

## Patterns of advertisement call evolution in toads and chorus frogs

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**Abstract.** Patterns of evolution in the acoustic signals of two groups of anuran amphibians were examined. Call character matrices for clades of *Bufo* (Bufonidae) and *Pseudacris* (Hylidae) were derived from analysis of tape-recorded calls, and these call characters were mapped onto phylogenetic trees based on morphological and biochemical data. It was found that the characters that make up a call evolve at different rates. In hylids, characters allied with the morphological aspects of sound production were more conservative than those based on the physiological or behavioural aspects of calling, while in bufonids divergence rates of these character types did not differ. Observed patterns of character change within sets of close relatives suggest a focus for process-oriented research by identifying the origin and direction of important changes in calling behaviour.

Patterns of behavioural evolution were a major focus of early ethology, and much of this literature shows an integration of behaviour and systematics (Whitman 1899; Lorenz 1941; Tinbergen 1959; Huxley 1966). This work laid the foundation for a continuing tradition of comparative studies in the evolution of behaviour (e.g. Milne & Milne 1939; Lack 1947; Spieth 1947; Johnsgard 1961; Evans 1962; Van Tets 1965; Crane 1966; Otte 1970). Recently, there has been increased interest among behavioural ecologists in conducting comparative studies within an explicitly phylogenetic framework (reviewed in Brooks & McLennan 1991; Harvey & Pagel 1991). Much of this interest has been motivated by the recognition that the lack of a proper phylogenetic framework can pose problems for comparative studies. Without information about phylogeny it is not possible to estimate the true number of evolutionarily independent events; thus sample sizes can be overestimated and conclusions might be based on improper statistical inference (Ridley 1983; Felsenstein 1985). The inclusion of phylogenetic inference is a welcome addition to behavioural ecology that helps ameliorate this problem.

There is another, perhaps more interesting aspect to phylogenetic approaches in behaviour that has received less attention. That is, rather

than collapsing tree structure into a set of independent events or contrasts, the full structure of the tree can be used to uncover patterns of behavioural evolution (Ewing & Miyan 1986; McLennan et al. 1988; Arntzen & Sparreboom 1989; Prum 1990; Langtimm & Dewsbury 1991). This use of comparisons among closely related species to address questions about the evolution of behaviour, especially display behaviour, was a preoccupation of traditional ethology (Daanje 1950; Kessel 1955; Morris 1957; Hinde & Tinbergen 1958; Tinbergen 1959; Blest 1961; Cullen 1966; Huxley 1966; Lorenz 1966). The relatively recent development of rigorous phylogenetic and comparative methods (Hennig 1966; Wiley 1981; Harvey & Pagel 1991) makes this approach much more powerful and calls for a re-examination of classical ethological questions about behavioural evolution. We use this approach in an investigation of patterns of evolution of vocal signals in two groups of anurans. In addition to investigating general patterns of call evolution, we address two specific questions. (1) Do different call characters evolve at similar rates, or are characters more closely allied with morphology more conservative than those more closely allied with behaviour and physiology, as has been suggested in other studies? (2) What predictions about evolutionary processes can be derived from uncovering evolutionary patterns?

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### Anuran Mating Calls

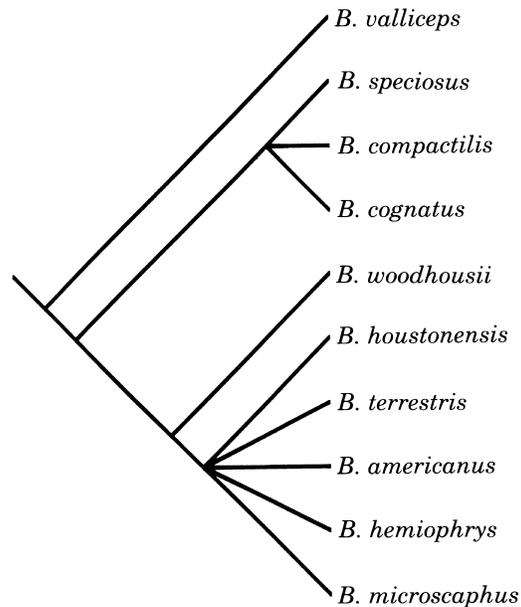
The acoustic signals of anurans are an excellent behaviour pattern for comparative studies. Calls are the primary mating display of anurans, and play an important role in their biology and evolution. The call advertises a male's presence to reproductive females, and in most taxa is the primary component of species recognition and mate choice. Typically, the call also plays a role in interactions between males, which may defend a calling site or territory from other males. Calling behaviour and the sensory system involved in call perception have been extensively studied for over three decades, making this among the best understood model systems for animal communication (reviewed in Fritzsche et al. 1988). The role of the call in mate attraction and social competition is well understood (reviewed in Straughan 1973; Littlejohn 1977; Wells 1977, 1988; Ryan 1985; Gerhardt 1988, 1991), and much is known about the structure of the auditory system and its relation to characteristics of the call (Capranica 1965; Fuzessery 1988; Walkowiak 1988; Zakon & Wilczynski 1988). Furthermore, calls are relatively short, repetitive acoustic signals whose features can be quantified using standard sound analysis methods. Measurements are objective and repeatable, eliminating problems of inter-observer differences and bias that can complicate comparative behavioural studies.

### METHODS

#### Groups Selected for Phylogenetic Analysis

An ideal group for comparative analysis of communication would be one in which there is a robust phylogeny, a detailed understanding of the communication system, and a series of well-documented tape-recordings. Among the anuran taxa that best meet these criteria are two clades, one within the North American toads (Bufonidae) and the other within treefrogs (Hylidae). Relationships of both groups have been derived using a wide range of data sources, and the communication system has been well studied in representative species. Furthermore, large series of tape-recordings exist in museum and private collections.

The systematic relationships of North American *Bufo* have received considerable attention,

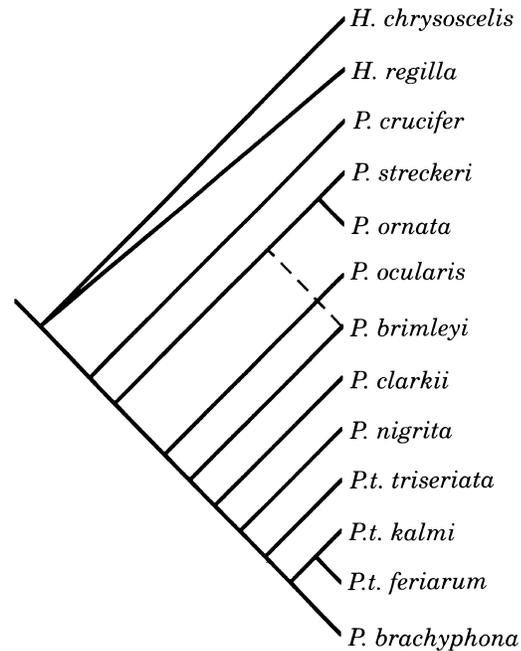


**Figure 1.** Proposed phylogeny of 10 North American *Bufo* species from Maxson et al. (1981).

although primarily at the species-group level. Species groups originally were established on the basis of morphology and laboratory hybridization, notably by Blair (1972) and his colleagues. Maxson et al. (1981) re-examined relationships among 14 species of North American *Bufo* using albumin immunological data. With the exception of one species (*B. alvarius*), these data confirmed the species groups previously defined. Maxson et al. (1981) also hypothesized phylogenetic relationships for most of the North American species groups based on immunological distance data. These proposed relationships were used as a working hypothesis for this study (Fig. 1). This clade includes two main branches: the *B. americanus* group, including *B. americanus*, *B. hemiophrys*, *B. houstonensis*, *B. microscaphus*, *B. terrestris* and *B. woodhousii*, and the *B. cognatus* group, including *B. cognatus*, *B. compactilis* and *B. speciosus*. Relationships within these species groups remain to be resolved. Two taxa suggested to be closely related to these taxa by Maxson et al. (1981) were not included in this study (*B. alvarius* and *B. boreas*) because we were unable to obtain adequate recordings. A member of the sister group lineage, the *B. valliceps* group, was included as an outgroup taxon for comparison.

Our primary reason for focusing on *Bufo* is Martin's (1972) pioneering study of call production systems in bufonids. Through experimental and comparative approaches he was able to relate characteristics of the emitted sounds to the associated components of the call-producing system. This work provides an excellent basis for comparative studies of vocalizations in this group.

