

Papéis Avulsos de Zoologia

PAPÉIS AVULSOS ZOOL., S. PAULO, VOL. 32 (15): 193-200

20. II. 1979

DESCRIPTIONS OF THE ADVERTISING CALLS OF *CYCLORAMPHUS ASPER* AND *CYCLORAMPHUS DUBIUS* (AMPHIBIA: LEPTODACTYLIDAE)

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ABSTRACT

The advertising calls of Cycloramphus asper and C. dubius are described. The calls of these two species are very similar. The advertising call of each species apparently maximizes location information at the expense of species coding information. The advertising calls of Leptodactylus melanonotus and L. wagneri, which also have a strong location component, differ from Cycloramphus calls in that they appear to package species coding information in such a way that location information is maximized. Advertising calls lacking a distinctive species coding component are rare in frogs; the only other reported instance occurs in members of the Australian genus Pseudophryne.

The specific status of the taxa *Cycloramphus asper* and *C. dubius* is confused in the literature. Bokermann (1951), the last person to revise the genus, considered the two distinct. Cochran (1955), in her faunal survey of southeast Brazilian frogs, synonymized *C. dubius* with *asper* with no explanation. Bokermann (1966) listed the two taxa as distinct in his type locality list of the amphibians of Brazil, without comment on Cochran's action. Both species of *Cycloramphus* occur at the biological station Boracéia in the Serra do Mar, State of São Paulo. Although overall aspects of all specimens are similar, differences in foot webbing as figured by Bokermann (1951) clearly distinguish individuals of the two taxa. The morphological and biochemical relationships of these taxa with each other and with other members of the genus are being explored in other studies in progress.

The purpose of this paper is to describe and compare the calls of sympatric males from Boracéia and, also, to compare the *Cycloramphus* calls with functionally similar calls of *Leptodactylus melanonotus* and *L. wagneri*.

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METHODS AND MATERIALS

The calls analyzed consist of individual notes given at irregular intervals. We recorded calls in the field with a Uher CR 134 cassette recorder. We recorded two notes for *C. dubius* and seven notes from two individuals *C. asper*. Individual notes were analyzed on a Kay Sonagraph 6061 B, a Hewlett Packard 7402A strip chart recorder and a Brüel and Kjaer 2121 frequency analyzer. Spectrum analyses of whole calls for Figures 2 and 3 were made by repeating calls from a tape loop into the B and K frequency analyzer set to minimum bandwidth (1%) and slow RMS meter function. Each dot in the analysis represents the peak meter reading for a discrete analyzer frequency setting. This type of frequency analysis is similar to the sectioner output of the Kay Sonagraph, but integrates frequency versus intensity to represent a whole call rather than a discrete instant of time.

DESCRIPTIONS OF CALLS

Cycloramphus asper. The call is a sharp click (Figure 1) with a duration of .03-.04s. The call is not finely tuned; energy is spread over a broad frequency range from about 200 to 5000 hz. There is considerable variation in frequency distribution among calls of a single individual and between individuals (Figure 2). The most intense frequency common to the two specimens of *C. asper* centers on 800 hz. Although there is considerable variation in the distribution of sound energy among calls from a single individual (Figure 2b), the available data suggest that there are characteristics of the sound energy distribution that differentiate calls of individual males. For example, the calls of the specimen represented in Figure 2b all have a notable energy component around 1500 hz. The calls of the specimen represented in Figure 2a do not have a notable frequency component around 1500 hz.

Cycloramphus dubius. The call sounds similar to that of *C. asper*, being a sharp click (Figure 1) and also has a duration of about .03s. The call is not finely tuned; energy extends from about 500 to 3500 hz. The energy distributions of the two notes available for analysis are quite different (Figure 2c), although high energy occurs in both notes at about 1400 hz and 2000 hz.

The calls of *C. asper* and *dubius* are more similar than different. The calls appear to differ in the most intense frequencies, however. The most intense frequency of the call in *C. asper* centers around 800 hz and around 2000 hz in *C. dubius*.

