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Acoustic communication in frogs: a personal and historical approach to the analysis of the structure and function of their calls

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Biographical summary
Murray is a pioneer in the application of audio recording to the study of sound communication in animals or bio-acoustics. His model system is acoustic signalling in frogs, particularly in species that occur in temperate Australia and in the southern United States. He commenced this research as a BSc Honours student in Zoology at the University of Western Australia in March 1954. After completing a PhD there in December 1957, he spent the next 18 months on post-doctoral studies at the University of Texas at Austin. He returned to Australia in October 1959 to take up a lectureship in Zoology at the University of Melbourne, where he remained until retirement at the level of Reader/Associate Professor in February 1998. He is continuing his association with the University of Melbourne in the honorary position of Principal Fellow in the Department of Zoology. In addition to numerous primary research publications in Australian and international journals, Murray has written a number of chapters in symposium volumes that consider the broader aspects of acoustic communication in evolutionary and behavioural biology.

Introduction

Acoustic communication plays an important role in the reproductive biology of frogs. Frogs belong to the Order Anura (which means "without tails") and are placed in the vertebrate Class Amphibia. There is no clear biological distinction between "frogs" and "toads" so that, except for established common names which include "toad" or the diminutive forms "toadlet" and "froglet", only the terms "frog" or "anuran" will be used.The two main signals in the repertoire are produced by breeding males (Littlejohn 1977, Wells 2007). The most conspicuous and commonly produced signal is the "advertisement call", which is associated with attraction of a mate (= mating function) and the repulsion of nearby calling males of the same and different species (= territorial function). The other less-frequent signal is the encounter call, which is produced by a resident male in response to the advertisement call of an encroaching calling neighbour - when received above a critical threshold of intensity - and is usually associated with agonistic behaviour if the acoustic interaction intensifies. Wells (2007) used the term "aggressive call" for this category of signal, but "encounter call" is preferred, because it is based on context only and not attributed to a specific function (Littlejohn 1977). In this essay, I will concentrate on the advertisement call, with emphasis on long-range acoustic communication through the atmosphere - which may be only a about a meter for small frogs. Littlejohn (1996) has written a concise general review of acoustic communication in frogs. For recent comprehensive accounts of the topic see Gerhardt and Huber (2002); Wells (2007); and Narins, et al., (2010); otherwise, only specific publications will be cited.

Figure 1. Calling male of the Spotted Marsh Frog (*Limnodynastes tasmaniensis*) showing the inflated vocal sac.

The following overview of vocalisation and audio reception should apply to most frogs, especially the smaller species that I have studied in southern Australia. The main anatomical structures involved in call production are: the muscles of the body wall which provide the power supply, the larynx which contains a posterior pair of vocal cords that produce the basic sound which can then be amplitude modulated by an anterior pair of arytenoid valves, the vocal sac which is inflated during calling and acts as a radiator to couple the acoustic system to the atmosphere (Figure 1), and the associated nervous connections and control centres in the brain. The advertisement calls are largely genetically determined, a conclusion that is based on the intermediate structure of calls of hybrids and the lack of parental contact after the eggs are laid or tadpoles metamorphose into frogs. The ears are located on the sides of the head, posterior to the mouth. There is no external ear or pinna so that the circular eardrum (tympanum) is flush with the body surface. The air-filled middle ear contains a mechanical linkage (columella or stapes) between the tympanum and the inner ear. Each middle ear is connected to the mouth cavity by the eustachian tube so that there is continuity between the inner surfaces of the two eardrums. The fluid-filled inner ear is a complex structure, but there are three main organs concerned with vibrational and acoustic reception. The first organ is the basillar papilla which processes air-transmitted sounds such as the advertisement call, and is narrowly tuned to the main frequencies of that sound so that it acts as a band-pass filter. The frequency range of detection by the basilar papilla lies between about 2000 and 4000 Hz for small frogs (body length < 35 mm), with the greatest sensitivity matching the spectral properties of the calls of each species. The second organ is the amphibian papilla - which responds to low frequencies (i.e., ca 300-1000 Hz) that can also be transmitted through the atmosphere and received at the tympanum, or from seismic vibrations transmitted through the substrate and conducted to it by way of a linkage of bones and muscles in the hands, arms, and pectoral girdle to the operculum of the inner ear. The third organ is the saccule which is sensitive to very low frequencies (< 300 Hz) and also responds to seismic stimuli which are conducted to the inner ear by the same linkage as serves the amphibian papilla. Thus there is no direct equivalent of the mammalian cochlea, but in some species the amphibian papilla has limited anatomically distributed properties of frequency resolution. Progress in understanding acoustic communication depended to a large extent on the development of instrumentation and procedures for recording, objective physical analysis and experimental documentation (e.g., Baker 2001). I have provided a personal perspective of the development of the equipment and procedures used in the recording and analysis of the calls of frogs over the period 1954 to 1997 - which began with a fully analogue approach that continued until 1982 when the transition to digital technology commenced (Littlejohn 1998). In the present account I will concentrate on the biological aspects and associated methodology of my research to complement the earlier personal perspective. This approach will be developed along the following lines: (1) a brief review of procedures used in recording and analysis, (2) descriptions of the calls and patterns of differentiation in components of the call within and between species, (3) determination of functional significance of differences in calls of closely related species that call at the same time and place, and (4) elucidation of problems of communication in complex acoustic environments. Examples from my research and that of my colleagues will be used to illustrate these points.

