COMMENTARIES

Progressive Analysis of Avian Vocal Repertoires with Special Reference to the Brown Noddy

NICHOLAS E. COLLIAS¹

Three steps are necessary in the study of avian vocal repertoires (aside from developmental and physiological aspects). (1) The various vocalizations and the situations (context) under which they are given must be identified and described under natural conditions. The description should be objective enough so the calls can be readily recognized by other observers. Tape recordings and sonographic study enable precise description of the calls. Common elements in the different situations in which a call is given will suggest the probable significance of each call. In graded signals and intermediate stimulus situations such continua can be arranged into opposite or antithetical extremes (Riska 1986a, b; Collias 1987). (2) An analysis should be made of the general situation or context in which a specific type of vocalization is given. Systematic variation of the stimulus situation under controlled experimental conditions is useful in the advance from correlational to causal analysis (Marler et al., 1986a, b). (3) Finally, one should analyze the response of the receiver to a given vocal signal, supplemented by experimental playbacks of this vocal signal and of synthetic sounds, in the appropriate context (Collias and Joos 1953).

Recently Riska (1986a, b) inventoried and described the vocal repertoire of young and adult Brown Noddy terns (*Anous stolidus*) in the Dry Tortugas. The terns were observed over four breeding seasons. This study is of special interest because it deals with a species having graded vocalizations.

J. W. Chardine (1987) criticized the study in effect for not taking the next logical step in the analysis. I believe it would be a disservice if readers with an interest in avian vocalizations were dissuaded by Chardine's commentary from reading Riska's articles. He mentions none of the numerous contributions of these articles: a great many noddies were color-banded for individual identification; the entire vocal repertoire was taped and video recordings made of the associated behavior patterns; and, the stimulus situations (context) for all the different calls were described concisely and tabulated. In the laboratory several spectrograms of each call were measured and analyzed by a new method which enabled a computer to read and record the x-y coordinates directly. The results showed the degree of overlap for the same call

in different aged chicks and for the different calls in the adults.

According to Chardine, Riska's "data were reported in such a way as to strongly imply there was a deterministic relationship between a stimulus (context) and the response in the chick or adult. For example, the statement 'Chicks that are alone on the nest Screech when an intruder appears' (Riska 1986a: 355) implies that the response always followed the stimulus." But nowhere does Riska claim 100% determination by the stimulus situation of any response. The inference I drew was of a characteristic relationship between a given situation and a given signal, not necessarily an invariable one. Furthermore, because the Screech was given only to an intruder at the nest (other noddy, Sooty Tern, or human) the evidence is certainly sufficient to establish a close connection with the presence of an intruder.

Chardine continues to quote Riska with reference to the Screech: "Chicks turn toward and face the intruder, spread the wings to one side, and Screech." He then comments "Always? Seventy-two percent of the time? Or does the probability change with chick age or type of intruder?" He suggests that the posture described by Riska is more characteristic of the response elicited by a human intruder. He cites unpublished observations that noddy chicks hide their bills when approached by a conspecific intruder, but he does not mention what proportion of the time they do this or Screech to the intruder.

One can decide the context under which a signal is given directly, and far more quickly, by repeatedly noting the situation (context) when the signal is given, as Riska did. One can then reverse the analysis and enumerate how often a specific vocal signal accompanies a specific context. This procedure might be useful for later analysis of stimulus situations, but I think we need first to establish what the vocal signals are and give a qualitative description of their correlated contexts, often complex and variable, before further analysis of the stimulus situation. We can then decide what is worth quantifying and how to do so.