DISCUSSION

As Wells (1977) recently summarized, vocalizations of male frogs advertise species identity, sex, reproductive state, and spatial location. Female *Cycloramphus* are not known to call, so when a *Cycloramphus* calls, it advertises its maleness. It seems unlikely that males call when not in reproductive condition. The call itself contains informa-

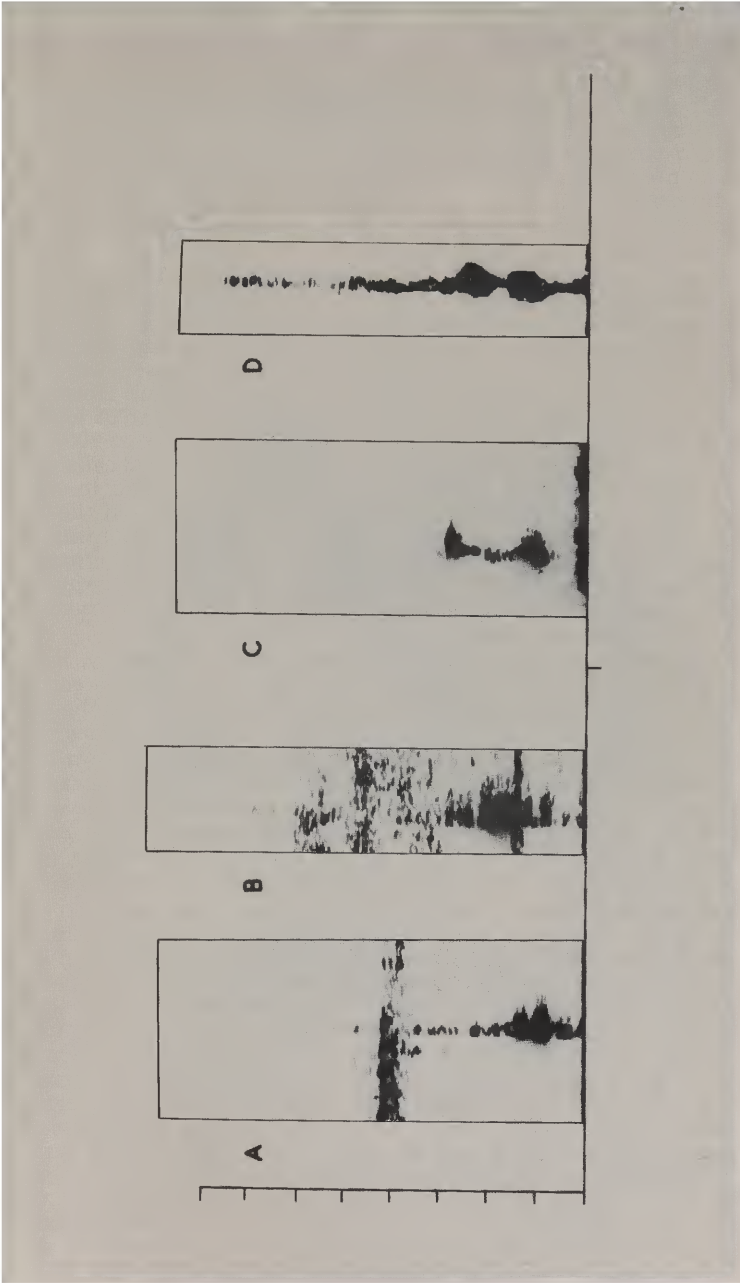


Fig. 1. Sonagrams of advertisement calls of (A) *Cycloramphus asper*, WRH field 4367, Brasil: São Paulo, Boracéia, air temperature 21.8°C; (B) *Cycloramphus dubius*, WRH field 4654, Brasil: São Paulo, Boracéia, air temperature 19°C; (C) *Leptodactylus wagneri*, Ecuador: Napo; Limoncocha (D) *Leptodactylus melanonotus*, Costa Rica. Vertical marks at 1000 Hz intervals, horizontal mark indicates 1 second. Background noise blocked out for *L. melanonotus* call only.

tion on species identity and spatial location. It is difficult to maximize these types of information simultaneously, however. A call that maximizes location information is of short duration, is poorly tuned (broad frequency), and has a sharp attack (the beginning of the call is of high intensity), like the sound produced by clicking two coins together. A call that maximizes species coding information is finely tuned (narrow frequency) and either of long duration or repeated at predictable intervals (see Straughan and Heyer, 1976, for further discussion). The calls of *Cycloramphus asper* and *C. dubius* both appear to maximize location information, with species coding information being of secondary importance.