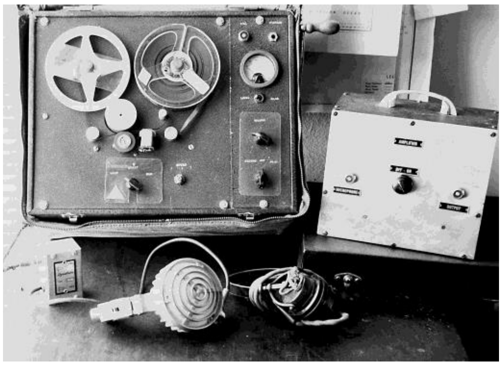

Figure 2. Custom-built tape recorder and pre-amplifier with Philips EL 6030 hyper-cardioid microphone and Dynatron 850 impedance-matching transformer. Photograph taken ca 1956.

Audio recording

In 1953, at the request of my future research supervisor A. R. (Bert) Main, the Australian Broadcasting Commission with their outdoor sound recording unit successfully demonstrated the feasibility of recording the calls of frogs on magnetic tape in the field (Main 1993). On this basis, and because of my interest in electronics, I agreed to undertake a research project to record and describe the calls of south-western Australian frogs for the BSc (Honours) degree in the Department of Zoology at the University of Western Australia. Recording the calls of frogs in the field started in the autumn of 1954 when a custom-built portable tape recorder driven by a spring motor and the essential accessories became available (Figure 2). It was only after my research project had commenced that I became aware of other studies of the objective analysis of acoustic signals of animals (e.g., Blair and Pettus 1954, Blair 1955a, Thorpe 1954). Initially an omni-directional piezo-electric microphone (Acos 19-4) was used, but this was later replaced by a directional dynamic microphone (Philips EL 6030 hyper-cardioid) and a custom-built preamplifier. Because of the weight of the recorder (about 17 kg), it was usually operated from a vehicle parked close by and a long microphone lead used (Figure 3). This set-up was used until the end of 1957 when my post-graduate studies were completed and I left Western Australia to begin a post-doctoral period with W. Frank Blair at the University of Texas at Austin. Blair was then using a mains-powered (120 volt, 60 Hz alternating current) studio recorder (Magnecord PT6 recorder and pre-amplifier) supplied by a frequency stabilised rotary converter and lead-acid storage battery for field recording. Soon after my arrival the first self-contained portable recorders were acquired by Blair (Amplicorp, Magnemite 610VU, with spring motor and battery powered electronics). The subsequent availability of compact and fully battery-operated recorders with better tape transport mechanisms and electronic specifications resulted in recordings of greatly increased quality (Littlejohn 1998). Improvement in the control of the nominal speed of tape through the replacement of centrifugal governors with electronic servo-controlled systems, especially those with a quartz oscillator as a reference, and the more-precise indication of the peak recording level to prevent over-modulation and associated distortion, were also very significant later developments (see Littlejohn 1998). It was also important to check the tape transport speed, especially of the early recorders, by calibration against a standard such as a frequency test tape and frequency counter in the laboratory, or with the addition of a short section of a tone from a portable standard frequency source (e.g., 1000 Hz) with the recordings in the field. The other important technical advance was the availability of highly directional microphones - which began with the acquisition of a short shotgun dynamic microphone of the cardioid-distributed port design (Electro-Voice 644 Sound-Spot) in 1968, and subsequently those that operated on the interference/pressure gradient principle (e.g., Sennheiser MKH 805); the result was an improved signal-noise ratio and enhanced rejection of the calls of adjacent frogs. Even so, a robust and shorter directional dynamic microphone (e.g., Beyer M 88 hyper-cardioid) remained the favourite for ease of placement close to the frog. This choice was also made to avoid the reduced signal strength and higher level of frequency distortion that could result if the shotgun microphone was placed slightly off-axis – as when the calling frog could not be seen because it was concealed in thick vegetation.

