"DISTRESS CALLS" OF CROCODILIANS—WHOM DO THEY BENEFIT?

MARK A. STATON*

Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, Texas 77843

Crocodilians are known to be highly vocal (Campbell 1973), and their hearing capacities, which are superior to those of other reptiles and on a par with those of many birds and most mammals (Bellairs 1971; Wever 1971), enhance vocal/auditory relationships between conspecifics. Young crocodilians often vocalize in a variety of situations: in the presence of food (Campbell 1973), while hatching (Alvarez del Toro 1974; McIlhenny 1935; Staton and Dixon 1977; Voeltzkow 1892), to establish and maintain contact with members of a group (Campbell 1973; Deitz, personal communication), in response to other calls (Campbell 1973), and in situations which might be perceived as dangerous, such as loud noises, rapid nearby movements, or the presence of or seizure by a predator (Campbell 1973; Neill 1971; personal observation). There are few or no differences in the auditory qualities of these calls (Campbell 1973), and their function is identified by the releasing situation. Calls elicited by dangerous circumstances may be given in the presence or absence of the parent female. (Protection of young in crocodilians is usually attributed to the parent female, although there have been suggestions [e.g., Neill 1971; Alvarez del Toro 1974; Hunt 1974] that adults other than the parent female protect juvenile crocodilians.) Correlatively, two main functions have been attributed to the call: (1) a distress call to attract the attention of the parent female, and (2) an alarm call to alert nearby conspecifics in the same pod (groups of young which remain together for varying periods of time after hatching). Subadults and adults of at least two species, *Alligator mississippiensis* (McIlhenny 1935) and *Caiman crocodilus* (personal observation), also give the call, but only rarely. At least in the young, the call may vary in pitch and intensity, depending on the degree of excitement of the animal (Neill 1971; personal observation). The call is frequently referred to as the "distress call," although Neill (1971) chose to restrict the use of this term to the louder, higher-pitched call evoked by a high degree of excitement, i.e., seizure by a predator. However, since the call may function before seizure and regardless of the degree of excitement, calls of different pitch and intensity will be considered together here. Hence, for the purpose of this note, the call will be referred to as the "distress call"; it should

* Present address: P.O. Box 37336, Houston, Texas 77036.

Amer. Natur. 1978. Vol. 112, pp. 327-332.

be borne in mind that this is more inclusive than but functionally similar to the distress call of Neill (1971) and that, at least in its low-pitch/low-intensity form, it does not appear to differ structurally from calls emitted under other circumstances.

The distress call has been recorded in 11 of the 21 extant species of crocodilians, and it probably occurs in all species (Neill 1971). That maternal protection (threats to or attack of potential predator) is evoked by the call is known for seven species (table 1). The adaptive significance to the calling individual is apparent as long as the protective female is nearby. Furthermore, since crocodilians remain together in pods for periods ranging from several weeks to perhaps 2 or 3 yr (Cott 1971; Campbell 1973), and since the parent female protects the young for only several weeks (Cott 1971) to 5 mo (Staton and Dixon 1977) after hatching, these calls undoubtedly serve an alarming function on occasion. From the time the young are abandoned by the parent female until the pod breaks up a call given by an alarmed individual can be of no direct benefit to the caller; it would probably further arouse many predators. During this time, distress calls will primarily benefit other members of the pod at the apparent risk of the caller's life.

The distress call is apparently much rarer in crocodilians past their first year or two of life, as reflected by the rarity of literature records of this phenomenon. On several occasions, I have heard subadult and adult *C. crocodilus* emit the distress call upon my approach; once, while following one closely in a canoe at night, I distinctly heard the caiman emit the vocalization in its low-pitch form. McIlhenny (1935) stated that the call exists throughout the life span of *A. mississippiensis*; he recounted having heard the distress call being emitted by a severely injured adult male who had been defeated by another. The reduced vocalization of the distress call during ontogeny may be related to the fact that as crocodilians grow older and larger they have fewer and fewer natural predators. Most mortality in crocodilians occurs early in life (Neill 1971; Staton and Dixon 1975). Hence, the number of situations that are dangerous to crocodilians and that might elicit the call decreases with age.

The question I pose here is whether the crocodilian distress call, in its alarming capacity, serves as an example of altruistic behavior. Charnov and Krebs (1975, p. 107) defined altruism (in reference to bird calls) as acts that increase "the survival chances of nearby conspecifics while placing the caller in greater immediate danger"; such acts run counter to the traditional neo-Darwinian concept of individual selection, termed "genic selection" by Williams (1966). Alarm calls of birds have been depicted as altruistic and explained as having evolved by group selection (Wynne-Edwards 1962). More in keeping with the concept of genic selection, Maynard Smith (1965) advocated kin selection as an explanation of the origin of avian alarm calls. Since crocodilian pods, at least early in life, consist mostly or entirely of siblings, it might seem reasonable to invoke kin selection as an explanation of the seemingly altruistic crocodilian calls, but only if the call contributes more to the fitness of the caller's relatives than to the caller's fitness.