The relationships of North American hylids, including the genus *Pseudacris*, have also received considerable attention. A variety of data sets have been applied to this problem, including osteology (Chantell 1968a, b; Gaudin 1969, 1973, 1974), laboratory hybridization (Mecham 1957, 1959, 1965; Ralin 1970), call similarity (Blair 1959, 1962), chromosome banding patterns (Wiley 1982; Anderson 1991), immunological distance (Wallace et al. 1971; Maxson & Wilson 1975; Swofford 1981), and allozyme electrophoresis (Hedges 1986; Highton 1991). These systematic data are reviewed by Cocroft (in press), who proposed a phylogenetic hypothesis based on a cladistic re-analysis of 47 morphological, chromosomal, and allozyme characters drawn from the literature. Four call characters were also included in that analysis, so for the purposes of this study an additional analysis was run without the call characters. The (minimal) effect on tree topology of inclusion or exclusion of these characters is discussed below. The combined analysis yielded 20 minimum-length trees, with consistency and retention indices of 0.81. The ingroup portion of a strict consensus tree is shown in Fig. 2. This study demonstrated that the two traditional species groups of chorus frogs constitute monophyletic groups. The *P. nigrita* species group includes *P. brachyphona*, *P. brimleyi*, *P. clarkii*, *P. nigrita*, *P. t. kalmi*, *P. t. feriarum*, *P. t. maculata* and *P. t. triseriata* (the nominal 'subspecies' of *P. triseriata* are here considered distinct species because there is evidence that they are not each other's closest relatives: Hedges 1986; Cocroft, in press; see also Platz & Forester 1988; Platz 1989). Basal to this clade is *P. ocularis*. The second chorus frog clade is the *P. ornata* species group, including *P. ornata* and *P. streckeri*. *Pseudacris crucifer* is the sister taxon to the rest of *Pseudacris*. The remaining Holarctic hylid species apparently represent either a sister group or are paraphyletic with respect to the ingroup species in this study (Maxson & Wilson 1975; Hedges 1986; Cocroft, in press). Calls of two outgroup Holarctic hylid



**Figure 2.** Proposed phylogeny of *Pseudacris* from Cocroft (in press). Note: for *P. brimleyi*, the dashed line indicates the position if call characters were excluded from phylogenetic analysis, and the solid line shows the position if call characters were included; all other relationships were unaffected by inclusion or exclusion of call characters.

species were included in this study, *Hyla chrysoscelis* and *H. regilla*; some studies have suggested that *H. regilla* is more closely related to *Pseudacris* than are other Holarctic hylids.

The approach used in this study was to map call characters onto trees derived from morphological and molecular data because trees based on non-call data provide an independent framework with which to interpret patterns of call character evolution. However, access to the data matrix used to estimate the tree for the hylid clade allowed us to perform a sensitivity analysis to determine how inclusion or exclusion of call characters into the phylogenetic analysis would affect tree topology. In fact, the same topology results whether or not call characters are included, with the exception of the position of one species (*P. brimleyi*). At the level of analysis used in this study, this minor difference does not affect the overall conclusions. However, because it is possible that inclusion of the call characters would in fact provide a better

estimate of phylogeny (Kluge 1989; Baum & Larson 1991), we indicate both potential placements of *P. brimleyi* in the phylogeny (Fig. 2) and point out where the difference in placement of this species would affect interpretations of character evolution.

### Call Variables

Within a species, calls exhibit consistent features that can be measured for each call of each individual. Differences in call features between species stem from several sources of variation, based on how acoustic energy is extracted from a moving airstream and how this energy is modified before being coupled to the environment. Features of the broadcast call are thus related to the morphological and neurophysiological programmes involved in producing the call (Martin 1972). At some level, then, differences in calls between species represent modifications of the sound-producing system, and every time an individual of a given species produces a call, that call will have certain characteristic features.

Signals do vary, however, between and within individuals in a population and between geographically separated populations of a single species (e.g. Fouquette 1975; Nevo & Capranica 1985; Gerhardt 1991; Ryan & Wilczynski 1991). Calls in this study were sampled in order to encompass variation at three levels within a species: within individuals, among individuals and among populations. When possible we sampled calls of males from two (or more) geographically separated populations, with five males per population and five calls from each male, for a total of 50 calls per species (Table I). Recordings were obtained from museum and private tape collections and from the authors' fieldwork (see Appendix). Recordings that lacked accurate locality and temperature information were excluded, as were those that showed evidence of distortion.

Table II contains a list of the call features that were measured in this study. This list includes traditional measurements known to be relevant in communication (e.g. dominant frequency, pulse rate, call length). It also includes other measurements that may or may not be of significance in communication (e.g. call rise time, pulse rate change) but which are equally consistent, valid descriptors of the call. For example, a rise in frequency within the call is a characteristic feature

**Table I.** Sample sizes for populations, individuals and calls

| Species                 | Populations | Males | Calls |
|-------------------------|-------------|-------|-------|
| <b>Bufonidae</b>        |             |       |       |
| <i>B. americanus</i>    | 2           | 10    | 50    |
| <i>B. cognatus</i>      | 2           | 8     | 27    |
| <i>B. compactilis</i>   | 1           | 4     | 12    |
| <i>B. hemiophrys</i>    | 1           | 5     | 25    |
| <i>B. houstonensis</i>  | 2           | 10    | 50    |
| <i>B. microscaphus</i>  | 2           | 10    | 48    |
| <i>B. speciosus</i>     | 1           | 10    | 50    |
| <i>B. terrestris</i>    | 2           | 10    | 50    |
| <i>B. valliceps</i>     | 2           | 10    | 50    |
| <i>B. woodhousii</i>    | 2           | 10    | 50    |
| <b>Hylidae</b>          |             |       |       |
| <i>H. chrysoscelis</i>  | 2           | 10    | 50    |
| <i>H. regilla</i>       | 2           | 5     | 25    |
| <i>P. brachyphona</i>   | 2           | 6     | 28    |
| <i>P. brimleyi</i>      | 3           | 10    | 50    |
| <i>P. clarkii</i>       | 2           | 10    | 50    |
| <i>P. crucifer</i>      | 2           | 10    | 50    |
| <i>P. nigrita</i>       | 3           | 10    | 50    |
| <i>P. ocularis</i>      | 3           | 10    | 50    |
| <i>P. ornata</i>        | 2           | 10    | 50    |
| <i>P. streckeri</i>     | 2           | 10    | 50    |
| <i>P. t. feriarum</i>   | 2           | 10    | 50    |
| <i>P. t. triseriata</i> | 2           | 10    | 50    |
| <i>P. t. kalmi</i>      | 3           | 5     | 25    |

of the signals produced by *Pseudacris*, but there is no evidence that this feature functions in communication (Doherty & Gerhardt 1984).

Calls were analysed using a Multigon Uniscan II real-time analyser and a DATA 6000A universal waveform analyser. The sampling rate for analysis was set at three to four times the highest frequency in the call, and thus the sampling rate varied between 10 and 20 kHz. Theoretical resolution for the time and frequency measurements reported here was within 3%, although in practice some additional minimal error could have been introduced if tape speed varied slightly among the recorders used for the original field recordings.

Because many call characteristics in frogs vary in a predictable, quantitative fashion with temperature, all relevant measurements were adjusted to a common temperature before comparison using standard regression methods. Means for individual males were used to evaluate temperature variation for each variable for each species; when a significant relationship was detected, the slope of the line was used to adjust the measurements of all individuals to a common temperature

**Table II.** List of call characters used in the study. Comments concerning only bufonids or only hylids are preceded by (B) or (H), respectively

| Variable                             | Measured characteristic  |
|--------------------------------------|--|
| Call length                          | Time from beginning to end of one call. Measured from waveform analyser screen or, for <i>Bufo</i> calls longer than 11.5 s, by stopwatch  |
| Pulse rate                           | (Total number of pulses – 1)/time from beginning of first pulse to beginning of last pulse. (H) Entire call; (B) 10 pulses from mid-call   |
| Dominant frequency                   | Frequency in call containing the greatest energy, determined from Fourier transform of (H) entire call; (B) 2-s section from mid-call  |
| Call rate                            | (Total number of calls – 1)/time from beginning of first call to beginning of last call  |
| Call rise time                       | Time from beginning of call to point of maximum amplitude. (B) Measured as length of initial transient (=first portion of call, during which frequency and amplitude increase, then stabilize)   |
| Pulse length                         | Time from beginning to end of one pulse from mid-call  |
| Pulse rise time                      | Time from beginning of pulse to point of maximum amplitude   |
| Pulse shape                          | Unitless variable derived by dividing pulse rise time by pulse length; provides an index of the overall shape of the amplitude envelope of the pulse   |
| Frequency modulation                 | Dominant frequency at end of call minus that at beginning of call. (H) Divided by call length; (B) applies to initial transient only rather than entire call   |
| Pulse duty cycle                     | Unitless variable derived by dividing pulse length by the interval between the beginning of one pulse and the beginning of the next pulse  |
| Pulse amplitude                      | Maximum amplitude of pulse (in mV; used only for within-call comparisons)  |
| Amplitude increase                   | (B) Ratio of pulse amplitude at beginning of call to that at mid-call  |
| Amplitude ratio                      | (H) Ratio of energy present in dominant frequency (=second harmonic) to energy present in fundamental. Because this measure can vary with recording conditions, it was separated into two broad categories: amplitude of the fundamental frequency was much less than or about equal to that of the dominant frequency |
| Pulse rate change                    | (H) Change in pulse rate during call, based on one pulse cycle from the beginning of call and one from the end of the call   |
| Pulse type                           | (B) Pulses containing interior amplitude modulation or not   |
| Call type                            | (H) Calls amplitude modulated or not   |
| Dominant=fundamental/higher harmonic | Dominant frequency approximately equal to the interval between harmonics or to some integer multiple of that interval  |