There are two basic ways to code species specificity in frog calls: through the broadcast channel used or through the duration and kind of repetition pattern (Littlejohn, 1977; Straughan, 1975). The duration of *C. asper* and *C. dubius* notes are the same and the notes are given at irregular intervals in both species. Thus, there is no time component coding for species specificity in either taxa. However, there may be a difference in broadcast frequency. If the ear of female *C. asper* is tuned to 800 hz and the ear of female *C. dubius* to 2000 hz, then female *C. dubius* probably could not hear male *C. asper* calls (see Figure 2). However, female *C. asper* could hear and respond to male *C. dubius* calls, since the *C. dubius* call has intense energy in the 800 hz range. Neurophysiological studies of other species (Capranica, 1977) suggest that a frequency of around 800 hz is not an effective species coding frequency since all frogs hear well in this frequency range. We postulate that any species coding information present in the calls of *C. asper* and *dubius* is partially effective at best.

The interpretation of the calls of *C. asper* and *C. dubius* as being location information calls (hence not having much species coding information) is consistent with the ecological distribution of the two species at Boracéia. If the species coding information does not effectively communicate species identity in the two taxa, the two taxa should not occur in the same place at the same time. At Boracéia, the two species are nocturnal and call at the same time of the year, but occur in different habitats. *Cycloramphus asper* occurs along small forest streams. *Cycloramphus dubius* occurs on the sheer rock walls of a quarry where water seeps over the rock wall surfaces.

Straughan and Heyer (1976) suggested that the kind of call produced by *Cycloramphus asper* and *dubius* results from a burst of air forced through the vocal cords. This produces a poorly tuned call with a sharp attack — a pulse of broad frequency noise. There are two features of this type of call that communicate location: (1) the sharp attack and brevity, and (2) the broad frequency band. In all frogs that have been tested, the female ear is tuned to two main frequency channels, a low frequency channel and a higher frequency channel correlating with the male mating call (Littlejohn, 1977; Straughan, 1973, Lombard & Straughan, 1974). These two channels do not receive at the same time (Lombard and Straughan, 1974). Unless the ear of female *Cycloramphus* differs from all other frog ears tested, it will be tuned to a rather narrow frequency. Thus most of the broad frequency band produced by the male would not be communicated to the female. Therefore, she would have to use the sharp attack and brevity of the call for location information. Perhaps the only way a

