

TEMPERATURE INFLUENCES ON HATCHLING CAIMAN CROCODILUS DISTRESS CALLS¹

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Hatchling *Caiman crocodilus fuscus* were tested for their tendency to emit a distress call and show an extension reflex as they were held by the base of the tail at cloacal temperatures (T_c) ranging from 7 to 36 C. The low T_c threshold for the distress call was about 9 C and for the extension reflex, 9.9 C. There is no apparent upper T_c threshold for the distress call. However, no vocalizations were emitted above 33 C, perhaps because gular pulsations overrode their expression. The duration of the distress call, which consists of three or four distinct bands between 0.2 and 2.4 kHz, and the duration of the intercall interval both decreased with increasing T_c . In contrast, repetition rate was stable over a broad range of T_c (18–33 C), and the spectral composition of the calls also was unchanged over a range of 12.8–33.0 C. Temperature independence of sound energy distribution and stability of repetition rate are deemed adaptations which reduce the ambiguity in the distress call signal to the receiver, provided that the auditory system of the receiver is similarly responsive to temperature. Low-temperature functioning of neuromuscular systems would appear to be advantageous for small crocodylians, whose body temperature fluctuates more than the body temperature of larger animals.

Crocodylians, like other reptiles, have definite temperature tolerances (Colbert,

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Cowles, and Bogert 1946) and behaviorally regulate their body temperature (Diefenbach 1975b; Lang 1975; Smith 1975). Also physiological functions, for example, heart rate (Smith 1975; Grigg and Alchin 1976) show a predictable dependence on body temperature. An equally important problem is whether crocodylian communicatory behaviors are

temperature dependent as they are in some frogs (Blair 1958; Zwiefel 1968) and insects (Walker 1975). Crocodylians are quite vocal, and recent research has suggested that the sounds made by adults (Garrick and Lang 1977) and young (especially their distress calls and grunts; Alvarez del Toro 1969; Pooley 1969, 1976; Campbell 1973; Kushlan 1973; Hunt 1975; Pooley and Gans 1976) are of significant adaptive value.

We therefore investigated the influences of changing body temperature primarily on the vocalizations but also on gular movements and a noncommunicative reflex of hatchling *Caiman crocodilus*. The temperature threshold for vocalization and its effects on the temporal and spectral qualities of the distress call were emphasized in order to suggest probable vocal mechanisms and the ecological significance of temperature on the communicatory behavior of crocodylians.

MATERIAL AND METHODS

Growing, hatchling *Caiman crocodilus fuscus* were studied during May, June, and July 1974 at the New York Zoological Park. Over this time mean body weights and total body lengths of 10 animals changed, respectively, from 35.7 to 49.1 g and from 23.7 to 25.4 cm. The caiman were housed in a large tub containing 2 inches of water (24.0–25.2 C) and were provided with a basking platform which was warmed by two red-bulb IR lamps from a distance of about 0.5 m. Other platforms without incident heat were also available. Air temperatures above the water varied from 23.6 to 29.8 C, and surface temperatures on the basking platform, which was usually wet, varied from 26.4 to 28.4 C. All animals fed at least three times per week on a balanced diet of beef liver, heart, and muscle and fish supplemented with bone

meal. All were healthy during the experimental period.

The caiman were observed through a one-way mirror, and while basking they were gently picked up and their cloacal temperature (T_c) measured with a Schultheis rapid-responding thermometer; at this time any vocalizations were also noted. The same thermometer was used for all T_c and other temperature measurements. Cloacal temperatures (no. = 30) of basking animals ranged from 24.4 (just beginning to bask) to 36.4 C; the mode was 27.0 C. These T_c 's overlap the range of voluntarily selected body temperatures of 150–350-g *C. crocodilus* (Diefenbach 1975b) and are important in interpreting the effects of changing temperature on their behaviors.

