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Vocal Diversity in Frogs of the South American Temperate Forest

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ABSTRACT.—**Mating calls and other vocalizations emitted in breeding areas by 11 leptodactylid and rhinodermatid species of the temperate austral forest in Chile were analyzed. Assemblages of sympatric calling species were always composed of a small number of species (4 maximum), which results in a simple acoustical environment relative to anuran communities in tropical rainforests. Acoustical separation among species is assured by differences in spectral and temporal components of the calls and diverse preferences for calling sites. Dominant frequencies were related to species size. The limited number of congeneric species coexisting in sympatry and the lack of mating calls in species of three leptodactylid genera contributes to the simplicity of the acoustical environment in southern Chile. Modes of call variation within and among genera suggest that the extant vocal diversity in this batrachofauna may have arisen during the course of independent evolutionary histories and that interactions among sympatric taxa have had a restricted role in these processes.**

Anuran vocalizations have evolved under a variety of influences. The role of acoustical interference in multispecies assemblages of calling frogs as a selective pressure for vocal divergence has been stressed by various authors (Hödl, 1977; Littlejohn, 1977; Duellman and Pyles, 1983). Acoustical differences among species that have close systematic affinities are particularly important in maintaining species identity. Physical properties of the environment for sound transmission also seem to affect characteristics of anuran mating calls; convergences in vocal patterns have been reported in species which live in similar habitats (Schiøtz, 1973; Leroy, 1977*a*). An extreme case of this kind of adaptation is the reduction in vocal repertoires with absence of mating call in frogs that inhabit biotopes with high levels of environmental noise, or in species with restricted distributions (Schmidt, 1970; Martin, 1972).

Because long-range vocalizations are under biotic and abiotic constraints, the usefulness of these signals as systematic characters is limited (Duellman, 1963; Brown and Littlejohn, 1972; Leroy, 1977*b*). However, some structural features of vocalizations are consistent with systematic arrangements within some leptodactylid genera (Barrio, 1965*a, b;* Straughan and Heyer, 1976; Ryan, 1988).

The batrachofauna of the temperate austral forest of southern Chile and adjacent Argentina is mostly composed of leptodactylid frogs of the subfamily Telmatobiinae, in the genera *Alsodes, Atelognathus, Batrachyla, Caudiverbera, Eupsophus, Hylorina, Insuetophrynus* and *Telmatobufo.* These taxa are poorly diversified and include a reduced number of species relative to other leptodactylid subfamilies, *Caudiverbera, Hylorina* and *Insuetophrynus* being monotypic genera.

The Telmatobiinae constitute a primitive group considered to be the base of the leptodactylid radiation in South America (Lynch, 1971, 1978; Heyer, 1975), whose early presence on the continent is documented by fossil records dating from the early Tertiary (Baez and Gasparini, 1979). The subfamily Leptodactylinae is represented in the region of the temperate forest by a single species of *Pleurodema,* a genus probably derived from *Eupsophus*-like stock of telmatobiines (Duellman and Veloso, 1977). Two species of *Rhinoderma* which make up the family Rhinodermatidae are also inhabitants of this region. The phyletic relationships of this genus remain uncertain; they are presumably related to the Bufonidae (Lynch, 1971).

Acoustical signals by leptodactylid and rhinodermatid frogs associated with the temperate austral forest have received limited attention. The calls of some of these species have been described as part of specific taxonomic diagnoses (Barrio, 1967*a, b;* Veloso, 1977; Formas and Vera, 1980) or their vocal repertoires in relation to ecological habits (Penna et al., 1983).

Vocalizations emitted in breeding areas and calling habits of a representative number of leptodactylid and rhinodermatid species of the temperate forest in Chile are described here. A comparative analysis of the ensemble of these ern Chile, *Telmatobufo australis* and *Atelognathus grandisonae,* have not been observed by us. These eight species have very restricted distributions; each is known to occur in a single locality in coastal or Andean elevations, where they are found along fast-moving streams.