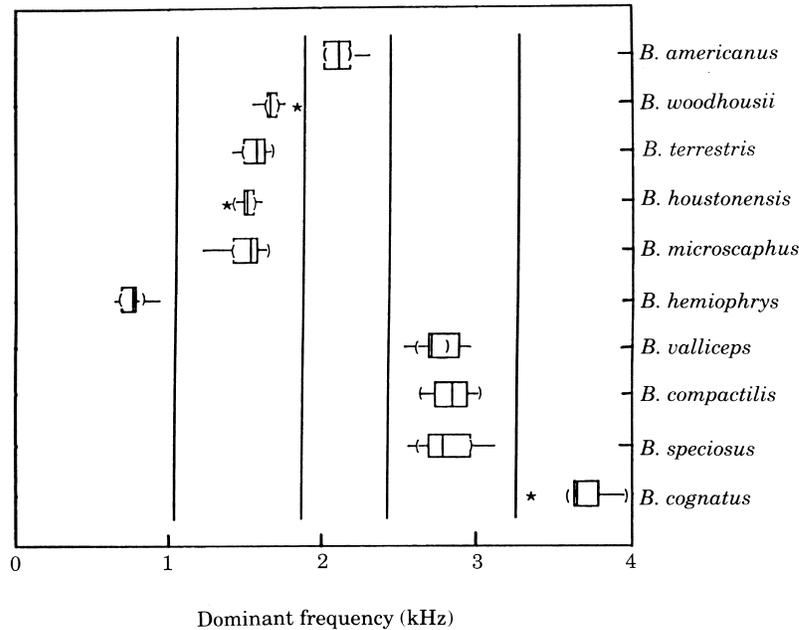
of 18°C. In four cases we used published regression equations available for larger samples from the same populations from which we had recordings (Michaud 1964; Zweifel 1968; Fouquette 1975; Platz 1989).

Some call variables, such as dominant frequency, can vary predictably with the size of the calling male. Because differences in these features between species might simply be a correlated effect of differences in body size, we examined the size–frequency relationship itself rather than frequency alone. Ideally, this relationship would first be determined within each species, but in a number of taxa we did not have adequate size data for the males whose calls we used in the analysis. Accordingly, we instead used species' means as data points in a linear regression analysis, and

used significant slopes to remove the effects of body size from the among-species comparison. Size information for each species was obtained by measuring the size (snout–vent length) of the recorded individuals or, when necessary, of museum specimens of adult males from the same or nearby localities as the recordings (for *Bufo*, data for additional species from Blair (1964) were also included).

### Call Character Coding

In this study we focus on variation in a single behaviour pattern, the mating call, between groups of related species. Most phylogenetic studies that examine behavioural characters have scored the presence or absence of a given display



**Figure 3.** Box plot of dominant frequency (adjusted for body size) in *Bufo*. Parentheses represent 95% confidence intervals. Vertical lines have been added between sets of overlapping species to indicate gaps.

(or other behaviour) within an entire repertoire (e.g. Lorenz 1941; Delacour & Mayr 1945; Otte 1970, 1974; Eisenberg & Leyhausen 1972; Mundinger 1979; Eberhard 1982; McLennan et al. 1988; but see Ewing 1975; Ewing & Miyan 1986; Heady 1987). Although examining the presence or absence of a display within a repertoire may provide a greater number of characters, some information is lost because this approach does not incorporate differences between species in the form of a particular display.

Variation in most call characters is quantitative rather than categorical. Although quantitative characters are often used in phylogeny reconstruction, methods of coding these characters for phylogenetic analysis continue to be debated (Archie 1985; Pimentel & Riggins 1987). For this study, we examined variation across species for each character using a box plot, which is a graphical analogue of an analysis of variance, partitioning the variation within and among species and exhibiting the median and 95% confidence intervals. We then used gap coding, with the criterion of non-overlap of 95% confidence intervals to define gaps. This divided each call variable into one or more sets of overlapping boxes, separated by gaps from

other such sets. Each set was coded as a single character state (Fig. 3 provides an example of this coding method). We chose this coding method because it provides a consistent way of comparing character change across taxa, provides a data set that can be treated using cladistic methods, and allows general patterns to be easily seen.

## RESULTS

### Call Variables

The call variables measured in this study appear in Tables III and IV, adjusted to a common temperature of 18°C. Only dominant frequency was significantly (negatively) correlated with size across species, in both groups (*Bufo*:  $r=0.75$ ,  $N=25$ ,  $P<0.01$ ; *Pseudacris*:  $r=0.79$ ,  $N=13$ ,  $P<0.001$ ). There was also a trend for a relationship between size and pulse rate in *Bufo* ( $r=0.60$ ,  $N=10$ ,  $P=0.07$ ). Because pulse rate and size appear to be correlated within this genus (Blair 1964), this regression was used to remove the effect of body size from differences in pulse rate before comparison. Other characters did not vary predictably with size.

**Table III.** Call measurement summary ( $\bar{X} \pm SE$ ) for *Bufo* species, adjusted to a common temperature of 18°C

| Species                | Call length (ms)  | Pulse rate (/s) | Dominant frequency (Hz) | Call rate (/m) | Call rise time (ms) | Pulse shape | Frequency modulation (Hz) | Amplitude increase |
|------------------------|-------------------|-----------------|-------------------------|----------------|---------------------|-------------|---------------------------|--------------------|
| <i>B. americanus</i>   | 9 635.5 ± 2586.5  | 39.5 ± 2.5      | 1714.4 ± 94.8           | 3.74 ± 0.52    | 552.5 ± 106.7       | 0.38 ± 0.04 | 408.4 ± 88.1              | 4.87 ± 1.93        |
| <i>B. cognatus</i>     | 20 548.2 ± 6203.5 | 12.5 ± 0.7      | 2307.2 ± 171.3          | 2.39 ± 0.69    | 300.0 ± 79.3        | 0.48 ± 0.07 | 396.4 ± 154.6             | 2.18 ± 0.78        |
| <i>B. compactilis</i>  | 23 875.0 ± 3408.2 | 11.7 ± 1.1      | 2115.8 ± 153.8          | 1.94 ± 0.39    | 130.3 ± 52.8        | 0.39 ± 0.02 | — 496 ± 2.9               | 1.34 ± 0.06        |
| <i>B. hemiophrys</i>   | 3 035.2 ± 1080.3  | 86.4 ± 2.2      | 1700.1 ± 111.2          | 6.77 ± 0.72    | 330.3 ± 67.8        | 0.44 ± 0.08 | 400.9 ± 113.8             | 4.98 ± 2.44        |
| <i>B. houstonensis</i> | 14 591.1 ± 3544.4 | 26.3 ± 1.9      | 2083.6 ± 71.5           | 2.16 ± 0.31    | 425.8 ± 121.1       | 0.39 ± 0.05 | 318.0 ± 57.4              | 4.00 ± 1.05        |
| <i>B. microscaphus</i> | 4 581.1 ± 1074.6  | 69.3 ± 2.2      | 1300.2 ± 119.7          | 2.88 ± 0.92    | 439.1 ± 98.9        | 0.43 ± 0.05 | 285.6 ± 89.0              | 7.44 ± 3.41        |
| <i>B. speciosus</i>    | 690.8 ± 426.4     | 35.6 ± 1.7      | 2620.6 ± 177.1          | 54.10 ± 13.65  | 65.4 ± 20.2         | 0.50 ± 0.05 | 0.9 ± 94.4                | 1.43 ± 0.44        |
| <i>B. terrestris</i>   | 9 944.8 ± 1240.8  | 43.2 ± 2.8      | 2138.4 ± 89.0           | 3.15 ± 0.48    | 306.8 ± 71.3        | 0.35 ± 0.04 | 648.3 ± 80.1              | 3.76 ± 1.18        |
| <i>B. variceps</i>     | 4 283.5 ± 1001.1  | 26.7 ± 3.2      | 1487.7 ± 133.0          | 4.73 ± 0.87    | 282.2 ± 56.8        | 0.11 ± 0.02 | 264.8 ± 40.6              | 4.58 ± 0.97        |
| <i>B. woodhousii</i>   | 1 962.9 ± 311.6   | 106.6 ± 9.0     | 1968.7 ± 80.5           | 8.57 ± 0.92    | 184.7 ± 28.5        | 0.40 ± 0.06 | 413.3 ± 64.7              | 3.34 ± 0.82        |

