Biogéographie de Madagascar, 1996 : 403-410

EXTENDED CALL REPERTOIRE OF A MADAGASCAR FROG

Peter M. NARINS [1] & Edwin R. LEWIS [2]

[1] *Department of Physiological Science, 621 Circle Drive South, Box 951527, University of California, Los Angeles, CA 90095-1527* U.S.A.

[2] *Department of EE & CS, University of California, Berkeley, CA 94720* U.S.A.

ABSTRACT.- The call repertoire of *Boophis madagascariensis* (Rhacophoridae) males was recorded in the natural habitat of this animal- the rain forest in eastern Madagascar. We have classified the calls made by males of this species into 28 types. Even if all « iambic » calls are considered variants of one type, there are still 8 call types produced by this species. This represents the largest call repertoire of any frog reported to date. Playback studies using a subset of the natural calls as stimuli were carried out to determine the functional significance of several of the call types. We found one sequence of call notes evoked increased call rates from males, other note sequences inhibited males from calling, whereas others appeared to have no effect on male calling rate. The evolutionary significance of an extended call repertoire is discussed.

KEY-WORDS.- Vocalizations, Rhacophorid frogs, *Boophis*, Playback studies

RESUME.- Les cris mâles du *Boophis madagascariensis* (Rhacophoridae) ont été enregistrés dans son milieu naturel, la forêt tropicale humide de l'est de Madagascar. Nous les avons classés ensuite en 28 types différents. Bien que tous les cris « iambiques » soient considérés comme les variantes d'un même type, cette espèce en compte 8 à son actif, ce qui représente le plus large répertoire jamais réalisé pour les grenouilles. Des extraits de la bande témoin ont été utilisés comme stimuli afin d'établir la signification fonctionnelle de quelques types. Une séquence de la bande témoin a pour effet d'accélérer la vitesse d'émission des cris mâles; une autre, de les suspendre alors que d'autres extraits ne modifient pas le son d'origine. La signification fonctionnelle d'un répertoire élargi des cris est discutée.

MOTS-CLES.- Vocalisations, Grenouilles Rhacophoridae, *Boophis*, Etudes en « playback »

INTRODUCTION

Most frogs and toads are vocal. Males typically produce a small number of stereotyped, repetitive vocalizations that have a restricted number of functions. At least five major call types were recognized by BOGERT (1960) including the mating call, the territorial call, the distress call, the warning call, and the release call. In addition, males of some territorial species produce a call when another frog, usually a male, is detected within their territory. This call is distinct from the mating call and is referred to an encounter call (MCDIARMID & ADLER, 1974), now more commonly referred to as a short-distance aggressive call (SALTHE & MECHAM, 1974). Generally, a frog's mating

In: W.R. LOURENÇO (éd.)
Editions de l'ORSTOM, Paris

call serves more than one function and so it is now referred to as the advertisement call (WELLS, 1977).

The advertisement call notes may be repeated in a periodic fashion for many hours and are often highly stereotyped in their structure. That is, the calls are redundant and are emitted with little spectral or temporal variation in their call parameters. These factors presumably confer the calls with increased localizability and noise immunity, both highly advantageous features in an environment such as a tropical rain forest, characterized by extremely high levels of ambient noise during the evening hours, when most anuran amphibans are actively calling.

Many anurans have advertisement calls that consist of a single repeated note or trill. However, some species have more complex advertisement calls consisting of multiple notes (NARINS & CAPRANICA, 1976; LITTLEJOHN, 1977; WELLS, 1988). For example, some hylids such as *Smilisca sila* are capable of producing single or multiple-note calls, but the notes are identical in both call types (TUTTLE & RYAN, 1982). In contrast, the advertisement call of the neotropical leptodactylid *Physalaemus pustulosus* (RAND & RYAN, 1981) consists of a « whine » note followed by a variable number of « chuck » notes, which are spectrally and temporally quite distinct. At the time of this observation, *Physalaemus* was thought to have one of the most complex vocalizations of any frog (TUTTLE & RYAN, 1982). Complexity is evident in the vocalizations of *Hyla ebraccata* as well, in which males respond to conspecific calls by increasing the proportion of their multi-note and aggressive calls (WELLS & GREER, 1981, SCHWARTZ & WELLS, 1984). In a more recent study, the striped morph of *Polypedates leucomystax*, a rhacophorid frog common in Peninsular Malaysia, appears able to produce an advertisement call with at least three distinct notes, suggesting yet greater complexity (NARINS *et al.*, 1996).