Analysis of Calls.—The vocalizations emitted by these leptodactylids have species-specific patterns. Oscillograms and spectograms of the calls are shown in Fig. 1, and Table 2 summarizes the quantitative information of the temporal parameters and dominant frequencies. Several species produce a single type of vocalization corresponding to an advertisement call. Other species, including *E. roseus, E. migueli* and *A. nodosus,* produce a second call of longer duration. *Hylorina sylvatica* also emits a second signal, a trill of notes, which we have not recorded. *Alsodes nodosus* and *H. sylvatica* gave such calls occasionally, interspersed in long sequences of mating calls. *Eupsophus roseus* and *E. migueli* were observed to emit their long calls when an intruder attempted to enter a cavity occupied by a calling male. Such vocalizations could correspond to territorial or encounter calls, used in interactions between males (Paillette, 1977; Wells, 1977).

The calls of these leptodactylids exhibit notable interspecific differences in their temporal structure. Most of the calls are composed of notes characterized by a gradual onset and decay. In contrast, *B. taeniata* and *H. sylvatica* produce notes with fast rise-times that reach their maximum amplitudes in less than 1 msec. The number of notes in a call varies widely among species. The extremes are the single note calls of *E. roseus* and *E. migueli* and the long trilled call of *Pleurodema thaul* with more than 60 notes per emission. Intra-note amplitude modulation is a characteristic of the call of *H. sylvatica.* In this species, each note is composed of 1–4 pulses of high periodicity (mean pulse rate 52.1 pulses/sec). The spectral structure of the calls is shown in sonagrams (Fig. 1). Calls generally have harmonic structure. In most of the species the dominant frequency, identified as a darker band in the tracings, coincides with the fundamental frequency. However in *E. vertebralis* and *C. caudiverbera* the dominant corresponds to a higher harmonic. These calls have a fundamental frequency of about 200 Hz and a fifth harmonic with the highest energy content. The mating calls of *E. roseus* and *E. migueli* have fundamental frequencies of 600–800 Hz and the dominant frequency is usually the second harmonic. In these frogs other harmonics adjacent to the dominant one also have a considerable energetic representation. In most species the spectral composition of the calls does not vary throughout sound emission. However, calls of *A. nodosus* are frequency-modulated. The first note of the short call is relatively high-pitched, and its dominant frequency and harmonics shift upwards. The second note has lower frequencies and its spectral structure is generally constant. These two note types are also recognized in the long call, in which they are repeated in an alternate mode. The second note type in this case is also modulated and shows an initial rise and subsequent decrease in its spectral components. A discrete frequency modulation also occurs in the short calls of *E. roseus* and *E. migueli,* however, these modulations lack the stereotyped structure of the call of *A. nodosus.*

Temporal parameters of the mating calls are affected by environmental temperatures. A tendency towards decrease in note and call duration and a note rate increase with temperature are generally observed, but the basic structure of each specific signal remains unaltered within the temperature ranges at which recordings were made. Numbers of individuals appropriate for regression analysis were sampled in *B. leptopus* ($N = 23$) and *P. thaul* ($N = 28$), in which the effect of temperature on temporal variables is clearly appreciated in note rate increase. Regression equations between temperature and note rate are $y = 4.93 + 0.38\times$, and $y = 7.98 + 0.57\times$, respectively (F test for linearity: $P < 0.005$ in both cases). Dominant frequency in *P. thaul* is also related to temperature, but the regression between the two variables is weaker and a considerable non-linear variation is also observed (regression equation: $y = 1.75 + 0.017\times$, F test for linearity: $P < 0.05$). In *B. leptopus* this spectral component of the call does not change with air temperature (F test for deviations from regression: $P < 0.005$). Water temperature has a similar effect on these acoustical components.

The relationship between species size and dominant frequency of the calls is illustrated in Fig. 2: the logarithm of the spectral variable varies inversely with the logarithm of animal size ($r = -0.911$).