The vocalizations of 10 individually marked caiman were tape recorded under controlled conditions. The caiman were either heated with a 250-W IR lamp or cooled in an ice bath (7–14 C), both of which were harmless procedures. Then their tendency to vocalize was tested by holding an animal firmly by the base of the tail in a normal dorsal-ventral orientation, during which it may vocalize and reflexly extend its limbs. Because specific sounds are evoked when the young animal is held and because these sounds attract adults (Kushlan 1973), this vocalization has been characterized as a distress call. There is conflicting opinion, however, as to whether the distress call is a discrete vocalization, part of a graded vocal system (Burghardt 1977), or the same as other juvenile vocalizations (Campbell 1973). For our purposes it is not necessary to address this question now. What is important is that we controlled the conditions for elicitation of the vocalization which enabled us to determine the causal relationship of T_c to the vocal parameters. Additionally, the strength of the extension

reflex and the rate of gular pulsations (movements of the gular region) were measured at different T_c 's in caiman during elicitation of the vocalizations.

Tape recordings of the distress calls were made at $3\frac{3}{4}$ inches/s on a Nagra IVL tape recorder using a Sennheiser condenser microphone (MKH 815). Analysis was conducted with a Kay Electric Sound Spectrograph using the wide band pass filter. The following parameters of the distress call were measured: (1) repetition rate, (2) call duration, (3) inter-call-interval duration, and (4) sound frequencies.

RESULTS

Effect of temperature on distress calls.--- Caiman distress calls are given, with the mouth open or closed, as a series of three or more sounds pronounced "ehh." The call is composed of three or four distinct bands, the fundamental and several harmonics, which may first rise sharply and

then decrease rapidly in frequency. Spectral composition of the three bands was independent of T_c (no. calls analyzed = 27) over a T_c range of 12.8–33.0 C. The median frequency composition of the first three bands was approximately 700–200 Hz for band 1 (which is here considered the fundamental), 1,200–400 Hz for band 2, and 1,800–800 Hz for band 3. Examples of calls at different T_c 's appear in figure 1. It is apparent that the difference between the maximum and minimum frequency of each band is greater in bands 2 and 3, but bands 2 and 3 are not always coincident in these examples. Also at $T_c = 31$ C the initial upswing of the call was absent.

Repetition rate (calls/10 s) did not show a simple linear dependence on T_c . Deviations from linear regression were significant ($P < .05$), perhaps due to heterogeneity about the regression line and/or a curvilinear relationship (Sokal and Rohlf 1969). The relationship was

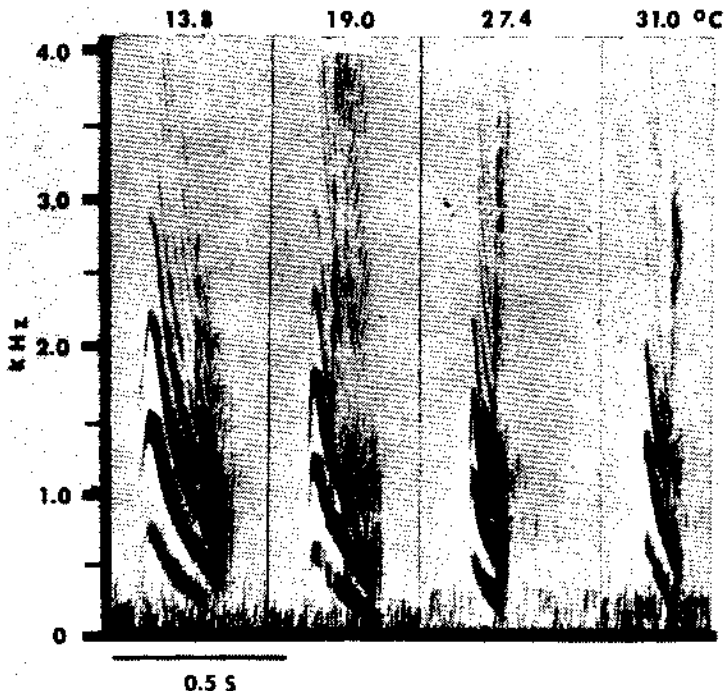


FIG. 1.—Sound spectrograms of the distress calls of one *Caiman* at different T_c 's (C)

not simplified by a semilog plot; however, an arithmetic plot (fig. 2) demonstrated that between 18 and 33 C repetition rate varied in no apparent pattern between 6 and 10/10 s.