Several authors recently have postulated explanations of the avian alarm call

TABLE 1

LITERATURE RECORDS OF "DISTRESS CALLS" IN CROCODILIANS AND OF MATERNAL PROTECTION EVOKED BY THE CALL

Species	Juvenile "Distress Call" Exists	Maternal Protection is Evoked by Juvenile's "Distress Call"	Distress Call Found in Adults and Subadults
Alligator mississippiensis	Kushlan 1973; Campbell 1973; McIlhenny 1935; pers. obs.	Kushlan 1973; McIlhenny 1934	McIlhenny 1935; Deitz (pers. commun.)
Caiman crocodilus	Campbell 1973; Neill 1971; pers. obs.	Pers. obs.	Pers. obs.
Crocodylus acutus	Campbell 1973; Neill 1971	Neill 1971	...
Cr. cataphractus	Neill 1971	...	...
Cr. moreletii	Hunt 1974	Hunt 1974, 1975	...
Cr. niloticus	Cott 1961; Neill 1971	...	...
Cr. novaeguinae	Neill 1946, 1971	Neill 1946, 1971	...
Cr. palustris	Neill 1971	Neill 1971	...
Cr. porosus	Neill 1971	...	...
Cr. siamensis (?)	Neill 1971	...	...
Melanosuchus niger	Campbell 1973	Hartwig 1873	...

in terms of the caller's benefits. Perrins (1968) noted that the alarm calls of the Great Tit (*Parus major*) were difficult to locate and that therefore calling did not jeopardize the caller's survival. Such "ventriloquial" qualities are not known in crocodilian calls, however, and this explanation cannot apply to them. Charnov and Krebs (1975) argued that calling by individual birds in a flock in response to aerial predators is manipulation of conspecifics to confuse the predator and hence is of benefit to the caller. The same could be argued for crocodilians according to the observations of Campbell on *Caiman* and *Crocodylus* (personal communication) and on *A. mississippiensis* (Campbell 1973, p. 2; personal communication): "In the field, vocalizations were usually accompanied by short lunges away from the source of disturbance. This would be repeated throughout the group with a resulting net movement away from the disturbance." Trivers (1971) has postulated that alarming the entire group to avoid predation of any member would ultimately benefit the caller, since it would prevent the predator from specializing on the caller's species and locality. As for the case made by Charnov and Krebs, Trivers's hypothesis explains the avian alarm call through its contribution to the caller's personal fitness, and these arguments are applicable to the crocodilian call.

Both Charnov and Krebs's and Trivers's hypotheses share a common mechanistic feature—they rely upon the call's effect on groups of conspecifics to explain its importance to the caller; an analysis of the ontogeny of the distress call of crocodilians provides an explanation of its alarming capacities based solely on the effects of the call on the caller, which is simpler and hence more desirable (Williams 1966). After the young have been abandoned by the parent female, calling in dangerous situations could be termed altruistic as defined by Charnov and Krebs (1975). The vocalization persists into adult life in situations deemed dangerous by the caller. Hence, altruism seems to be a component of individual behavior in crocodilians, a component which is disadvantageous to the caller. However, during the initial months of the life of a crocodilian, which are usually spent in care of the parent female (the most crucial months, since this is when mortality is the greatest [Staton and Dixon 1975]), the distress call contributes overwhelmingly to the caller's personal fitness—to the extent that later disadvantages are overridden. It is true that during these initial months the alarming capacity of the call may be beneficial to other members of the pod, but such benefits are less than the survival value inherent in their own call coupled with the care of the parent female. Furthermore, any negative effects of the call in its supposedly altruistic role would be nullified by the presence of the protective female. A caller at any stage of its lifetime would be calling because its life is endangered, and selection has favored calling in such situations. Nonmaternal benefits received by individuals throughout their lifetime would probably "average out." Neither group selection nor kin selection need be invoked to explain the origin and retention of the call. That calling may, after crocodilians are no longer in the care of their female parent, be of value to kin (when in unprotected pods) or to unrelated conspecifics (when in congregations as adults or subadults) is a fortuitous effect.