When dominant frequency and note rate are combined, a number of species are seen to be acoustically separated as illustrated in Fig. 3. Dominant frequency and note rate were the acoustical components considered in the analysis because their relevance for signal recognition has been demonstrated by behavioral (Littlejohn, 1977; Gerhardt, 1982) and neurophysiological studies (Capranica and Rose, 1983) in different anurans. Calling site preferences contribute an additional means of reproductive isolation among these species (Fig. 3)

Overlaps in note rate and dominant frequency occurred within 4 pairs of species. Differences in other features of the vocalizations or

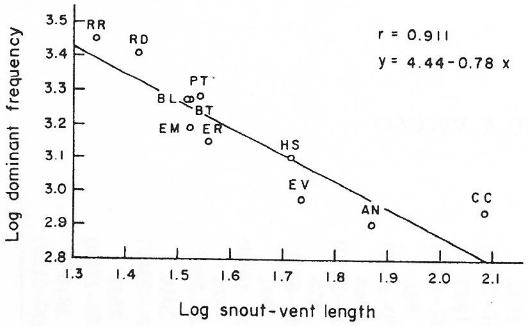

FIG. 2. Relation between mean snout-vent length and mean dominant frequency of the calls in anuran species of the temperate austral forest. Snout-vent length measurements correspond to samples of males from localities where recordings were made. Abbreviations (sample sizes in parentheses): RR, *Rhinoderma rufum* (10); RD, *R. darwini* (4); PT, *Pleurodema thaul* (4); BL, *Batrachyla leptopus* (11); BT, *Batrachyla taeniata* (7); EM, *Eupsophus migueli* (short call) (9); ER, *E. roseus* (short call) (4); HS, *Hylorina silvatica* (3); EV, *E. vertebralis* (9); AN, *Alsodes nodosus* (short call) (3); and CC, *Caudiverbera caudiverbera* (6). For *A. nodosus* the mean frequency was calculated between the extreme values of both frequency-modulated notes.

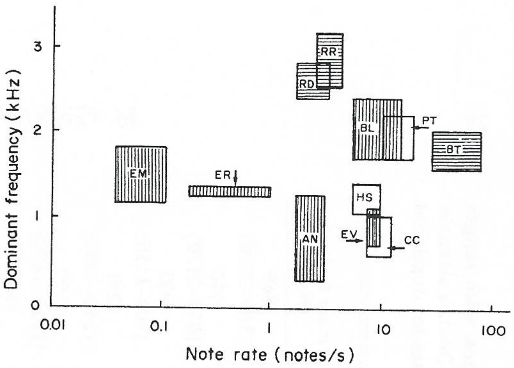

FIG. 3. Calling site preferences and variation in dominant frequency and note rate of mating calls in anurans of the temperate austral forest in Chile. Absolute ranges for both acoustical parameters are represented for each species. Abbreviations of species names as in Fig. 2. Note that rate (notes/sec) was calculated from call rate (calls/min) for the single-note calls of *E. roseus* and *E. migueli.* Calling site preferences are indicated by different hatchings, as follows: horizontal stripes = soil surface; vertical stripes = inside cavities; open = aquatic.

in preferred sites for calling precluded interference in three of these cases (Fig. 3). Vocal identification between *B. leptopus* and *P. thaul* is assured by a distinct number of notes, and the call of *P. thaul* is also identified by its intranote amplitude modulation. The overlap between *E. vertebralis* and *C. caudiverbera* is counteracted by the distinct number of notes in their calls. A slight superposition in dominant frequency and note rate is also observed between *H. sylvatica* and *E. vertebralis,* but call patterns in this particular case are totally different; notes in *H. sylvatica* have a fast rise time and are composed of separated pulses. Numbers of notes are also dissimilar between these frogs. *Rhinoderma* species constitute the only case in which spectral and temporal variables, calling sites and call patterns coincide. Call patterns are also coincident between *E. roseus* and *E. migueli,* but no overlap in note rate occurs between these forms. This lack of superposition could result from differences in temperatures at which both species were recorded (Table 2).