Call duration varied inversely with increasing T_c (figs. 1, 3), ranging from 0.344 to 0.082 s for the corresponding T_c range of 12.8–33.0 C. Analysis of variance for linear regression (Sokal and Rohlf 1969) demonstrated a highly significant ($P < .001$, $F[1, 17] = 165.25$) inverse dependent relationship of call duration on T_c . The duration of the intercall interval also was inversely dependent on T_c (fig. 4). The same analysis showed a highly significant relationship ($P < .001$, $F[1, 15] = 19.57$). The range of the duration of the intercall interval was 3.67–0.97 s between 12.8 and 33.0 C. Call duration and intercall-interval duration did not vary with T_c in a constant relationship. As demonstrated by the ratio of regression coefficients, .076/.011 ~ 7 , intercall interval decreased more rapidly in duration than did the call duration.

Elicitation of distress calls at different T_c 's.—Distress calls were not elicited at every attempt or at all T_c 's over a range of 7–36 C. Data were grouped into 5 C classes beginning at 7 C. The proportion of trials resulting in vocalization was clearly associated ($P < .005$) with the temperature group (table 1; *G*-test, Sokal and Rohlf [1969]). One result was that caiman within the extreme-temperature groups vocalized less (table 1). For instance, within the 7–12 C group two vocalizations occurred in the 9 C class,

TABLE 1
PROPORTION OF CAIMAN VOCALIZING WITHIN EACH TEMPERATURE GROUP (T_c)

Group °C (T_c)	No. Vocalizing	No. Tests	Proportion Vocalizing*
31–36.....	3	15	.200
25–30.....	20	69	.289
19–24.....	15	39	.385
13–18.....	38	85	.447
7–12.....	7	63	.111
Total.....	83	271	...

NOTE.— $G = 23.026$, $\chi^2 = 14.86$ ($P < .005$, $df = 4$).
* $\bar{x} = .307$.

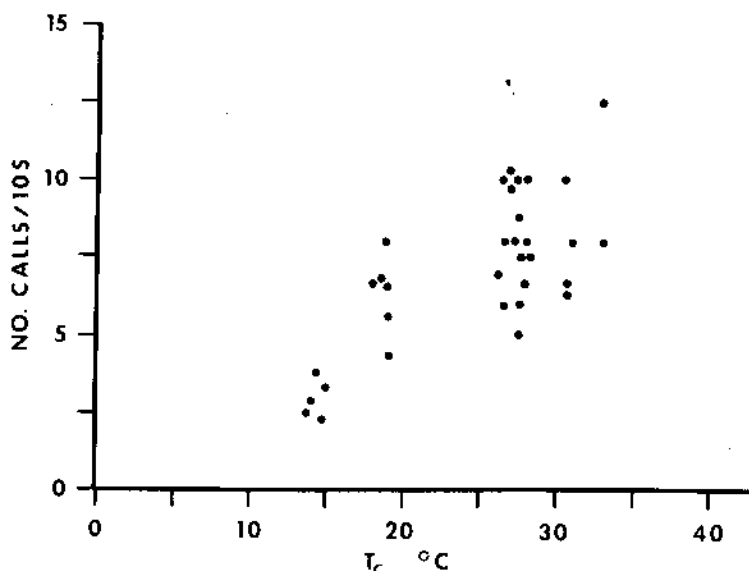


FIG. 2.—Relation of distress call repetition rate to T_c (no. = 33)