**Table IV.** Call measurement summary ( $\bar{X} \pm SE$ ) for hylid species, adjusted to a common temperature of 18°C

| Species                 | Call length (ms) | Pulse rate (/s) | Dominant frequency (Hz) | Call rate (/s) | Call rise time (ms) | Pulse shape | Frequency modulation (Hz/s) | Pulse duty cycle | Pulse rate change (%) |
|-------------------------|------------------|-----------------|-------------------------|----------------|---------------------|-------------|-----------------------------|------------------|-----------------------|
| <i>H. chrysoscelis</i>  | 829.0 ± 50.7     | 40.7 ± 1.3      | 2425.5 ± 119.7          | 0.23 ± 0.07    | 737.3 ± 49.4        | 0.45 ± 0.04 | 56.3 ± 53.7                 | 0.59 ± 0.06      | - 11.1 ± 3.3          |
| <i>H. regilla</i>       | 168.1 ± 9.9      | 135.6 ± 7.2     | 2124.9 ± 174.2          | 1.27 ± 0.34    | 137.9 ± 18.5        | 0.27 ± 0.04 | 1604.3 ± 247.7              | 0.91 ± 0.04      | 14.3 ± 1.0            |
| <i>P. brachyphona</i>   | 180.2 ± 84.4     | 104.8 ± 3.2     | 2393.8 ± 150.4          | 1.21 ± 0.05    | 370.4 ± 133.5       | 0.16 ± 0.03 | 2286.7 ± 288.6              | 0.65 ± 0.19      | 42.3 ± 27.0           |
| <i>P. brimleyi</i>      | 187.4 ± 23.9     | 71.0 ± 4.4      | 2921.6 ± 154.0          | 0.84 ± 0.15    | 228.2 ± 30.6        | 0.18 ± 0.03 | 1996.9 ± 370.2              | 0.50 ± 0.10      | 75.4 ± 41.8           |
| <i>P. clarkii</i>       | 227.9 ± 14.4     | 63.4 ± 3.7      | 3071.5 ± 147.2          | 1.07 ± 0.14    | 167.4 ± 16.5        | 0.20 ± 0.03 | 1367.3 ± 397.0              | 0.69 ± 0.12      | 65.5 ± 28.6           |
| <i>P. crucifer</i>      | 170.6 ± 57.5     | —               | 3000.5 ± 290.9          | 0.87 ± 0.29    | 16.9 ± 8.7          | —           | 1996.7 ± 973.3              | —                | —                     |
| <i>P. nigrita</i>       | 777.6 ± 98.8     | 12.0 ± 0.84     | 3149.2 ± 305.3          | 0.43 ± 0.05    | 317.7 ± 260.8       | 0.19 ± 0.05 | 576.0 ± 279.8               | 0.10 ± 0.03      | - 41.5 ± 6.9          |
| <i>P. ocularis—A</i>    | 34.9 ± 1.3       | —               | 5929.9 ± 316.9          | 0.91 ± 0.44    | 3.3 ± 1.0           | —           | 5954.1 ± 1487.8             | —                | —                     |
| <i>P. ocularis—B</i>    | 72.6 ± 9.7       | 41.5 ± 4.3      | 6159.1 ± 289.5          | 0.91 ± 0.44    | 1.3 ± 0.5           | 0.20 ± 0.07 | 2980.6 ± 433.4              | 0.28 ± 0.05      | 13.3 ± 14.0           |
| <i>P. ornata</i>        | 28.4 ± 8.6       | —               | 2650.6 ± 183.2          | 2.47 ± 0.62    | 6.8 ± 2.6           | —           | 2299.1 ± 501.1              | —                | —                     |
| <i>P. streckeri</i>     | 43.7 ± 14.5      | —               | 2290.7 ± 131.2          | 2.90 ± 1.04    | 7.5 ± 1.8           | —           | 1861.4 ± 1133.3             | —                | —                     |
| <i>P. t. feriarum</i>   | 732.6 ± 240.1    | 26.5 ± 11.1     | 2976.5 ± 181.7          | 0.53 ± 0.08    | 618.7 ± 168.0       | 0.19 ± 0.04 | 725.6 ± 298.0               | 0.18 ± 0.06      | - 35.5 ± 4.8          |
| <i>P. t. kalni</i>      | 721.5 ± 207.5    | 21.8 ± 0.6      | 2971.7 ± 122.7          | 0.67 ± 0.07    | 501.6 ± 224.4       | 0.21 ± 0.01 | 474.5 ± 327.7               | 0.17 ± 0.06      | - 43.0 ± 6.7          |
| <i>P. t. triseriata</i> | 516.6 ± 187.4    | 20.4 ± 1.4      | 2776.3 ± 127.8          | 0.37 ± 0.04    | 571.4 ± 104.6       | 0.23 ± 0.03 | 398.2 ± 80.3                | 0.20 ± 0.02      | - 40.5 ± 8.4          |

Call components in *P. ocularis* are listed separately.

|     | Characters |   |   |   |   |   |   |   |   |    |    | Taxa                   |
|-----|------------|---|---|---|---|---|---|---|---|----|----|------------------------|
| (a) | 1          | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |                        |
|     | 1          | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1  | 1  | <i>B. valliceps</i>    |
|     | 1          | 1 | 2 | 1 | 2 | 2 | 2 | 3 | 1 | 3  | 3  | <i>B. speciosus</i>    |
|     | 1          | 1 | 2 | 1 | 1 | 3 | 2 | 2 | 1 | 3  | 3  | <i>B. compactilis</i>  |
|     | 1          | 1 | 2 | 1 | 1 | 3 | 1 | 4 | 2 | 1  | 2  | <i>B. cognatus</i>     |
|     | 1          | 1 | 2 | 2 | 1 | 1 | 2 | 9 | 4 | 1  | 1  | <i>B. woodhousii</i>   |
|     | 1          | 1 | 2 | 2 | 1 | 3 | 1 | 6 | 4 | 1  | 1  | <i>B. houstonensis</i> |
|     | 1          | 1 | 2 | 2 | 1 | 3 | 1 | 2 | 4 | 2  | 1  | <i>B. terrestris</i>   |
|     | 1          | 1 | 2 | 2 | 1 | 3 | 1 | 5 | 3 | 1  | 1  | <i>B. americanus</i>   |
|     | 1          | 1 | 2 | 2 | 1 | 1 | 1 | 7 | 5 | 1  | 1  | <i>B. hemiophrys</i>   |
|     | 1          | 1 | 2 | 2 | 1 | 1 | 1 | 8 | 4 | 1  | 1  | <i>B. microscephus</i> |

| (b) | 1 | 2 | 3 | 4 | 5 | 6   | 7 | 8 | 9   | 10 | 11 | 12 | Taxa                   |
|-----|---|---|---|---|---|-----|---|---|-----|----|----|----|------------------------|
|     | 1 | 1 | 1 | 1 | 1 | 1   | 1 | 1 | 1   | 1  | 1  | 1  | <i>H. chrysoscelis</i> |
|     | 1 | 2 | 2 | 2 | 1 | 3   | 1 | 7 | 1   | 1  | 2  | 3  | <i>H. regilla</i>      |
|     | 1 | 2 | ? | 2 | 2 | 4   | 2 | ? | 2   | 2  | ?  | ?  | <i>P. crucifer</i>     |
|     | 1 | 2 | ? | 2 | 4 | 5   | 2 | ? | 2   | 2  | ?  | ?  | <i>P. streckeri</i>    |
|     | 1 | 2 | ? | 2 | 3 | 5   | 2 | ? | 2   | 2  | ?  | ?  | <i>P. ornata</i>       |
|     | 1 | 2 | 2 | 2 | 1 | 4,5 | 2 | 1 | 1,2 | 2  | 3  | 3  | <i>P. ocularis</i>     |
|     | 1 | 2 | 2 | 2 | 1 | 3   | 1 | 5 | 1   | 2  | 1  | 4  | <i>P. brimleyi</i>     |
|     | 1 | 2 | 2 | 2 | 1 | 2   | 1 | 4 | 1   | 2  | 1  | 4  | <i>P. clarkii</i>      |
|     | 1 | 2 | 2 | 2 | 1 | 1   | 1 | 3 | 1   | 2  | 4  | 2  | <i>P. nigrita</i>      |
|     | 1 | 2 | 2 | 2 | 1 | 1   | 1 | 2 | 1   | 2  | 4  | 2  | <i>P.t. triseriata</i> |
|     | 1 | 2 | 2 | 2 | 1 | 1   | 1 | 2 | 1   | 2  | 4  | 2  | <i>P.t. kalmi</i>      |
|     | 1 | 2 | 2 | 2 | 1 | 1   | 1 | 2 | 1   | 2  | 4  | 2  | <i>P.t. feriarum</i>   |
|     | 1 | 2 | 2 | 2 | 1 | 2   | 1 | 6 | 1   | 2  | 1  | 4  | <i>P. brachyphona</i>  |

**Figure 4.** (a) Call character distributions in *Bufo*. Characters are (1) dominant frequency=fundamental frequency; (2) frequency modulation within pulses; (3) pulse shape; (4) pulses with or without amplitude modulation; (5) call rate; (6) call length; (7) call rise time; (8) pulse rate; (9) dominant frequency/body size relationship; (10) transient frequency change; (11) transient amplitude change. (b) Call character distributions in hylids. Characters are (1) dominant frequency=second harmonic; (2) frequency modulation within call; (3) pulse shape; (4) dominant frequency/body size relationship; (5) call rate; (6) call length; (7) call rise time; (8) pulse rate; (9) pulsed/pure-tone call; (10) dominant frequency/fundamental frequency amplitude ratio; (11) pulse duty cycle; (12) pulse rate change within call. Because *P. ocularis* has two call components, it was scored as having both states for relevant characters.