The primary objective of Riska's study was a precise, quantitative description of the vocal signals. Their interpretation in relation to context reflected an author's privilege to make conclusions from such data as have been gathered, to discuss the implications of the data, as well as to indicate possible leads for future work (CBE Style Manual 1978: 11). For example, Riska

¹ Department of Biology, University of California, Los Angeles, California 90024 USA.

tabulated seven different situations or contexts in which the Harsh Cheep was given and then took the common element in the various contexts to deduce that the Harsh Cheep is given when a chick is in motion or out of the nest (p. 356). Adults respond to these calls by approaching the chick, brooding, shading, and preening it, and usually by giving a special call; hence the need to provide such care is the meaning to the adult, as interpreted. Chardine's discussion of message and meaning is somewhat confusing since he does not make it clear that (sensu Smith 1977) "message" refers to the signaler, "meaning" to the receiver. Messages (of the signaler) and meanings (to the receiver) are not just redundant statements of contexts and responses because they often represent generalizations.

Chardine continues his critique: "the author stated without qualification that the Frequency-modulated Cheep, produced by the chick and observed in the context of a close parent, 'means' the chick is hungry. Clearly, it is a very broad leap to suggest that a particular behavior such as this is a good external 'marker' for an internal motivational and physiological state such as hunger." What Riska wrote (p. 357) was a bit different: "The message of the caller is that it is hungry, and the meaning to the adult is that it should feed the chick on the nest" (italics my own). I don't find the idea that the Frequency-modulated Cheep is a good external marker of hunger at all a broad leap of the imagination, judging from all the associated foodbegging behavior along with the customary sequelae of being fed by the adult. Additional data showing that "the probability of a chick producing its vocalization increases with time since the last feeding or that the probability of an adult feeding the chick upon hearing the chick is high," as Chardine recommends, might be useful verification and in continuing the analysis.

In any time-limited project, there are practical limits to the amount of data that needs to be gathered in order to accomplish the primary purpose of the study. In her study of the vocal repertoire of the Brown Noddy, Riska describes 12 vocal signals given in a total of 45 contexts. The further analysis of the stimulus situations in quantitative terms is obviously a large and separate project for the future.

LITERATURE CITED

- CHARDINE, J. W. 1987. Brown Noddy vocal behavior. Auk 104: 790.
- COLLIAS, N. E. 1987. The vocal repertoire of the Red Junglefowl: a spectrographic classification and the code of communication. Condor 89: 510–524.
- , & M. JOOS. 1953. The spectrographic analysis of sound signals of the domestic fowl. Behaviour 5: 175–188.
- COUNCIL OF BIOLOGY EDITORS STYLE MANUAL. A guide for authors, editors, and publishers in the biological sciences. 1978. 4th ed. A CBE publication.
- MARLER, P., A. DUFTY, & R. PICKERT. 1986a. Vocal communication in the domestic chicken: I. Does a sender communicate information about the quality of a food referent to a receiver? Anim. Behav. 34: 188–193.
- , ____, & ____. 1986b. Vocal communication in the domestic chicken: II. Is a sender sensitive to the presence and nature of a receiver? Anim. Behav. 34: 194–198.
- RISKA, D. E. 1986a. An analysis of communication in young Brown Noddies (*Anous stolidus*). Auk 103: 351–358.
- 1986b. An analysis of communication in the adult Brown Noddy (*Anous stolidus*). Auk 103: 359-369.
- SMITH, W. J. 1977. The behavior of communicating. Cambridge, Masssachusetts, Harvard Univ. Press.

Received 21 January 1988, accepted 22 March 1988.

Female Song in Willow Flycatchers

DAVID E. DAVIS

The note by Seutin (Auk 104: 329-330, 1987) discusses what the author calls "female song." Unfortunately the vocalization to which he refers is the "position" note given by both male and female Empidonaces (Davis, Auk 71: 164-171, 1954; Davis, Wilson Bull. 71: 73-85, 1959). The advertising song is given at dawn or dusk and is an elaborate performance. The bird rises above the treetops, utters a variety of strange notes including position notes, and tumbles down, like a butterfly, to the trees (Davis, Wilson Bull. 71: 73-85, 1959; MacQueen, Wilson Bull. 62: 194-205, 1950; McCabe, Wilson Bull. 63: 89-98, 1951). The individuals are presumably males but identification of sex is impossible in the dim light and the rapid flight. I heard the

¹ 777 Picacho Lane, Santa Barbara, California 93108 USA.