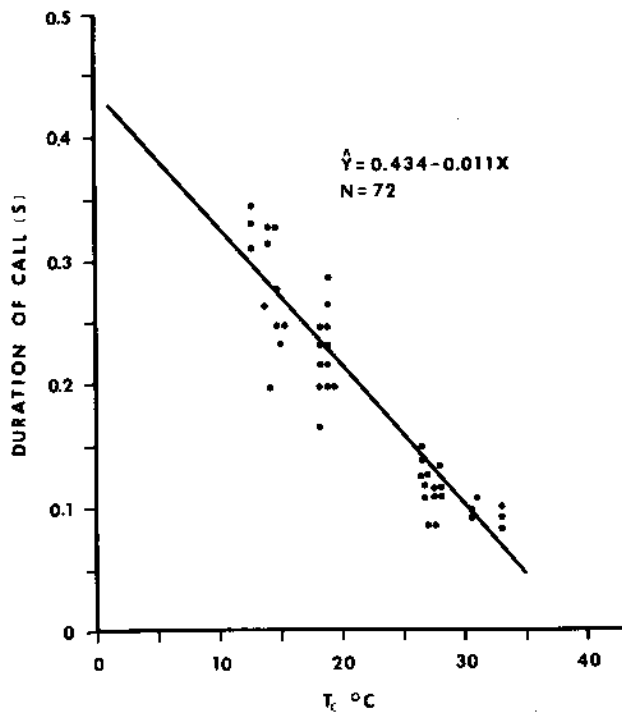


FIG. 3. Relation of call duration in seconds (s) to T_c . The standard error of the regression coefficient (b_{y-x}) is .00087. Multiple entries at one T_c are represented by a single closed circle.

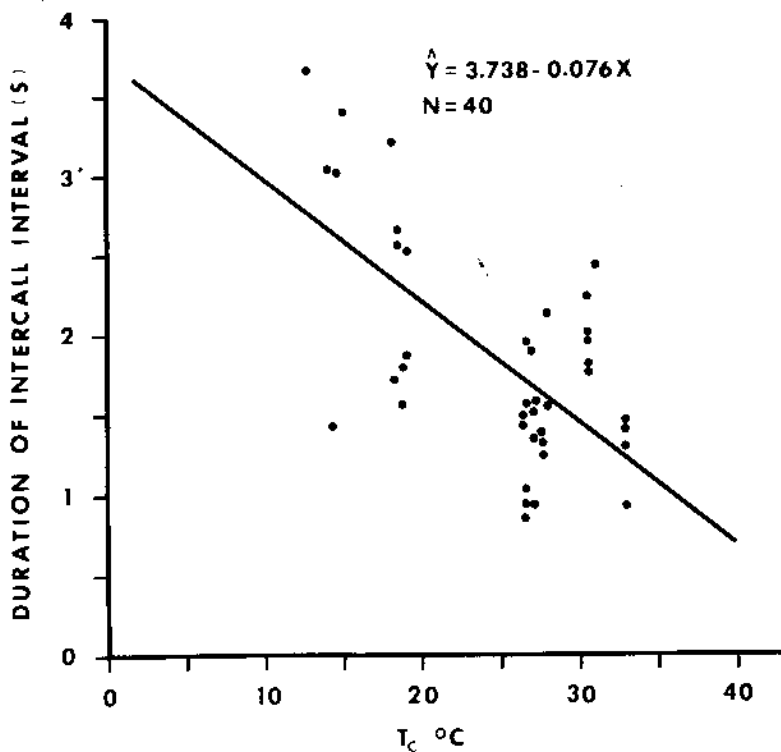


FIG. 4. Relation of the duration of the intercall interval in seconds (s) to T_c . The standard error of the regression coefficient is .01718.