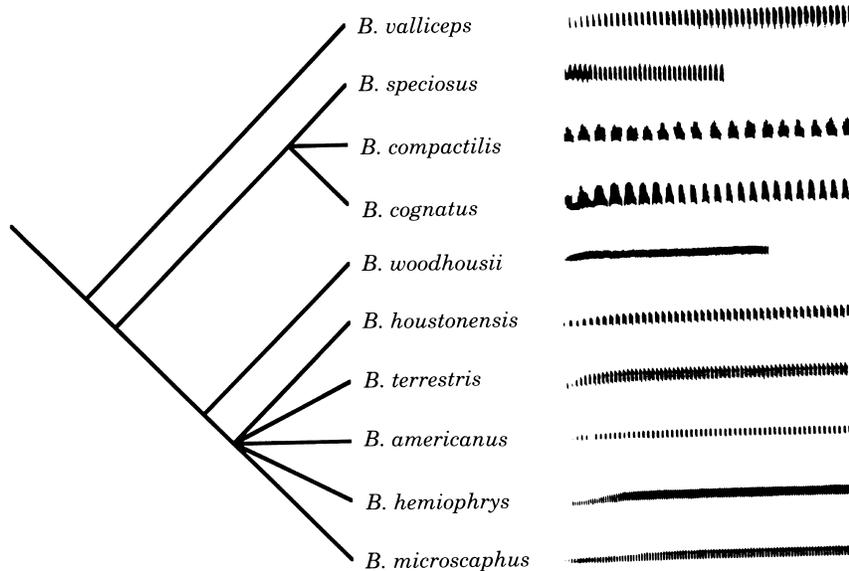
Coding of call variables produced a matrix of 11 characters for *Bufo* (Fig. 4a) and 12 characters for hylids (Fig. 4b). The number of character states ranged from one to nine.

#### Within-group Patterns: *Bufo*

Advertisement calls in these closely related *Bufo* species share a suite of structural features. The call of each species consists of a long train of pulses, given in a relatively narrow band of frequencies, with an initial transient in which amplitude and

dominant frequency change gradually and then stabilize (Fig. 5). The dominant or carrier frequency of the call is the fundamental frequency of vibration of the vocal cords (character 1). Within pulses, the dominant frequency rises slightly and then falls, creating an inverted U-pattern of frequency modulation repeated in each pulse throughout the call (character 2). These features represent behavioural characters shared by every species within the clade.

Other call features are also shared by sets of related species, although on a more restricted



**Figure 5.** Audiospectrograms of *Bufo* calls (only the first 1 s of each call is shown). Audiospectrograms display the energy in each frequency across time; in this figure the axes were removed to facilitate comparison of general call features. Calls were recorded at about 18°C.

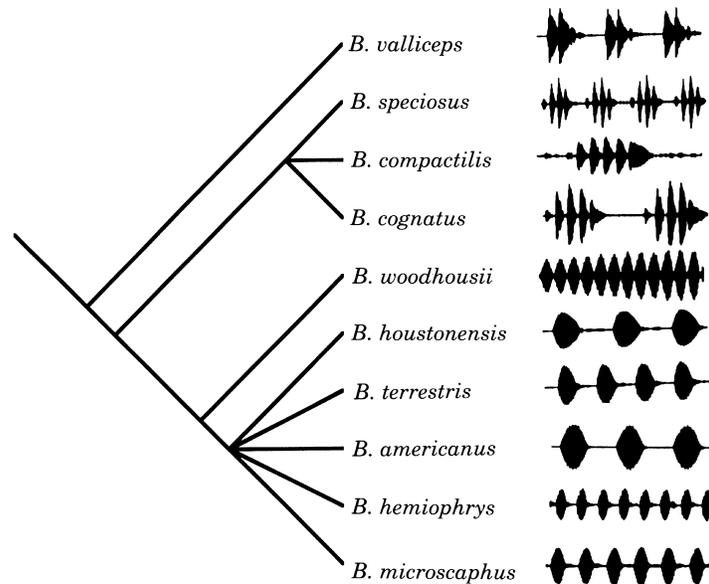
scale. Within this group of *Bufo* there are two basic types of pulses: one divided into sub-pulses, the other not (character 4). This feature is not distributed randomly with respect to relationships; the outgroup and the *B. cognatus* clade have pulses with interior amplitude modulation, while the *B. americanus* clade has calls with simple, unmodulated pulses (Fig. 6).

The strategy by which males package their acoustic output also falls into two broad classes. Most of the species in this study deliver long calls at relatively low rates, between about two and nine calls per minute. Although this range is substantial, call rate varies considerably between individuals and call rates broadly overlap among species (character 5). Within the *B. cognatus* clade, however, two distinct patterns are found: two species give very long calls at about two calls per minute, while the third species, *B. speciosus*, delivers short calls at over 50 calls/min.

Characteristics of the initial transient of the call (the beginning portion of the call during which frequency and amplitude have not yet stabilized) are conservative, although they do show some change within and between clades. The length of this transient is similar in most species, although it is relatively short in two *B. cognatus* group species

and one *B. americanus* group species (character 7). Calls of all species also begin at a low amplitude that gradually increases; however, the difference between the initial and final amplitudes is less in the *B. cognatus* group (character 11). Dominant frequency also rises gradually throughout the initial transient in most species; however, in *B. speciosus* and *B. compactilis*, the dominant frequency in this initial portion of the call typically starts at about mid-call level, rises, and then falls again to the same frequency (character 10).

The dominant frequency/size ratio is less conservative, showing more divergence within close relatives (character 9). The dominant frequency is lower in relation to body size in the *B. americanus* group than in the *B. cognatus* group or *B. valliceps*, and is lowest in *B. hemiophrys*. Call length also diverges within and between species groups (character 6). This pattern is extreme in the *B. cognatus* group, in which calls of two species average over 20 s in length, while calls of the third species are less than 1 s in length. The most divergent character is pulse rate (character 8), which exhibits a different character state for nearly every species in the study (this is true whether or not pulse rate is adjusted for body size).



**Figure 6.** Waveforms showing pulse structure in *Bufo* calls. Note the loss of amplitude modulation within pulses in the *B. americanus* species group. Waveforms display changes in amplitude over time; here each trace represents 100 ms from the middle of the call shown in Fig. 5.

#### Within-group Patterns: *Pseudacris*

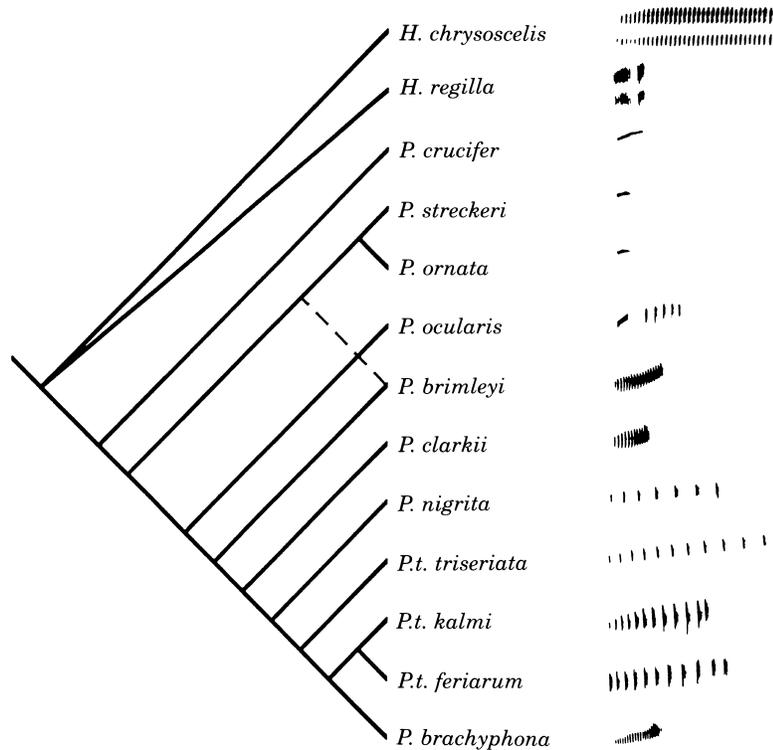
As in *Bufo*, calls of closely related species share basic structural features. However, these features differ in important ways between the two clades. First, in the hylid species, the dominant frequency is the second harmonic of the vocal cord vibration frequency (character 1), instead of the fundamental as in *Bufo*. Second, in the ingroup hylid species, air flows in only one direction during the call (R. B. Cocroft, personal observation), and thus the length of the call is limited by the volume of air in the lungs. As a result, calls are much shorter than those of most of the *Bufo* examined in this study, in which air can shuttle back and forth across the larynx during the call (Martin 1972).