Species involved in the six situations of sympatry reported here (Table 1) had divergent call patterns. Moreover, acoustical separation is in most cases reinforced by calling site preferences.

DISCUSSION

The South American temperate forest constitutes a relatively simple acoustical environment as compared to tropical forests in which assemblages of about 15 species calling in a breeding area occur commonly. Acoustical separation among sympatric frogs of the temperate forest results from variation in more than one call component, a redundancy that is also observed among frogs calling in assemblages in tropical forests (Hödl, 1977; Passmore, 1981; Drewry and Rand, 1983; Duellman and Pyles, 1983).

The frequency range in which frogs of the temperate austral forest communicate is restricted relative to communities in tropical forests; the upper limit for call dominant frequency is at about 3000 Hz in *Rhinoderma rufum,* whereas dominant frequencies of up to about 6, 8 and 9 kHz have been reported in tropical aggregations by Hödl (1977), Drewry and Rand

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FIG. 1. Sound spectrograms and osciollograms of anuran calls in the temperate austral forest of Chile. Air temperatures of recordings in parentheses. (A) *Batrachyla taeniata* (8 C), (B) *B. leptopus* (8 C), (C) *Eupsophus vertebralis* (12 C), (D) *E. roseus* (short call) (13 C), (E) *E. roseus* (long call) (13 C), (F) *E. migueli* (short call) (10 C), (G) *E. migueli* (long call) (9 C), (H) *Hylorina sylvatica* (15 C), (I) *Caudiverbera caudiverbera* (15 C), (J) *Alsodes nodosus* (short call) (15 C), (K) *A. nodosus* (long call) (15 C), (L) *Pleurodema thaul* (10 C), (M) *Rhinoderma darwini* (18 C), (N) *R. rufum* (15 C). Spectral markings: 1 kHz (0–8 kHz). Time scale at bottom = 1 sec. Spectral and time scales are the same for all graphs.

(1983), and Duellman and Pyles (1983), respectively.

Overlap in dominant frequencies among species is similar between frogs of the temperate austral forest and tropical communities. A maximum of four Chilean species overlap in their dominant frequencies at about 1700 Hz (Fig. 3, Table 2). *Batrachyla antartandica*, a species not included in this analysis, has been reported by Barrio (1967*a*) to have a dominant frequency in this range, making up a total of five superimposed species. In the Amazonian assemblage studied by Hödl (1977) a maximum of four species overlap in their calls at about 2500 Hz; in the community studied by Duellman and Pyles (1983) in Ecuador, a maximum of five species overlap in their dominant frequencies at about 1600 Hz; and in the Puerto Rican communities of *Eleutherodactylus* analyzed by Drewry and Rand (1983), a maximum of six species overlap in their calls at about 3300 Hz.

The relative simplicity of the sound environment in the temperate forest, resulting from the limited number of calling species in an assemblage and the restricted frequency range in which these frogs communicate, has a counterpart in a restricted variety of the calling sites used in this geographical area relative to tropical environments; the arboreal stratum is left unoccupied in southern Chile.

The distinctiveness of calls of sympatric species that have close phylogenetic affinities is important to maintain species identity. Vocal divergence among congeneric anurans is considered to arise when incipient species become geographically isolated. Further call divergence could occur by selection for increasing reproductive isolation upon reencounter of the formerly isolated populations, a mechanism which presumably has operated in anuran species whose calls diverge more in sympatric populations than in allopatry. Calls among these species differ mainly by a single acoustical component (Blair, 1974; Littlejohn, 1977). Additional support for the occurrence of reinforcement of reproductive isolation is provided by the fact that closely related species living in sympatry have calls that diverge more than do those of related allopatric species (Duellman and Pyles, 1983).