Wilson (1975, p. 123) has listed the four hypotheses advanced to account for avian warning calls, and two of these (group selection and kin selection) have been rejected for crocodilians on the basis of parsimony. With the important difference that the mechanism advanced herein deals with juveniles rather than adults, it resembles portions of the other two hypotheses listed by Wilson: "Warning calls function in the breeding season to protect the mate and young and are simply extended into the off season because it burdens the DNA to encode a seasonal adjustment . . .," and "Warning calls evolved by individual selection because, in spite of first appearances, they actually help the bird giving the call." In the case of crocodilians, the warning call is also a distress call to elicit the protection of the parent female. In spite of first appearances during most of the animal's life, the call is unmistakably of overwhelming importance to the caller in its critical initial months, and genic selection explains the call's existence. That the distress call is not as frequently vocalized in later life substantiates this conclusion. Most warning calls discussed in the literature are those of adults, and attempts to explain the evolution of these vocalizations have examined the advantages and disadvantages of the call in the adult stage. It is possible that, instead, such calls evolved in early life with a function and effects similar to those of crocodilian distress calls and that, in some species, the function of the call has been renovated in the adult stage. This possibility should be investigated.

ACKNOWLEDGMENTS

I am especially indebted to J. D. McEachran for critically examining several drafts of the manuscript. D. Deitz, J. Farlow, F. Medem, H. Campbell, and J. Dixon provided valuable comments on the ideas presented in this note, although they do not necessarily agree with them in their entirety. I thank F. Wills and R. Thomas for editorial comments. R. Fish and my wife, Allison, have been most dependable field companions. My work on crocodilians has been financed by Sr. Tomas Blohm of Venezuela, a grant from the Office of Endangered Species and International Affairs (with J. Dixon), and a 9-mo NSF traineeship from the graduate school of Texas A&M University.

LITERATURE CITED

Alvarez del Toro, M. 1974. Los crocodylia de Mexico. Instituto Mexicano Recursos Naturales Renovables, Mexico, D.F.

Bellairs, A. d'A. 1971. The sense of crocodilians. Pages 181–191 *in* Crocodiles. Proc. 1st Meeting of Crocodile Specialists. Intern. Union Conserv. Natur. Publ., N.S., Suppl. Paper 32.

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

Charnov, E. L., and J. R. Krebs. 1975. The evolution of alarm calls: altruism or manipulation? Amer. Natur. 109:107–112.

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.

———. 1971. Parental care in the crocodilia, with special reference to *Crocodylus niloticus*. Pages 166–180 *in* Crocodiles. Proc. 1st Meeting of Crocodile Specialists. Intern. Union Conserv. Natur. Publ. N.S., Suppl. Paper 32.

Hartwig, G. 1873. The tropical world: aspects of man and nature in equatorial regions of the globe. Longmans & Green, London.

Hunt, R. H. 1974. Hatching and rearing of the morelet's crocodile, *Crocodylus moreletii*. Proc. Amer. Ass. Zool. Parks Regional Conf., Arlington, Tex.

———. 1975. Maternal behavior in the morelet's crocodile, *Crocodylus moreleti*. Copeia 1975:763–764.

Kushlan, J. A. 1973. Observations on maternal behavior in the American alligator, *Alligator mississippiensis*. Herpetologica 29:256–257.

McIlhenny, E. A. 1934. Notes on incubation and growth in alligators. Copeia 1934:80–88.

———. 1935. The alligator's life history. Christopher, Boston.

Maynard Smith, J. 1965. The evolution of alarm calls. Amer. Natur. 94:59–63.

Neill, W. T. 1946. Notes on *Crocodylus novae-guinae*. Copeia 1946:17–20.

———. 1971. The last of the ruling reptiles. Columbia University Press, New York.

Perrins, C. M. 1968. The purpose of the high-intensity alarm call in small passerines. Ibis 110:200–201.

Staton, M. A., and J. R. Dixon. 1975. Studies on the dry season biology of *Caiman crocodilus* from the Venezuelan llanos. Mem. Soc. Cienc. Natur. La Salle 35:237–265 (Caracas).

———. 1977. The breeding biology of the spectacled caiman, *Caiman crocodilus crocodilus*, from the Venezuelan llanos. Fish and Wildlife Service, Wildlife Res. Rep. 5.

Trivers, R. L. 1971. The evolution of reciprocal altruism. Quart. Rev. Biol. 46:35–57.

Voeltzkow, A. 1892. On the oviposition and embryonic development of the crocodile. Ann. and Mag. Natur. Hist. 9:66–72.

Wever, E. G. 1971. Hearing in the crocodilia. Proc. Nat. Acad. Sci. 68:1498–1500.

Williams, G. C. 1966. Adaptation and natural selection. Princeton University Press, Princeton, N.J.

Wilson, E. O. 1975. Sociobiology, the new synthesis. Belknap, Cambridge, Mass.

Wynne-Edwards, V. C. 1962. Animal dispersion in relation to social behavior. Oliver & Boyd, Edinburgh.