Calls of the ingroup species are characterized by a gradual rise in dominant frequency throughout the call (character 2; see also Fig. 7). Furthermore, all of the ingroup species show a similar size-frequency relationship; although dominant frequency varies among species, most of this variation is explained by variation in size (character 4). In all of the ingroup species with pulsed calls (and in *H. regilla*), pulses have an abrupt

onset and gradual decay; this contrasts with *H. chrysoscelis*, in which pulses have a gradual onset (character 3; see also Fig. 8). Finally, in the two outgroup taxa, the fundamental frequency contains almost as much energy as the dominant frequency, while in the ingroup the fundamental is much lower in amplitude than the dominant (character 10).

Call rise time (character 7) is similar in most species, although it is in general more rapid in species with pure-tone calls (e.g. the *P. ornata* group) than in species with pulsed calls (Table IV). In the ingroup species with pulsed calls, pulse repetition rate changes during the call (character 12). The direction of change appears to be correlated with the absolute pulse rate: in species with slower average pulse rates, pulse rate decreases within the call, while in species with faster average pulse rates, pulse rate increases within the call.

Calls of *P. crucifer* and the *P. ornata* group species consist of a pure tone, while calls of the *P. nigrita* group species consist of a train of pulses (character 9). *Pseudacris ocularis*, which arises between these two groups, has a call that contains both components, a pure tone followed by a train of pulses. However, for this character,



**Figure 7.** Audiospectrograms of *Pseudacris* calls. Note the upward frequency sweep in calls of the ingroup species. Time scale is identical for each call; for reference, the call shown for *P. brimleyi* is 200 ms long. (Not all calls in this figure were recorded at the same ambient temperature, but basic call structure is not affected by temperature differences.)

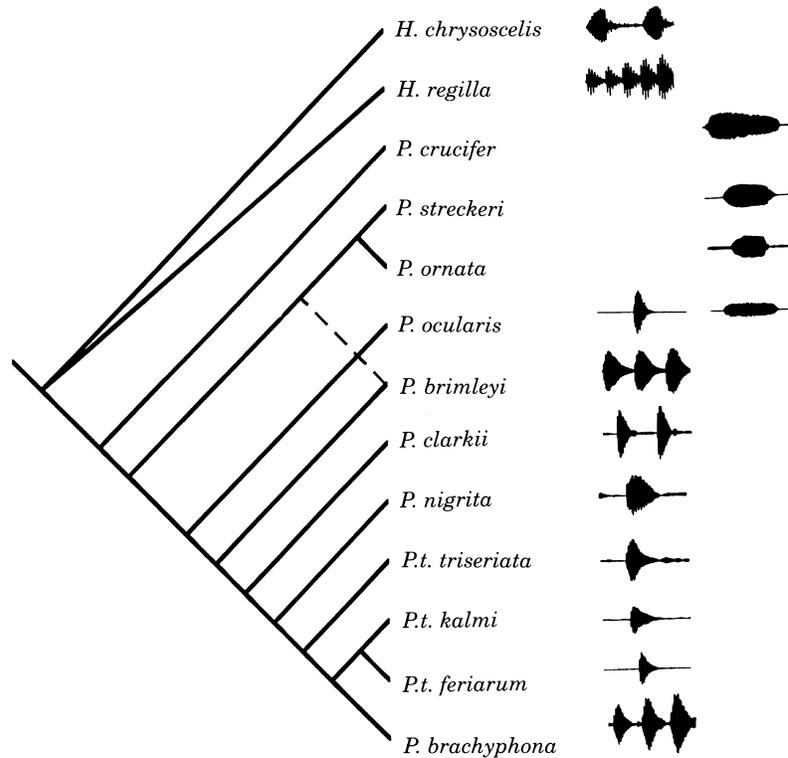
interpretation differs depending on whether or not call characters are included in the tree: if *P. brimleyi* does arise at the base of the *P. ornata* group rather than within the *P. nigrita* group (tree with call data excluded), then either the pulsed component or the pure-tone component must have arisen twice.

Other characters, as in *Bufo*, are more divergent. For example, pulse rates are seldom shared among taxa; within the ingroup species with pulsed calls, only the three nominal *P. triseriata* 'subspecies' share the same character state (character 8). Furthermore, while the overall calling pattern within *Pseudacris* appears conservative (acoustic output packaged into short signals with relatively high repetition rates), call length diverges within and between clades (character 6). Call rate is less divergent, although there is a trend in *P. crucifer* and especially in the *P. ornata* group towards higher rates of calling (character 5).

## DISCUSSION

### Patterns of Character Evolution

Although an anuran mating call is often considered a single, stereotyped unit of behaviour, calls do not evolve in a unitary fashion. Instead, because there are multiple sources of variation in the call-producing system, calls comprise a set of characters, and these characters evolve at different rates. Some characters are conserved through repeated speciation events, while others show change. Our analysis of character evolution in two clades of anurans allows us to examine these patterns of character change at two levels. Initially, we can compare rates of change among characters within a single clade. We then can look for evidence of general trends by looking for shared patterns between the two groups we analysed and by comparing these with other data sets available in the literature.



**Figure 8.** Waveforms from *Pseudacris* calls. Note the similarity in pulse shape within the ingroup. In the first column, showing pulse structure, each trace represents 30 ms from mid-call; in the second column, showing overall amplitude envelope of pure-tone calls, the X-axis length is 200 ms for *P. crucifer* and 50 ms for *P. streckeri*, *P. ornata* and *P. ocularis*.

One index of character conservation is the likelihood that close relatives will share the same character state. Table V contains a summary of the probability that two ingroup species selected at random will share the same character state (i.e. out of all possible different ways of drawing two taxa out of a group, the proportion in which the two taxa will share the same state for a given character). A value of 1.00 would indicate that all members of a group share the same state, and thus that the character has been conserved. A value of 0.00 would indicate that each member exhibits a different state, and thus that the character has diverged within the group. This index is equally applicable to both groups, despite differences in the degree of resolution of relationships. An alternative index of character change would be to use the number of steps (evolutionary transitions from one character state to another) observed for each character optimized on the tree. We also

examined the hylid clade using this method; however, this approach is not appropriate for the *Bufo* clade because the lack of resolution within species groups makes estimating the number of steps problematical.

Within each group, index values for call characters range from 1.00 to nearly zero, spanning a range from highly conserved to highly divergent. Clearly, there are very different modes of character change within the set of characters that make up a call. It is perhaps surprising that variation along so many axes is phylogenetically conservative, as evidenced by the characters that are shared by every member of a monophyletic group. This is unexpected, given that mating calls usually are considered to be both a highly diagnostic, species-specific behaviour (Blair 1964) and one that would be expected to diverge rapidly under the influence of social selection (West-Eberhard 1983). Other characters do show evidence of rapid divergence,

**Table V.** Summary of character change indices among ingroup *Bufo* and *Pseudacris*

| Bufonidae                      |       |      | Hylidae               |       |      |
|--------------------------------|-------|------|-----------------------|-------|------|
| Character                      | Index | Type | Character             | Index | Type |
| DF=first harmonic              | 1.00  | M    | DF=second harmonic    | 1.00  | M    |
| Pulse shape                    | 1.00  | M    | Pulse shape           | 1.00  | M    |
| FM within pulses               | 1.00  | M    | FM within call        | 1.00  | (?)  |
| Call rate                      | 0.78  | P/B  | DF/size relationship  | 1.00  | M    |
| AM within pulses               | 0.50  | M    | DF/FF amplitude ratio | 1.00  | M    |
| Call rise time                 | 0.50  | P/B  | Call rate             | 0.51  | P/B  |
| Transient: change in amplitude | 0.44  | P/B  | Call rise time        | 0.49  | P/B  |
| Transient: change in frequency | 0.44  | P/B  | Pulse rate change     | 0.32  | P/B  |
| Call length                    | 0.36  | P/B  | Pulse duty cycle      | 0.32  | P/B  |
| DF/size relationship           | 0.19  | M    | Call length           | 0.20  | P/B  |
| Pulse rate                     | 0.03  | P/B  | Pulse rate            | 0.11  | P/B  |

Characters are listed in decreasing order of index value. Character types are listed as M if change in character is based on change in morphology, P/B if character change is based on change in physiology or behaviour. AM: Amplitude modulation; DF: dominant frequency; FF: fundamental frequency; FM: frequency modulation.

with a different state in nearly every species within a clade.

What might explain these differences in rates of change among characters? Ryan (1988) suggested, based on two relatively small data sets, that characters whose variation was linked to variation in morphology might be more conservative than characters whose variation was based on variation at the level of behaviour or physiology. Table V provides a summary of whether evolutionary change in each character is based on change in morphological aspects of the sound-producing system or on physiological or behavioural aspects. For example, in *Bufo*, the presence of amplitude modulation within pulses depends on the presence or absence of a morphological feature in the larynx (Martin 1972), whereas call length can vary within an individual and depends on active, behavioural regulation of call duration.