Such a preponderant role for selection for reproductive isolation among sympatric populations has been criticized by Paterson (1978, 1982), who has put forward the notion that species isolation arises incidentally from the operation of Specific Mate Recognition Systems (SMRS) which facilitates the encounter of conspecific sexual partners. According to this view, the interspecific diversity of the signals and responses operating between males and females of the same species does not result from interactions among species in sympatry. Passmore (1981) has applied this notion in analyzing vocal diversity in South African frogs of the genus *Ptychadena*. Sympatric species of this taxon show marked differences in various temporal and spectral components of their calls, a pattern of divergence which is more likely to have arisen during the independent evolutionary histories of the various forms and concomitant with the development of their respective acoustical recognition mechanisms, rather than from selective pressures for increasing reproductive isolation.

Divergence in mating calls among congeneric frogs of the temperate forest occurs only in *Eupsophus* and *Batrachyla*, and within both groups qualitatively distinct structural patterns are found. In *Eupsophus*, the call of *E. vertebralis* is composed of various notes while *E. roseus* and *E. migueli* produce single-note mating calls of similar structure, and also have entirely similar encounter calls. In *Batrachyla*, although spectral structure of the calls is similar, marked differences in temporal components determine distinct qualitative structural patterns: *B. taeniata* produces notes with a fast rise time, while in *B. leptopus* the notes have a gradual increase in amplitude. The call of *B. antartandica*, the third species in the genus, is composed of notes of fast rise time as in *B. taeniata*, but these clicks are produced at a much slower rate (about 4 notes/sec) (Barrio, 1967*a*).

Vocal diversity within these genera suggests that call divergence has resulted from independent evolutionary history rather than from selective processes for increasing reproductive isolation, following a mode of acoustical divergence of the kind proposed by Passmore. Support for this alternative is provided by the coincidence of vocal and systematic divergence in *Eupsophus*: *E. migueli* and *E. roseus* have entirely similar vocal repertoires and are likely to represent a recent stage of speciation, being distant from *E. vertebralis* in morphological, karyological and electrophoretic traits (Formas et al., 1983). Such a clear relationship between systematics and call structure does not occur in *Batrachyla*; electrophoretic patterns are similar between the three forms of this genus and chromosomal differences are restricted to inconspicuous secondary constrictions (Diaz and Veloso, 1979). However, geographical variation of the calls in this genus is consistent with a mode of independent acoustical divergence between species; calls of *B. taeniata* from the locality of Melipilla (latitude 33°42′S) in central Chile, where *B. leptopus* does not occur, have the same pattern as those produced by a population from Chamiza (latitude 41°27′S) in the area of overdeficit (Lynch, 1978; Diaz, 1982; Penna et al., 1983). *Alsodes nodosus,* the only frog which emits a mating call among these species, could represent an alternative, less extreme modality of adaptation to noisy environments. Stream inhabitants of the subgenus *Paa* (genus *Rana*) in Nepal and of the genus *Heleophryne* in South Africa also emit whistle-like vocalizations, a spectral characteristic which facilitates call detection in noisy backgrounds (Dubois, 1977; Passmore, 1981).

Dominant frequencies of most of the calls of frogs of the temperate austral forest are between 1–4 kHz. Frequencies within this range have been shown to be better transmitted than are frequencies beyond these limits in open and forested habitats, in studies conducted in both temperate and tropical latitudes (Marten and Marler, 1977; Marten et al., 1977; Wiley and Richards, 1982). The high predictability of call dominant frequency by size here reported is comparable to that found in neotropical frogs (Hödl, 1977; Duellman and Pyles, 1983). The strictness of the relationship between these two variables indicates that spectral divergence is constrained by factors determining animal size, and that this limitation occurs widely among anurans. The call of *C. caudiverbera,* which has the lowest dominant frequency in the group (average 866 Hz), is probably appropriate for transmission across the large bodies of water in which this species calls; large water surfaces attenuate the propagation of low frequencies to a lesser extent than do porous substrates (Wiley and Richards, 1982).