Boophis madagascariensis (Rhacophoridae) is endemic to Madagascar where it is restricted to the eastern half of the island. It is a large (60-80 mm snout-to-vent) brown treefrog with large dermal flaps on the elbows and heels. Males are smaller than females (PETERS, 1874). During the day, they may be found in the leaf axils of large plants, but at night males call from shallow water, at the border of pools or slow-moving streams or from elevated perch sites on the vegetation. Male calls are easily recorded since they are not readily disturbed by the sounds of investigators in their vicinity. They may be found calling from sunset until 0100-0200 hours during November.

Our goal in this study was to record and characterize the vocal repertoire of *Boophis madagascariensis*. In addition, we used acoustic playback experiments with natural calls as stimuli to determine both the functional significance of some of the call types as well as the effect of increasing call intensity on the evoked calling responses.

MATERIALS & METHODS

Field recordings and playback experiments were conducted during October, 1993 at a location about 0.8 km east of the entrance to Ranomafana National Park (21.25°S, 47.3°E), approx. 240 km south of Antananarivo, Madagascar. At the study site (altitude: 900m), several species of frogs could be found calling from the ground along the roadside or from the emergent vegetation up to several meters above the ground. Ambient temperature and relative humidity were consistently between 18°-22°C and

88%-95%, respectively. All experiments were carried out between 18h45 and 00h25 hours, local time, when calling activity was most intense.

Calling males of *Boophis madagascariensis* were located in their natural habitat. Ambient temperature, relative humidity, a description of the calling site, estimate of nearest-neighbor distances, and any vocal interactions with neighboring males were noted for each individual studied. Two minutes of spontaneous vocalizations were registered with a directional microphone (Audio-Technica AT-835 or AKG CK8) that was placed 10-35 cm from each calling male and recorded onto a portable cassette recorder (Sony Walkman Pro WM D6C). All recordings were made using low-noise tape (TDK Type II).

Following this, we broadcast acoustic stimuli consisting of natural call sequences (see below) using the Sony Walkman driving a speaker-amplifier (Calrad 20-257) and a 10-cm diameter loudspeaker, fixed at the end of a boom on a tripod. This arrangement allowed the loudspeaker to be placed 110 cm from the calling male without disturbing him. The stimuli were simultaneously recorded on one channel of a stereo tape-recorder (Marantz PMD 430), while the male's vocalizations were recorded on the other channel.

Four stimuli were used in the playback experiment. Stimulus 1 consisted of a 6-click « iambic » note, repeated 4 times in a 6.1s period, followed by 11.5s of silence. This sequence was repeated continuously for three minutes, followed by a 2-minute period of no stimulus. The same stimulus was then rebroadcast to the test male for another 3-minute period, but at a higher playback level. Levels at the eardrum of the male under test ranged between 69 and 95.9 dB SPL, were incremented in steps of 6 dB, and were calibrated using a precision sound level meter (GenRad 1982) and the known distance from the loudspeaker to the test male. Stimulus 2 was a « rip » note repeated 4 times in a 6.5s period, followed by 12.1s of silence. The repetition period for stimulus 2 was the same as that for stimulus 1. Stimulus 3 consisted of three notes presented sequentially and repeated for 30 minutes. Note 1 was a 7-click « iambic » note, followed by 20.3s of silence. Note 2 was a long « rip » note followed by 23.4s of silence and note 3 was a long « rip » followed immediately by a 6-click « iambic » note followed by 19.6s of silence. Stimulus 4 has the same structure as stimulus 3, but the notes are: (1) 3 quick tocs, (2) a 6-click iambic note, and (3) 3 quick tocs followed by a 6-click iambic note. The stimuli and the note timings are presented in figure 1.

RESULTS

Twenty-eight different call notes were recorded from a total of 10 calling males of *Boophis madagascariensis*. This number was contained in the 24 hours of recordings that we analyzed. These calls were distiguished by their voltage waveforms (Fig. 2) as analyzed on a DSP Sona-graph (Kay 5500) and printed on a Gray Scale Printer (Kay 5510), as well as their acoustic signatures (how they sounded). Even if the click-like sequences (Fig. 2i-2bb) which we term « iambic » sounds are considered as merely one call « type » with different numbers of clicks (I3-I23), there are still at least 8 distinct call notes contained in the males' advertisement call. However, not all males produced all 28 calls. For example, one male produced 14 distinct call notes while all others produced a fewer number. In addition, none of the 10 males ever produced an I21 note, although there is no reason to suppose that males are not capable of producing this particular note (since they can produce I3-I23 notes). Moreover, we believe that the complete repertoire of call note types for this species has not yet been completely documented.