In the hylid clade, characters whose variation is based on change in the morphological basis of call production are in fact more conservative than characters whose variation is based on changes in the behaviour and physiology of calling. This is reflected in the character conservation index values from Table V; the median score is significantly higher for morphological than for behavioural/physiological characters in *Pseudacris* (Mann-Whitney *U*-test,  $U=18.0$ ,  $N_1=6$ ,  $N_2=3$ ,

$P<0.05$ ). Comparison of the number of steps observed for each character optimized on the tree yields the same results for both topologies shown in Fig. 2 ( $U=18.0$ ,  $N_1=6$ ,  $N_2=3$ ,  $P<0.05$ ). In *Bufo*, this difference is not significant ( $U=13$ ,  $N_1=6$ ,  $N_2=3$ , NS). The most salient difference between the two groups is that in *Pseudacris*, the dominant frequency/body size relationship is essentially constant within the ingroup, while in *Bufo* it is not. In both groups, however, the three most highly conserved characters are morphologically based, while the most divergent character is physiologically based. Note that in this quantitative comparison, two characters from each group were not included. Characters 4 (*Bufo*) and 9 (*Pseudacris*) are categorical rather than quantitative, and characters 2 (*Bufo*) and 10 (*Pseudacris*) could not be measured precisely, as were the other characters. Both of these factors could bias the scoring of characters towards a lower number of states, and thus these characters were excluded from the statistical analysis.

Conservatism in certain features suggests that details of the call-production system are similar among close relatives. For example, whether the dominant frequency of the call is the fundamental frequency of the vocal cords or its second harmonic is a feature that characterized all members of a clade. Whether or not calls are pulsed, and, if so, what shape of amplitude envelope the pulses

exhibit, are additional features shared by groups of related species. In some cases, the morphological basis of this similarity among close relatives is particularly evident. For example, in the *Bufo* clade, the outgroup species (*B. valliceps*) and the *B. cognatus* group produce pulses that contain interior amplitude modulation; species in the *B. americanus* group produce pulses without this additional level of amplitude modulation (see Fig. 6). As shown by Martin (1972) in his comparative study of call production in bufonids, this subdivision of pulses is due to the action of arytenoid valves in the larynx, which have been lost in the *B. americanus* group. Thus a change in a morphological element of the sound-producing system (which parsimony suggests occurred in the common ancestor of the *B. americanus* group) is reflected in a feature of the emitted calls of the species in this clade.

Some call characters show a more divergent pattern among close relatives. However, changes in these features among species do not necessarily require changes in the design of the sound-producing system (see Heyer 1980 for discussion of a similar example in Neotropical hylids). For example, although species in the *B. americanus* group produce the same kind of pulses, each species produces them at a different rate. Martin (1972) suggested that in many *Bufo* (including all of the species in this study), differences in pulse rate among species can be accounted for by differences in the rate of active muscular contractions along the vocal tract, particularly the thoracic musculature (see also Martin & Gans 1972), rather than requiring change in the morphological configuration of the system. In fact, pulse rate is the most divergent character in both lineages (Table V). Interestingly, female preference functions for the pulse repetition rates of male calls tend to be narrowly tuned (Gerhardt 1991), and pulse rate has been shown to be one of the most important call features involved in conspecific mate recognition (Littlejohn 1971; Loftus-Hills & Littlejohn 1971). Thus rapid divergence in this character could result in the rapid evolution of pre-zygotic reproduction isolation (a pattern seen in *Drosophila*; Coyne & Orr 1989). A second character that is highly divergent in both lineages is call length. Although the ability to produce extremely long calls in *Bufo* reflects morphological specialization for a two-way flow of air during the call, differences in call length

among species within each clade are clearly related to active, behavioural aspects of call production.

The patterns of character variation evident in these North American bufonids and hylids may be a general feature of the evolution of anuran communication. Ryan (1988) derived data from the literature for call characters in two groups of frogs for which phylogenies were available (the hyperoliid genus *Kassina* and the hylid genus *Smilisca*). Using unit character consistencies as an index of how evolutionarily conservative characters were, he found that the dominant frequency/body size relationship in *Smilisca* was highly conserved, as was true in this study for *Pseudacris* (though not for *Bufo*). In both groups he examined, pulse rate or amplitude modulation was relatively less conserved, as it was for the groups we studied. Zweifel (1985) examined calls in the context of evolutionary relationships in two clades of Australian microhylid frogs. As in this study, close relatives shared basic features of call structure: in one group, calls consisted of repeated, frequency-modulated pure tones, while in the other group calls were a train of broad-band pulses. Within each group, however, calls of related species differed quantitatively from each other, primarily in pulse rate and note rate. Zweifel (1985) noted that these differences in repetition rate did not appear to reflect relationships established on the basis of morphological characters; in fact, pulse repetition rates in two cases were widely divergent between sister taxa.

A similar pattern occurs in the bufonid genus *Atelopus*. Details of basic call structure have been highly conserved among related species, but calls differ in pulse rate, dominant frequency and call length (Cocroft et al. 1990). Straughan & Heyer (1976) made a comparative study of calls in the leptodactylid genus *Leptodactylus*; in most of the species groups they examined, calls were similar in structure within a group but differed in the presence or absence of amplitude modulation. In the *Physalaemus pustulosus* species group (Leptodactylidae), males of each species produce whine-like advertisement calls consisting of a set of harmonically related tones that descend in frequency (Ryan & Drewes 1990; Ryan & Rand 1993a). However, while these species share a similar basic call structure, whine calls of different species differ in length, fundamental frequency and rates of frequency modulation.

Calls of males in the genus *Bombina* (Bombinatoridae) are produced, unlike those of most frogs, as air travels from the vocal sack back into the lungs. Species in this genus all produce short, tonal mating calls; however, between species, calls differ in length, frequency and repetition rate (Schneider et al. 1986). Structural features of calls appear to be shared among close relatives in many other anuran groups as well, such as centrolenids (R. W. McDiarmid, personal communication); sooglossids (Nussbaum et al. 1982); New World microhylids (Nelson 1973); the hyliid genus *Sphaenorhynchus* (R. B. Cocroft, unpublished data); and the pelobatid genus *Scaphiopus* (McAlister 1959).

There is, then, evidence of qualitatively similar patterns of call variation among a diversity of anuran groups. This suggests that the results of this detailed study of two clades may be indicative of general features of the evolution of anuran communication. Patterns of advertisement call variation across a broad range of taxa reveal that anurans possess a diversity of calling mechanisms, whose characteristics dictate the range of variation possible in the calls of species sharing that system. It would be worthwhile, as more systematic, behavioural and functional morphological data become available, to identify modifications or evolutionary shifts from one call-production system to another. Examination of such transitions would shed light on the sources of selection involved in the shift from one call-production system, with a given range of call variation, to another system with a potentially very different range of variation (see Ryan & Drewes 1990).

Some features of call evolution in anurans may be characteristic of other groups. Acoustic communication in crickets (Gryllidae) has been extensively investigated and from a comparative standpoint constitutes among the best-studied communications systems (see Alexander 1962; Huber 1989). Because signals are produced with external structures whose movements can be observed, the morphological and behavioural bases of signal production are particularly accessible to study. In crickets, call structure has also been conservative, in fact much more so than in anurans. All signalling crickets possess the same basic stridulatory apparatus, which is unique in producing a pure-tone signal (Alexander 1962). Calls vary primarily along a single axis: temporal

differences resulting from variation in timing of wing strokes during calling. A secondary axis of variation consists of intensity differences between successive pulses in some species (Ewing 1989). Thus, basic similarities in cricket signals also result from sharing a common sound-producing system, and much of the variation between species results from active, behavioural aspects of signal production.

### Observed Patterns and Predictions about Process

Comparative studies can identify patterns of divergence between closely related species and reveal both the origin and the direction of character change. Such identified patterns provide a context for focusing process-oriented research on important transitions (see McLennan 1991).

For example, in *Bufo*, female preferences for longer calls and faster call rates have been demonstrated in some species, including the outgroup species in this analysis (*B. valliceps*; W. Wagner & B. Sullivan, personal communication). This pattern of preference provides alternative and mutually exclusive pathways to increased attractiveness to females. Given that total acoustic output is limited (Taigen & Wells 1985), males of a given species can package their acoustic output into longer calls at lower rates or into shorter calls at higher rates. The mutually exclusive nature of these alternative pathways might lead to divergence in signalling strategies among lineages in which the female preferences exist. Such a pattern appears to be present within the *B. cognatus* group. Two species exhibit the longest calls and the lowest call rates of any species in the study, while the third species exhibits the shortest calls and the highest call rate (although basic pulse structure has been conserved). This pattern of within-group variation raises the possibility that sexual selection through female choice may have influenced the marked divergence of mating signals between these closely related species, a possibility that can be investigated with studies of female preference and male mating success in the set of close relatives showing the ancestral and derived character states. Similar directional female preferences are taxonomically widespread (Ryan & Keddy-Hector 1992), and thus these alternative pathways of signal evolution might occur in other groups.