one in the 10 C, and two each in the 11 and 12 C classes. Hence the low T_c threshold for distress calls was between 9 and 9.9 C, the same as for the extension reflex (see below). Within the highest temperature group (31–36 C), only three distress calls were emitted, none above 33 C. The paucity of calls above 33 C appears related to the occurrence of gular pulsations. Specifically, between 31 and 36 C distress calls were emitted only once in 11 trials when gular pulsations also occurred, but calls were emitted twice in four trials in the absence of gular movements. However, the frequency of occurrence of the calls was not significantly different from chance in either case ($P > .05$, 2×2 test of independence). Likewise, there was no statistically significant effect of gular movement on the frequency of vocalizations over a T_c range of 25–36 C ($P > .05$, no. gular movements = 41).

The rates of gular pulsations varied from 8 to 12/5 s (no. = 11) between 26.2 and 36.4 C. Similar rates of "gular fluttering" in *Caiman* at the same body temperatures were found by Diefenbach (1975b).

Temperature effects on the extension reflex.—When a caiman was held by the base of the tail, it extended its limbs, lifted its head, and arched its tail. Often an orientational component followed the extension reflex; that is, the animal turned and attempted to bite the experimenter's hand. The extension reflex was slight or partial at T_c 's of less than 9.9 C but much stronger at T_c 's from 9.9 to 16.5 C (no. = 10). No vocalizations occurred during these 10 trials, and only one vocalization was emitted during nine additional trials from 16.5 to 21.5 C when biting also occurred. Biting was attempted first at 13.0 C, and a strong bite was delivered at 17.7 C and all higher T_c 's.

DISCUSSION

Repetition rate of the distress call was relatively stable between 18 and 33 C, whereas call duration and intercall-interval duration both decreased linearly with increasing T_c (figs. 3–4). These results are plausible because any time period t_x can be divided into t_c (call duration) and t_i (intercall interval), so that $t_c + t_i = t_x$, and this expression is independent of repetition rate. Hence these three parameters account for all of the relevant temporal measures of these vocalizations.

A significant deviation from linear regression for repetition rate might be explained by the uncontrolled state of the caiman during testing, but it is probably not explained by differential handling contributing to the heterogeneity of the data. A more interesting possibility is that repetition rate and body temperature vary in a curvilinear relationship, with a plateau between 18 and 33 C. Stability of repetition rate over a 15 C range would be adaptive because it would reduce the temporal ambiguity in the distress call, provided, that is, that the receiver's hearing is similarly responsive to temperature.

Some temporal parameters of the vocalizations of some reptiles and amphibians respond to temperature changes similarly to caiman, whereas others do not. For example, Zweifel (1968) found that repetition rate (= pulse rate) of *Bufo americanus americanus* and *B. woodhousii fowleri* mating calls increased but call duration decreased with increasing body temperature. Similarly, the mating call of the gray tree frog (*Hyla versicolor*, Blair 1958), several species of chorus frogs (*Pseudacris*), and the southern toad (*B. terrestris*, Bellis 1957) show the same trends in repetition rate and call duration, but with air temperature. Marcelini (1974) reported that the repetition

rate of the multiple chirp call of the gekkonid lizard, *Hemidactylus frenatus*, varied positively with air temperature measured at the time of the call.

The frequency structure and repetitive pattern of the *Caiman* distress call should make it easily locatable (Marler and Hamilton 1966). The sound energy in the major bands (0.2–2.4 kHz; fig. 1) of the distress call, which is similar to frequencies of juvenile *C. crocodilus* calls reported by Campbell (1973), changed relatively little over the T_e range 12.8–33.0 C. Unchanging partitioning of sound energy of the distress call over a broad range of T_e is adaptive because it reduces ambiguity in the call and increases locatability for the potential receiver, which may be an aid-giving adult (Kushlan 1973) or another juvenile (Pooley and Gans 1976). In contrast to the temperature independence of these call frequencies, Blair (1955, 1958) found that middle or dominant frequencies of mating calls of *Microhyla olivacea*, *M. carolinensis*, and *Hyla versicolor* increased with increasing air temperature. Additional experiments are required to determine if the *Caiman* call functions adaptively at different body temperatures of both sender and receivers.