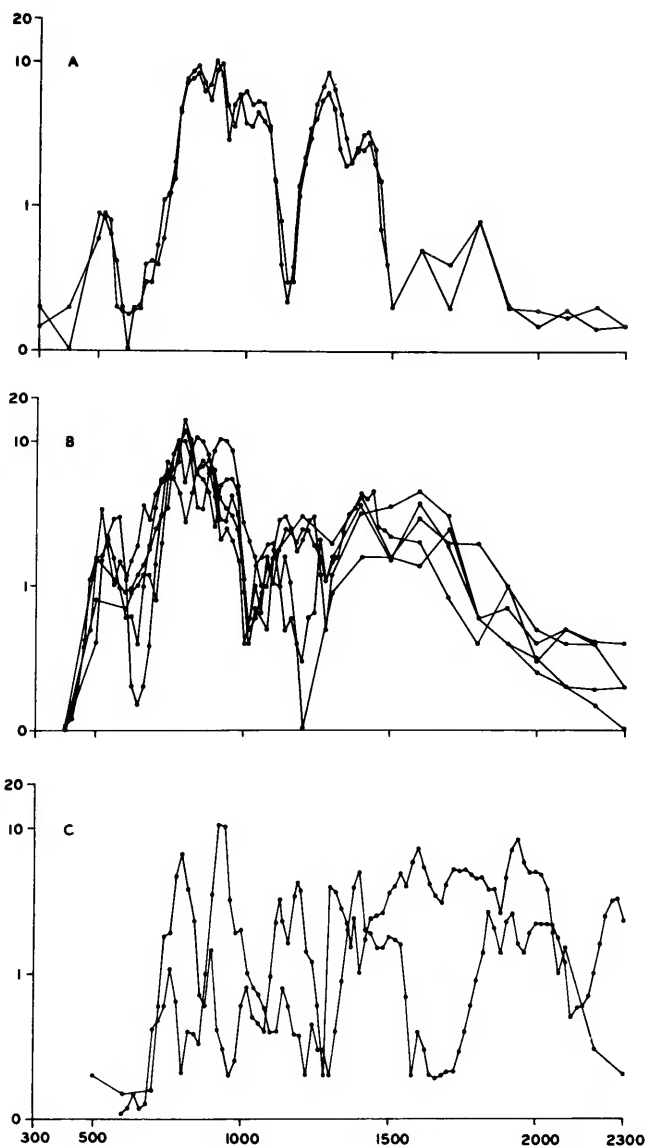


Fig. 2. Energy distribution for (A) two calls of *Cycloramphus asper*, WRH field 4367, (B) five calls of an individual (not captured) *Cycloramphus asper*, (C) two calls of *Cycloramphus dubius*, WRH field 4654. Vertical scale is relative intensity read from voltmeter of frequency analyser plotted logarithmically. Horizontal scale (linear) in hertz. Each dot represents the frequency where a reading was taken.

male *Cycloramphus* can produce a sharp attack call is by forcing a burst of air over the vocal cords. The broad frequency band of the call may be an unavoidable consequence of the anatomical system used to produce a sharp attack call.

The calls of *Leptodactylus melanonotus* and *L. wagneri* both appear to have sharp attacks and a broad frequency range when analyzed on the sonograph (Figure 1). The calls do have a broad frequency range (Figure 3), but the calls appear to be produced quite differently from those of *C. asper* and *C. dubius*. As seen on the oscilloscope strip chart recordings (Figure 4), the call of *C. asper* is not composed of a single sine wave, because the entire broad frequency band is analyzed simultaneously. The call does have a sharp attack. In contrast, the call of *L. wagneri* is composed of a lower frequency, pulsatile sine wave followed by a higher frequency, nonpulsatile sine wave (Figure 4). The shortness of each component and their juxtaposition produces a single note sound to the human ear (and is so produced on the sonogram). Furthermore, the *Leptodactylus wagneri* call is well tuned and does not have as sharp an attack as the *Cycloramphus* call (Figure 4). The calls of *L. melanonotus*, *L. wagneri*, *C. asper* and *C. dubius* all appear to maximize location information. However, the location information is produced differently in these two genera. The *Cycloramphus asper* and *dubius* calls appear to be maximizing locality information at the expense of species specific information. The *L. melanonotus* and *wagneri* calls appear to be packaging species specific information in a manner that maximizes location information. As an aside, the call of *L. wagneri* appears to have two messages. It would be interesting (and possible) to determine if the lower frequency unit contains territorial information broadcast to other males and the higher frequency unit contains mating information for females as in *Rana catesbeiana* and *Eleutherodactylus coqui* (Capranica, 1977).

No information can be derived from the calls of *C. asper* and *C. dubius* to determine whether the calls are convergent or reflect close relationship of the two taxa. Similarities of frog calls are often due to convergence (Schiotz, 1973) because frogs have limited morphological ways of producing calls.