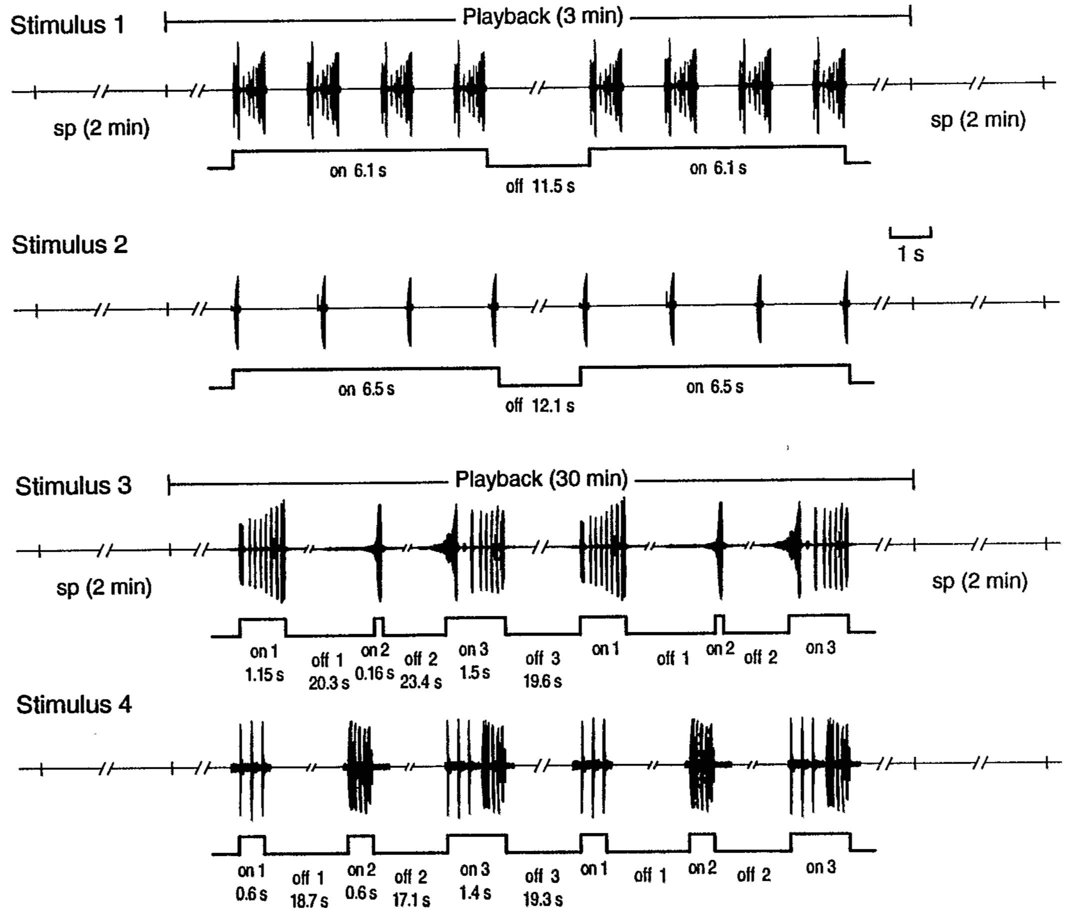

Fig. 1. Oscillograms and timing ot the four acoustic stimuli used in the playback experiments. For details, see text. Sp= spontaneous activity- the period during which no stimulus was presented.

Playback studies with stimulus 1 and 2 both resulted in increased calling rates from the males under test, with increasing playback levels (Fig. 3). Using stimulus 3 and 4 as stimuli resulted in similar results except in the case of stimulus 4 presented at relatively low levels (85 dB SPL), the three « toc » notes clearly inhibited the production of iambic calls from the test males. The other two components of stimulus 4, namely the 6-click iambic note and the 3 tocs followed by the 6-click iambic note, had no obvious effect on the production of rips or iambic notes from the test males. Thus, we have demonstrated that playback of the males' own call notes may result in increasing, decreasing or non-changed calling rates from the males under test. Moreover, there is some evidence that playback of particular call notes results in a higher probability of the test male producing those same call notes in response. More data analysis will be needed to substantiate this claim.