In considering the design of such studies, we already know that juvenile *C. crocodilus* demonstrate maximum auditory sensitivity within a range of 0.2–2.0 kHz (Manley 1970; Wever 1971; Campbell 1973), indicating a perceptual match with the distress call frequencies reported above. The next step might be to test auditory sensitivity at different body temperatures. This procedure has merit because of the profound effect of temperature on the reptilian auditory system (Campbell 1969; Verner 1972, 1976). However, analysis of the two components of the cochlear potential of *C. crocodilus* showed that the CM_+ com-

ponent was relatively temperature independent and would function anaerobically (Kauffmann 1974); its significance for hearing or behavior has not been demonstrated. Final evaluation of temperature effects on acoustic behavior might involve playback of the distress calls, which have been recorded at different body temperatures, to juveniles and adults held at different constant body temperatures.

It became evident during the study that certain motor acts may effectively override the emitting of these distress calls. The first suggestion was that gular pulsations may be incompatible with sound production between 31 and 36 C. (But a small sample size was the likely cause of the probability of occurrence being statistically nonsignificant [Sokal and Rohlf 1969].) At these body temperatures the rates of gular pulsations are similar to rates in alert *Caiman* (Flanigan, Wilcox, and Rechtschaffen 1973) and rates during the nonventilatory phase of respiration (Naifeh, Huggins, and Hoff 1970), during which the gular movements ventilate the olfactory epithelium (Huggins, Parsons, and Pena 1968; Gans and Clark 1976). These T_e 's (31–36 C) are between the "preferred range" (28.5–31.5 C) and the maximum voluntary tolerated T_e (36 C) for small caiman (Diefenbach 1975b) and within the basking range of our animals. Moreover, vocalizations were not emitted during the extension reflex (9.9–16.5 C) and emitted only once when attempted or actual biting occurred (16.5–21.5 C). Surely these observations deserve more attention because they imply, first, that the distress call can be overridden at a high but nonetheless common T_e level and, second, that other motor acts compete with the expression of this vocalization at T_e 's between 9.9 and 21.5 C.

Anatomical considerations.—The rela-

tive temperature independence of repetition rate and call frequency and their divergence from the temperature-dependent relationships of call duration and intercall interval suggest that anatomical investigations would be rewarding. The larynx, because it gives structure and pattern to the airstream, is a place to focus. Although no direct evidence indicates which of the laryngeal structures determine the call patterns, they may be inferred from descriptions of the actions of the muscles during respiration and vocalization (Naifeh et al. 1970, 1971a, 1971b; Naifeh, Huggins, et al. 1970; Gans and Clark 1976).

Basically, *Caiman* respiration on land involves active expiration and inspiration and full inspiratory breath holding. The inspiratory breath holding (nonventilatory phase), which does not always occur (Gans and Clark 1976), results from the action of the glottal sphincter muscle shutting the glottis (Naifeh, Huggins, et al. 1970). Rhythmic glottal opening appears to be under the control of the glottal dilator muscle, which is situated at the anterior margin of the glottal opening, and the posterior portion of the glottal sphincter muscle (Naifeh, Huggins, et al. 1970). These muscles probably determine the temporal aspects of the vocalization, that is, the call duration and repetition rate, which appear to be differentially affected by temperature. Last, by inference, the glottal aperture, which opens moderately at expiration (Naifeh, Huggins, et al. 1970)

and is modulated by glottal dilators and sphincter, shapes the spectral composition of the call. Supposedly the mechanism determining glottal aperture is little affected by changing temperature.