The extant acoustical diversity in frogs of the temperate austral forest includes dissimilar call patterns and repertoires within *Batrachyla* and *Eupsophus,* coincident call structure within *Rhinoderma,* and exclusive vocal repertoires in the monotypic genera *Caudiverbera* and *Insuetophrynus.* The nature of this diversity suggests that acoustical divergence in this batrachofauna has been mainly related to independent evolutionary processes, and that interactions among related taxa in sympatry have had a limited importance. This anuran group has a long evolutionary history, with early generic differentiation documented by fossil records of *Caudiverbera* and *Eupsophus* dating back to the Oligocene (Schaeffer, 1949; Baez and Gasparini, 1979). Conditions for further acoustical diversification in isolation existed during Pleistocene glaciations, during which time the reduced areas free of ice provided scattered refugia for the survival of vegetation and fauna (Vuilleumier, 1968; Müller, 1973; Heusser, 1974). The severe climatic conditions prevailing during this period probably exterminated a number of taxa, permitting the survival of forms restricted to remote and dispersed refugia (Formas, 1979). The resultant poor intrageneric diversification and vocal reductions in this batrachofauna contribute to the relatively simple acoustical environment observed at present.

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Herpetofauna of the Ipswichian Interglacial Bed (Late Pleistocene) of the Itteringham Gravel Pit, Norfolk, England

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ABSTRACT.—**At least four species of anurans, one tortoise and one snake were identified from the Ipswichian interglacial bed (Late Pleistocene) of the Itteringham Gravel Pit, Norfolk, England. A tree frog (*Hyla* sp.) is reported for the first time as a British fossil. The herpetofauna indicates that the major habitat was a lentic one. The occurrence of the tree frog (*Hyla* sp.), continental water frogs (*Rana*), and the European pond tortoise (*Emys orbicularis*) indicates a continental climate with warmer summers than occur in England today.**

The mammalian fauna of the British Pleistocene has been well-studied (Stuart, 1982), but the British Pleistocene herpetofauna has been largely neglected until recently. These recent works include reports of the European pond tortoise from interglacial sites (Stuart, 1979, 1982), and short herpetofaunal papers on Cromerian (Holman, 1987*c*; Holman et al., 1988), Hoxnian (Holman, 1987*a*), Ipswichian (Holman, 1987*b*), Devensian/Flandrian (Holman, 1988) and Flandrian (Holman, 1985, 1987*a*) localities.

Studies of fossil herpetofaunas are important in making paleoecological interpretations, for modern amphibians and reptiles have specific ecological requirements and most Pleistocene species have modern equivalents that have been well-studied in Britain and on the continent. Moreover, certain species may be particularly important in indicating specific environmental conditions because of stringent climatic reproductive constraints (Stuart, 1979).

The Ipswichian Interglacial Stage.—Except for the Flandrian, the Ipswichian is the best known of the British interglacials. The Ipswichian (ca. 120,000–110,000 years before present) occurs between the cold glacial times of the older Wolstonian stage and the younger Devensian stage. Stuart (1982) provides a general discussion of the most important Ipswichian sites and their vertebrate fauna. The presence of fossils of the African hippo (*Hippopotamus amphibius*) is generally accepted as diagnostic of the Ipswichian. Some other mammals which no longer are native to Britain but do appear in the Ipswichian are the horse (*Equus ferus*), spotted hyena (*Crocuta crocuta*) and the lion (*Panthera leo*). The Ipswichian has also yielded the European pond tortoise (*Emys orbicularis*) from many of its sites. The type site of the Ipswichian is Bobbitshole, Ipswich, England.

The Itteringham Deposit.—The Itteringham Gravel Pit (National Grid Reference 139305) is located beside the River Bure in the parish of Oulton, 6 km west of Aylsham, Norfolk, England. Deposits belonging to four distinct climatic stages have been identified. The uppermost valley deposits (mostly peat) belong to the present (Flandrian) interglacial. Beneath these are gravels and clays with fossil and sedimentary indications of intense cold and these are assigned to the last (Devensian) glacial. Stratigraphically lower are detrital muds and organic sands which are fully interglacial in character.