Certain sympatric species of the Australian frog genus *Pseudophryne* do not contain clear-cut species specific coding information in their calls (Pengilley, 1971). This is the only other case known to us of advertising calls maximizing information other than species coding information. The *Pseudophryne* species involved produce a variety of calls, some of which resemble the *Cycloramphus* calls in structure. Pengilley (1971) designated these calls, given when a female was within sight of the male, as courtship calls. Males call from burrows in mossy or grassy situations, so location information is at a premium. In contrast to *Cycloramphus*, the *Pseudophryne* species are not separated by habitat differences and Pengilley (1971) postulates that other differences act as premating isolating mechanisms, such as time of breeding, color and pattern.

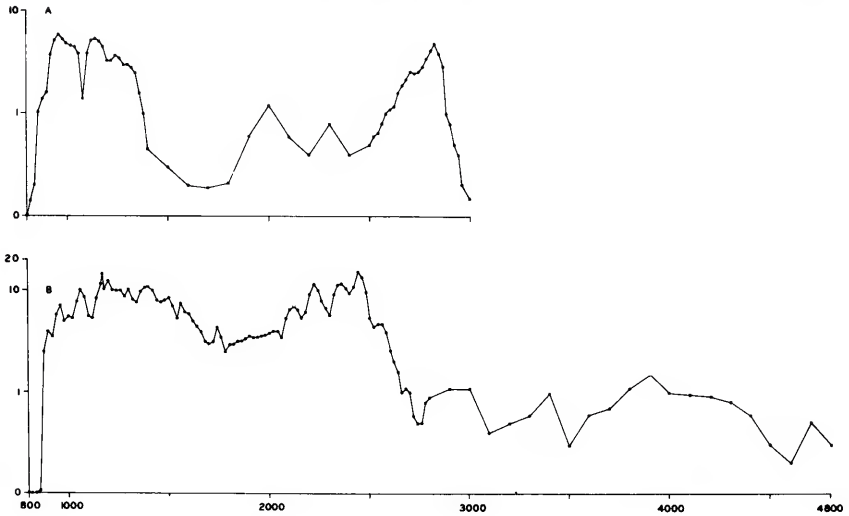


Fig. 3. Energy distribution for (A) a call of *Leptodactylus wagneri* and (B) *Leptodactylus melanonotus*. Vertical scale is relative intensity read from voltmeter of frequency analyser plotted logarithmically. Horizontal scale (linear) in hertz. Each dot represents the frequency where a reading was taken.

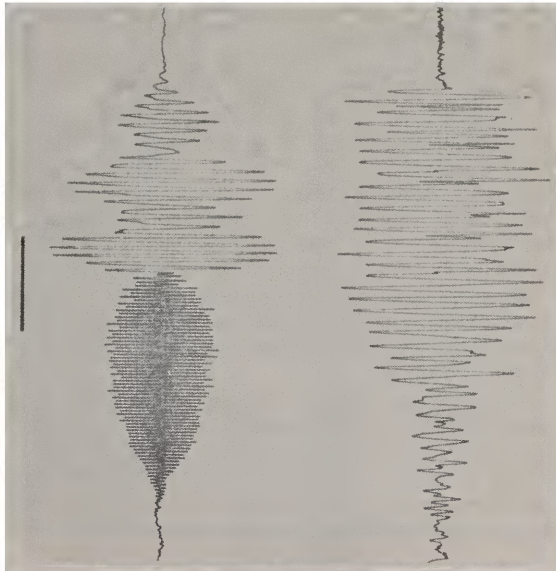


Fig. 4. Oscilloscopic strip chart recordings of calls of *Cycloramphus asper* (upper) and *Leptodactylus wagneri* (lower). Line equals 0.01 second.

ACKNOWLEDGEMENTS

George R. Drewry provided advice during the analysis and interpretation of the calls and critically read the manuscript. Kentwood D. Wells and George R. Zug also read the manuscript. We thank them for their comments.

This is a contribution to the research project, "Evolutionary Zoogeography of the Atlantic Forest System of Brazil: The Anuran Examples", supported jointly by the Museu de Zoologia da Universidade de São Paulo and the Smithsonian Institution's Amazon Ecosystem Research Program.

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