Ecological significance.—That the distress call and extension reflex both have low T_c thresholds near 10 C suggests adaptation to low temperature. There is some evidence bearing on this supposition: smaller *Caiman* (Diefenbach 1975a), American alligators (Joanen and McNease 1972), and *Crocodylus niloticus* (Pooley and Gans 1976) feed at lower body temperatures (at about 15 C) than larger members of their species. Also Pooley (1962) found that only 75% of a group of juvenile Nile crocodiles were paralyzed at a low body temperature of 7 C. These observations show that some small crocodilians feed and locomote at body temperatures 15–20 C below their ‘normally’ selected levels. Small crocodilians may benefit from low-temperature functioning of physiological systems by gaining more time for energy assimilation. Additionally, because small *Caiman* heat and cool faster than larger juveniles and adults (Diefenbach 1975b), the T_c of small crocodilians should fluctuate more. Thus, based on their thermal properties alone, toleration of low body temperatures would be adaptive. In this regard, McNease and Joanen (1975) found that, compared with adults, juvenile American alligators were more often active during cold periods.

LITERATURE CITED

- ALVAREZ DEL TORO, M. 1969. Breeding the speckled caiman (*Caiman crocodilus*) at Tuxtla Gutierrez Zoo. *Int. Zool. Yearbook* 9:35–36.
- BELLIS, E. D. 1957. The effects of temperature on salientian breeding calls. *Copeia* 1957:85–89.
- BLAIR, W. F. 1955. Mating call and stage of speciation in the *Microhyla olivacea*-*M. carolinensis* complex. *Evolution* 9:469–480.
- . 1958. Mating call in the speciation of anuran amphibians. *Amer. Natur.* 42:27–51.
- BURGHARDT, G. 1977. Of iguanas and dinosaurs: social behavior and communication in neonate reptiles. *Amer. Zool.* 17:177–190.
- CAMPBELL, H. W. 1969. The effects of temperature on the auditory sensitivity of lizards. *Physiol. Zool.* 42:183–210.