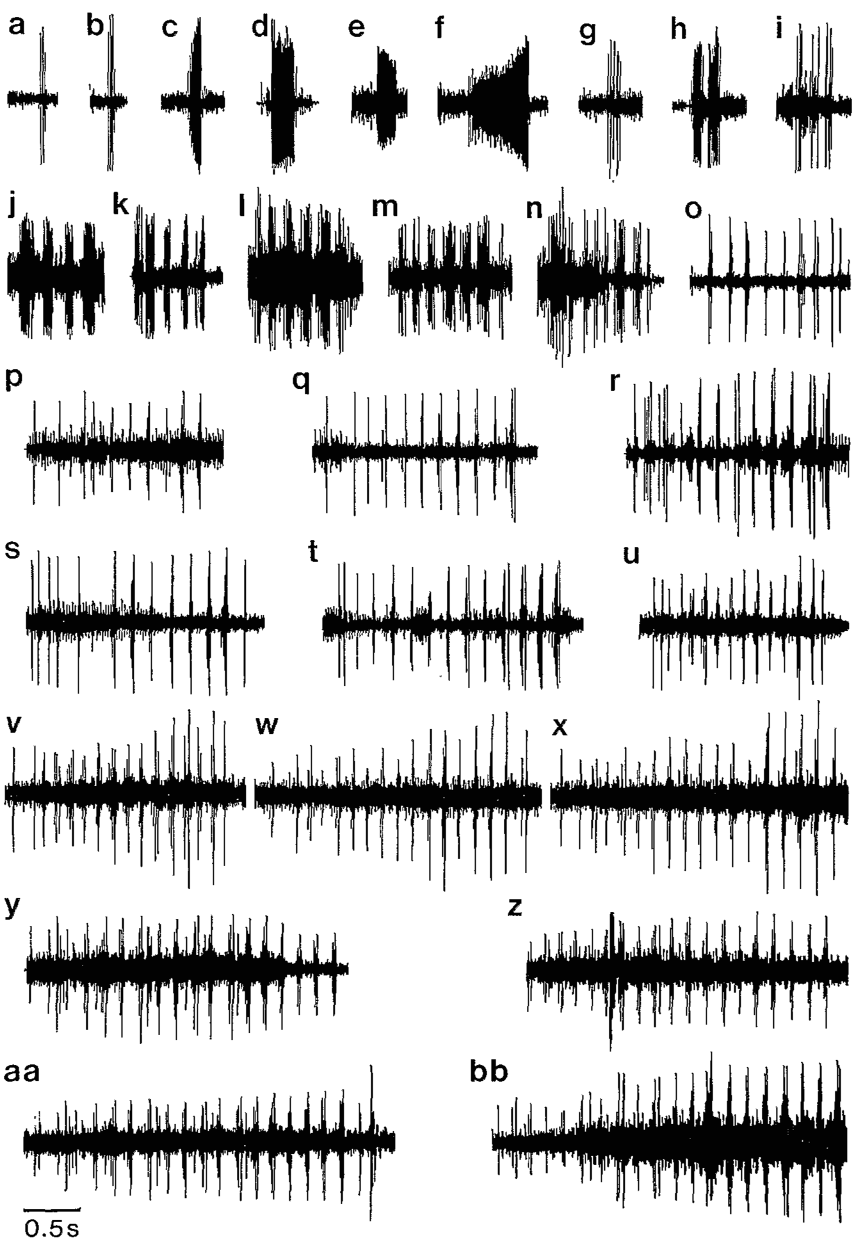

Fig. 2. Oscillograms of 28 call notes produced by males of *Boophis madagascariensis*. Ambient temperature ranged from 18°-22°C. (a) « toc » note, (b) « click » note, (c) « rip » note, (d) « loud click » note, (e) tone-like note with a frequency of 670 Hz, (f) « long rip » note, (g) « creak » note, and (h) to (bb) are « iambic » notes with increasing numbers of clicks.

How can a frog produce such a wide repertoire of calls? Preliminary morphological analysis of the vocal musculature of *B. madagascariensis* reveals no unusual adaptations that would facilitate rapid glottal opening or closing, for example (B. McClelland, pers. comm.). This suggests that the neural control system driving the vocal musculature in this species must be quite specialized and clearly deserves additional study.