In the hylid clade, one surprising pattern is the presence of frequency modulation in the calls of all of the ingroup species: the dominant frequency sweeps upward during the call. This is unexpected because Zakon & Wilczynski (1988) argue convincingly that small species with high-pitched calls (like these hylids) should not encode information in frequency changes. Because calls in these species will be perceived primarily by the basilar papilla, whose fibres are all broadly tuned to about the same best frequency, changes in frequency will only be perceived as changes in intensity rather than as frequency modulation per se. The prediction of Zakon & Wilczynski (1988) is supported by the findings of Doherty & Gerhardt (1984) that female *Pseudacris crucifer* did not discriminate between constant-frequency and frequency-modulated synthetic calls. One interpretation is that this frequency modulation may be unapparent to conspecific receivers and that, as Doherty & Gerhardt (1984) argue, the change in frequency in *P. crucifer* calls has no functional significance.

What then might explain the ubiquitous distribution of this character among these small species? The frequency changes in the calls of the hylids in this study may be an unselected consequence of some other feature of call production, or they may have a functional significance that previous experiments were not designed to explore. In *P. crucifer*, the basilar papilla of females is tuned to lower frequencies than that of males (Brenowitz et al. 1984). Zakon & Wilczynski (1988) suggest that this mismatch in auditory sensitivity may be a common pattern because basilar papilla tuning is closely related to body size, and sexual size dimorphism is prevalent in anurans. We hypothesize that the frequency modulation in these hylid calls may function to offset this mismatch in tuning by distributing call energy through a wider range of frequencies. Higher frequencies at the end of the call should be more audible to males than the lower frequencies at the beginning of the call (see Narins & Capranica 1980). Thus, frequency modulation in calls of these species may represent a compromise, allowing the call to be audible to two sets of receivers tuned to different frequencies.

This hypothesis of the function of frequency modulation has not been investigated experimentally in this clade of anurans. Given the explicit

comparative context, an observed function for this character in existing species can also be mapped onto the tree, revealing whether it would represent an adaptation or an exaptation (Gould & Vrba 1982) that may have originated as a correlated effect of some other aspect of call production (Brooks & McLennan 1991).

A second intriguing pattern found within the hylid clade is the shift from pure-tone advertisement calls to pulsed advertisement calls. *Pseudacris ocularis* arises between the group with pure-tone calls and the group with pulsed calls, and its advertisement call consists of a pure-tone component (similar to the pure-tone calls of the *P. ornata* group) followed by a pulsed component (similar to the pulsed calls of the *P. nigrata* group). Does this represent an intermediate stage, and, if so, has there been a shift in one component in the relationship between structure and function? Experimental studies of call function in this group, focusing especially on *P. ocularis*, may provide an answer.

The advertisement signals of the two anuran groups we examined represent only a small window into the tremendous diversity of animal signals. Understanding how this diversity has arisen remains a central question in ethology and behavioural ecology. On one hand, some of the most important insights into the structure of this diversity have come from studies that span broad taxonomic groups and look for evidence of convergence (Marler 1955, 1988; Collias 1960; Morton 1975, 1977; Wiley 1991). On the other hand, it seems clear that the contrasting approach taken in this paper, that of looking at patterns of divergence within individual clades, provides a different and complementary set of insights. Studies of within-group patterns of divergence in communication signals can tell us what features of signals are most likely to change evolutionarily (Ryan 1988; this study); can provide insight into the processes involved in that divergence (Basolo 1990; Prum 1990; Proctor 1993; Ryan & Rand 1993b); and can identify evolutionary transitions and innovations that suggest a focus for process-oriented studies (Otte 1974; Hoy 1990; McLennan 1991; this study). Knowing what patterns actually characterize the evolution of animal signals should guide us to ask the right questions about the processes that produced them, questions we otherwise might not know to ask.

## APPENDIX

## Sources and localities for recordings used in call analysis

| Species                 | Locality                            | No. | Recorder     | Catalogue no.*      |
|-------------------------|-------------------------------------|-----|--------------|---------------------|
| <b>Bufonidae</b>        |                                     |     |              |                     |
| <i>B. americanus</i>    | NJ: Bergen Co.                      | 5   | R. Zweifel   | AMNH 111            |
|                         | MA: Concorde                        | 5   | B. Causey    | —                   |
| <i>B. cognatus</i>      | AZ: Maricopa Co.                    | 5   | B. Sullivan  | —                   |
|                         | MN: Traverse Co.                    | 3   | —            | TMM 120, 122        |
| <i>B. compactilis</i>   | Mexico: Jalisco                     | 2   | J. Bogart    | TMM 329             |
|                         | Mexico: Distr. Fed.                 | 2   | —            | TMM 484             |
| <i>B. hemiophrys</i>    | MN: Traverse Co                     | 5   | —            | TMM 118, 121        |
| <i>B. houstonensis</i>  | TX: Bastrop Cp.<br>(two localities) | 10  | R. Cocroft   | USNM 196, 197       |
| <i>B. microscaphus</i>  | AZ: Maricopa Co.                    | 5   | B. Sullivan  | —                   |
|                         | UT: Washington Co.                  | 5   | —            | TMM 92A,B<br>TMM 94 |
| <i>B. speciosus</i>     | TX: Caldwell Co.                    | 10  | —            | TMM 107<br>TMM 101  |
| <i>B. terrestris</i>    | FL: Alachua Co.                     | 5   | —            | TMM 101A            |
|                         | GA: Baker Co.                       | 5   | —            | TMM 162A,B          |
| <i>B. valliceps</i>     | TX: Bastrop Co.                     | 4   | R. Cocroft   | USNM 168, 170       |
|                         | TX: Travis Co.                      | 4   | W. Wagner    | —                   |
|                         | TX: Travis Co.                      | 3   | —            | TMM 138B            |
| <i>B. woodhousii</i>    | NJ: Bergen Co.<br>(two localities)  | 10  | R. Zweifel   | AMNH 86, 115        |
| <b>Hylidae</b>          |                                     |     |              |                     |
| <i>H. chrysoscelis</i>  | IN: Brown Co.                       | 5   | M. Morris    | —                   |
|                         | TX: Travis Co.                      | 5   | R. Cocroft   | USNM uncat.         |
| <i>H. regilla</i>       | MT: Rock Creek                      | 1   | —            | AMNH 87             |
|                         | CA: Shasta Co.                      | 4   | —            | AMNH 167<br>TMM 95  |
| <i>P. brachyphona</i>   | AL: Auburn                          | 2   | M. Fouquette | —                   |
|                         | GA: Dawson Co.                      | 4   | C. Gerhardt  | —                   |
| <i>P. brimleyi</i>      | SC: Jasper Co.                      | 2   | M. Fouquette | —                   |
|                         | SC: Dorchester Co.                  | 2   | C. Gerhardt  | —                   |
|                         | GA: Chatham Co.                     | 7   | C. Gerhardt  | —                   |
| <i>P. clarkii</i>       | TX: Travis Co.                      | 5   | R. Cocroft   | USNM 201            |
|                         | TX: Bastrop Co.                     | 5   | R. Cocroft   | USNM 166–168        |
| <i>P. crucifer</i>      | NY: Suffolk Co.                     | 5   | R. Zweifel   | AMNH 163            |
|                         | NJ: Bergen Co.                      | 1   | R. Zweifel   | AMNH 163            |
|                         | NJ: Burlington Co.                  | 4   | —            | AMNH 69             |
| <i>P. nigrita</i>       | FL: Alachua Co.                     | 5   | M. Fouquette | —                   |
|                         | FL: Calhoun Co.                     | 4   | M. Fouquette | —                   |
|                         | FL: Union Co.                       | 1   | M. Fouquette | —                   |
| <i>P. ocularis</i>      | FL: Gadsden Co.                     | 2   | —            | AMNH 161            |
|                         | FL: Levy Co.                        | 2   | —            | TMM 102             |
|                         | GA: St Catherine's Is.              | 6   | R. Zweifel   | AMNH 162, 196       |
| <i>P. ornata</i>        | NC: Carterette Co.                  | 4   | —            | FMNH 472            |
|                         | FL: Alachua Co.                     | 6   | D. Lee       | FMNH 106, 404       |
| <i>P. streckeri</i>     | TX: Washington Co.                  | 4   | —            | TMM 316             |
|                         | TX: Travis Co.                      | 1   | —            | TMM 40              |
|                         |                                     | 5   | R. Cocroft   | USNM 196            |
| <i>P. t. feriarum</i>   | FL: Calhoun Co.                     | 5   | M. Fouquette | —                   |
|                         | TX: San Jacinto Co.                 | 5   | R. Cocroft   | USNM 201            |
| <i>P. t. kalmi</i>      | NJ: Cape May                        | 1   | —            | AMNH 150            |
|                         | NJ: Bergen Co.                      | 2   | —            | AMNH 86             |
|                         | NJ: Burlington Co.                  | 1   | —            | AMNH 69             |
| <i>P. t. triseriata</i> | KS: Cherokee Co.                    | 5   | J. Platz     | —                   |
|                         | KS: Cowley Co.                      | 5   | J. Platz     | —                   |

\*Museum abbreviations follow Leviton et al. (1985).

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