- —. 1973. Observations on the acoustic behavior of crocodylians. *Zoologica (N.Y.)* 58:1-11.
- COLBERT, E. H., R. B. COWLES, and C. M. BOGERT. 1946. Temperature tolerances in the American alligator, and their bearing on the habits, evolution, and extinction of the dinosaurs. *Bull. Amer. Mus. Natur. Hist.* 86:333-373.
- DIEFFENBACH, C. O. DA C. 1975a. Gastric function in *Caiman crocodilus* (Crocodylia: Reptilia). I. Rate of gastric digestion and gastric motility as a function of temperature. *Comp. Biochem. Physiol.* 51A:259-265.
- —. 1975b. Thermal preferences and thermoregulation in *Caiman crocodilus*. *Copeia* 1975: 530-540.
- FLANIGAN, W. F., R. H. WILCOX, and A. RECHTSCHAFFEN. 1973. The EEG and behavioral continuum of the crocodylian, *Caiman sclerops*. *EEG Clin. Neurophysiol.* 34:521-538.
- GANS, C., and B. CLARK. 1976. Studies on ventilation of *Caiman crocodilus* (Crocodylia: Reptilia). *Respiration Physiol.* 26:285-301.
- GARRICK, L. D., and J. W. LANG. 1977. Social signals and behaviors of adult alligators and crocodiles. *Amer. Zool.* 17:225-239.
- GRIGG, G. C., and J. ALCHIN. 1976. The role of the cardiovascular system in thermoregulation of *Crocodylus johnstoni*. *Physiol. Zool.* 49:24-36.
- HUGGINS, S. E., L. C. PARSONS, and R. V. PENA. 1968. Further study of the spontaneous electrical activity of the brain of *Caiman sclerops*: olfactory lobes. *Physiol. Zool.* 41:371-383.
- HUNT, R. H. 1975. Maternal behavior in the Morelet's crocodile, *Crocodylus moreletii*. *Copeia* 1975:763-764.
- JOANEN, T., and L. MCNEASE. 1972. Propagation of the American alligator in captivity. Pages 106-116 in *Proceedings of the Southeastern Association of Game and Fish Commissioners, 25th Annual Conference* 1971.
- KAUFFMANN, G. 1974. Zurabhängigkeit der Cochleapotentiale des Kaimans vom Stoffwechsel, von aktiven Transporten und von der Temperatur. *J. Comp. Physiol.* 90:245-273.
- KUSHLAN, J. A. 1973. Observations on maternal behavior in the American alligator, *Alligator mississippiensis*. *Herpetologica* 29:256-257.
- LANG, J. W. 1975. Thermoregulatory behavior of adult American alligators. *Amer. Zool.* 15:797 (Abstr.).
- MCNEASE, L., and T. JOANEN. 1975. A study of immature alligators on Rockefeller Refuge, Louisiana. Pages 482-500 in *Proceedings of the Southeastern Association of Game and Fish Commissioners 28th Annual Conference, 1974*.
- MANLEY, G. A. 1970. Frequency sensitivity of auditory neurons in the caiman cochlear nucleus. *Z. vergl. Physiol.* 66:251-256.
- MARCELLINI, D. L. 1974. Acoustic behavior of the gekkonid lizard, *Hemidactylus frenatus*. *Herpetologica* 30:44-52.
- MARLER, P., and W. J. HAMILTON III. 1966. *Mechanisms of animal behavior*. Wiley, New York.
- NAIFEH, K. H., S. E. HUGGINS, and H. E. HOFF. 1970. The nature of the ventilatory period in crocodylian respiration. *Respiration Physiol.* 10:338-348.
- —. 1971a. The nature of the non-ventilatory period in crocodylian respiration. *Respiration Physiol.* 11:178-185.
- —. 1971b. Study of the control of crocodylian respiration by anesthetic dissection. *Respiration Physiol.* 12:251-260.
- NAIFEH, K. H., S. E. HUGGINS, H. E. HOFF, T. W. HUGGINS, and R. E. NORTON. 1970. Respiratory patterns in crocodylian reptiles. *Respiration Physiol.* 9:31-42.
- POOLEY, A. C. 1962. The Nile crocodile *Crocodylus niloticus*: notes on the incubation period and growth rates of juveniles. *Lammergeyer* 2:1-55.
- —. 1969. Preliminary studies on the breeding of the Nile crocodile *Crocodylus niloticus* in Zululand. *Lammergeyer* 10:22-24.
- —. 1976. Mother's day in the crocodile pool. *Anim. Kingdom*, 79:7-13.
- POOLEY, A. C., and C. GANS. 1976. The Nile crocodile. *Sci. Amer.* 234:114-124.
- SMITH, E. N. 1975. Thermoregulation of the American alligator, *Alligator mississippiensis*. *Physiol. Zool.* 48:177-194.
- SOKAL, R. R., and F. J. ROHLF. 1969. *Biometry*. Freeman, San Francisco.
- VERNER, Y. L. 1972. Temperature effects on inner-ear sensitivity in six species of iguanid lizards. *J. Herpetol.* 6:147-177.
- —. 1976. Optimal temperatures for inner-ear performance in gekkonid lizards. *J. Exp. Zool.* 195:319-352.
- WALKER, T. J. 1975. Effects of temperature on rates in poikilotherm nervous systems: evidence from the calling songs of meadow katydids (Orthoptera: Tettigoniidae: Orchelimum) and reanalysis of published data. *J. Comp. Physiol.* 101:57-69.
- WEVER, E. G. 1971. Hearing in the Crocodylia. *Proc. Nat. Acad. Sci. USA* 68:1498-1500.
- ZWEIFEL, R. G. 1968. Effects of temperature, body size, and hybridization on mating calls of toads—*Bufo a. americanus* and *Bufo woodhousii fowleri*. *Copeia* 1968:269-285.