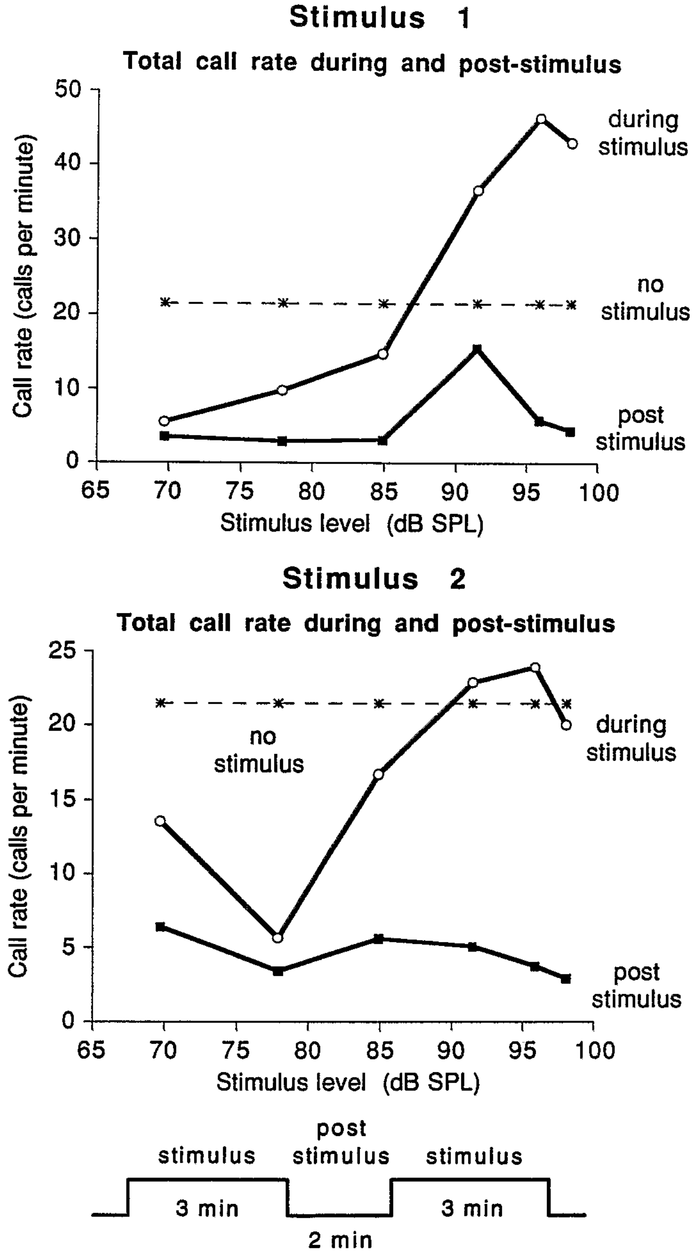

Fig. 3. Playback results for stimuli 1 and 2 presented an increasing levels. Data are averages for 10 frogs. Both stimuli cause an increase in evoked call rate with increasing playback intensity, but neither stimulus was effective at increasing call rate during the « post-stimulus » period. The dashed lines represent the average spontaneous calling rate for one frog recorded for 90 minutes. Ambient temperature for the spontaneous calling: 18°C.

The total number of calls in a frog's vocal repertoire varies from species to species. The extent of the repertoire reflects the selection pressure for premating reproductive isolation within the species, the ecological environment in which it resides, and the development of its social behavior (CAPRANICA, 1976). The discovery of a frog with the ability to produce more than two dozen different call notes suggests the potential to signal subtle state variations heretofore unknown among the anurans.

CONCLUSIONS

We have demonstrated that the call repertoire of male *Boophis madagascariensis* in eastern Madagascar consists of a minimum of 28 distinct call notes. Moreover, playback studies using natural call notes and note sequences revealed that some of the notes evoked increased call rates from males, other notes caused inhibition of the frog's calling and still other notes had no observable effect on the rate of call production by males.

Many neotropical frogs in the families Hylidae or Leptodactylidae produce stereotyped vocalizations. In these families there are species whose vocal repertoire has been characterized and extensively studied. For example, males of the Puerto Rican coqui, *Eleutherodactylus coqui* (Leptodactylidae) produce a stereotyped, two-note call in which the first (Co) note is used by males in aggressive interactions whereas the second (Qui) note is used to attract females (NARINS & CAPRANICA, 1976). In this species, the Co note is produced either alone or followed by the Qui note. The Qui note is never given alone, and moreover the Qui note never preceeds the Co note, *i.e.*, the temporal order of the notes is fixed. A fixed temporal note order is the rule in many species of Hylids and Leptodactylids, as well as in many other families of anuran amphibians. We have observed that *B. madagascariensis* appears able to « choose » from a pool of call notes and produce these notes in a great number of ordered sequences. In this sense, *B. madagascariensis* is unusual among frogs. We do not suggest that this species is unique in this sense, but we hope that more information on the vocal behavior of this and other species endemic to Madagascar becomes available before its habitat is completely destroyed.

ACKNOWLEDGMENTS

The authors wish to thank Dr. Patricia Wright from the Institute for the Conservation of Tropical Environments for her support of our project. David Narins also assisted in getting the project off the ground. Thanks are also due to Benjamin Andriamihaja, Gervais Sylvestre Rakotoarivelo, Richard Randriamampionona and Freddy Raymond for logistical support in the field. This research was supprted by a Guggenheim Fellowship and NIH Grant no. DC00222 to PMN and NIH Grant no. DC00112 to ERL.

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