair showed consistent differences in roar structure and pattern (Tables 1, 2 and 3; Fig. 1). Furthermore, in certain parameters, namely the mean inter-roar interval/bout and mean duration of a three-roar bout, NYZP ♂ is more like NYZP ♂ than NYZP ♀. Thus roars may be consistently different between sexes without any apparent immediate physiological concomitant, and therefore represent the result of complex developmental processes of which hormonal factors may be only one. The significance of this dichotomy in voice is that males could usually be distinguished from females. Such a system might have obvious advantages in a habitat where visibility is low, as in a marsh or swamp, and in a weakly dimorphic species that is believed to hibernate in a manner in which the sexes are separate but with the females aggregated and the males solitary (Brazaitis, 1968). Upon emergence from hibernation roaring might ultimately serve to attract potential mates.

Evidence of motivational information related to reproduction was observed early in the courtship period, 1965, when NYZP ♂ approached NYZP ♀ and attempted to mount her after she had roared (Brazaitis, pers. comm.). Roaring usually preceded courtship but was not a precondition for mounting. Moreover, except for two in-

stances when NYZP ♀ oriented towards or approached NYZP ♂ no overt social behavior was associated with the roars. The NYZP pair were never aggressive before, during or after roaring as suggested for an American alligator by Beach (1944).

Interpreted another way these roars may contain information identifying the individual. For example, duration and spectral measurements that were useful in suggesting sexual differences could result from size differences and distinct vocal development. Another alternative is that the repetition rate, or number of roars/bout may carry such information. However, without data on the social organization of Chinese alligators it is premature to suggest a selective advantage for individual information content in their roars. Obviously, to answer many of these questions of crocodylian communication natural populations of these rapidly vanishing forms should be studied.

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LITERATURE CITED

- BEACH, F. A. 1944. Responses of captive alligators to auditory stimulation. *Am. Nat.* 78:481-505.
- BRAZAITIS, P. 1968. *T'o. Anim. Kingdom* 71: 24-27.
- CAMPBELL, H. W. 1973. Observations on the acoustic behavior of crocodylians. *Zoologica* 58: 1-11.
- MARLER, P. 1961. The logical analysis of animal communication. *J. Theor. Biol.* 1:295-317.
- MCLHENNY, E. A. 1935. *The alligator's life history.* Christopher Publ. House, Boston.
- NEILL, W. T. 1971. *The last of the ruling reptiles.* Columbia Univ. Press, New York.
- SCOTT, J. P. 1968. Observation, p. 17-30. In T. A. Sebeok [ed.] *Animal communication.* Indiana Univ. Press, Bloomington.

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WEIGHT-LENGTH RELATIONSHIPS IN THIRTEEN SPECIES OF SNAKES IN THE SOUTHEASTERN UNITED STATES

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ABSTRACT: Regression equations of the form $y = ax^b$ were calculated for the relationship between body weight (y) and snout-vent length (x) in 13 species of snakes from the southeastern United States. All species except two (*Crotalus horridus* and *Heterodon platyrhinx*) had slopes which were not significantly different from 3.00. The effect of season on weight-length relationships was examined in four species and found to be a significant factor in one (*Natrix sipedon*). Sex was found to have a significant effect on the relationship in only two species, *C. horridus* and *Coluber constrictor*. Tail ratios (tail length/total length) were greater in ♂♂ than in ♀♀ for adults of all species. The percentage of the sample with broken tails in each species was positively correlated with the mean tail ratio for each species.

WEIGHT-LENGTH relationships have been studied in many poikilotherms, e.g., fish (Carlander, 1969; Kaufman and Beyers, 1972), turtles (Lagler and Applegate, 1943;

Mosimann, 1958; Dunson, 1967) and lizards (Minnich, 1971). The relationship between weight and length is useful in describing surface area-volume ratios and the subse-