Recording was carried out at breeding sites at night when the frogs were calling strongly. A calling individual was located by direct observation or by triangulation - a technique widely used by herpetologists - where the caller is located at the intersection of the narrowly focussed beams of the lights of two observers who are standing about 2-3 m apart in the general vicinity of the frog and directed towards the source of the sound. As described earlier, frogs have very sensitive seismic detectors of ground vibrations; thus they usually cease calling with the approach of the investigator, and will only resume after a few minutes if there are no more vibrations. If the subject

Figure 3. Patsy Littlejohn operating the custom-built tape recorder (Figure 2) from a vehicle. Photograph taken ca 1956.

was calling while floating, and more that about 1 m from the shore, then a shotgun microphone with its greater working distance was preferred. This procedure allowed recordings to be made from the bank because the ripples produced by an investigator when stepping into the water and wading out towards the frog usually resulted in the frog ceasing to call and submerging or swimming away. Thus we preferred to record frogs that were calling on the ground or in low vegetation along the banks, or if in water then close to the shore, so that we could use a hyper-cardioid dynamic microphone. The microphone was then placed within about 15-20 cm of the subject, either on the ground facing the frog, or attached to a stand and pointed downwards towards the frog from a similar distance. After a series of calls had been recorded, an attempt was then made to capture the frog for examination and to avoid recording the same individual again.

The body temperature of a frog and its associated metabolism vary with the ambient temperature. As some components of the advertisement call, such as duration and pulse rate, are influenced by the temperature of the emitter (Gayou 1984), the temperature of the subject when the recording was made is a critical value for comparative studies. The recorded specimens of the species that we were investigating were usually too small (i.e., < 35 cm) to allow accurate direct measurement of body temperatures. Removal of the specimen from its micro-environment and then holding it while attempting to obtain a core temperature by insertion of a fine thermometer probe into the mouth or hind gut may result a different value – either higher through transfer of heat from the hand of the collector, or lower because of an increased rate of evaporation from the body surface in the elevated and exposed position (Fouquette 1980). Thus some other temperature must be measured as a proxy to provide an estimation of body temperature. If calling in water, then the frog is assumed to be at thermal equilibrium with this medium, and the temperature of the adjacent water would then closely approximate that of the frog (Fouquette 1980). Most amphibians have moist freely evaporating skins, so that the wet-bulb air temperature at the calling site is the preferred measurement to obtain of a frog calling in air (Mellanby 1941). This effective temperature can then be used to determine its influence on a call attribute by regression analysis (see below).

Acoustic analysis

Once the technique of recording had been established, we then had to face the problem of physical analysis so that the calls could be described objectively and quantitatively to allow their comparison. There are two aspects to consider in acoustic analysis of the recordings - temporal (time) and spectral (frequency). Two main approaches to acoustic analysis were available in 1954; the recorded signal could be replayed and the output of the recorder sent to either: (1) a cathode ray oscilloscope and a photographic image of the trace obtained on a continuously recording camera to reveal its temporal structure (as an oscillogram or waveform), with resolution based on the speed of the film (Figure 4); or (2) an audio-spectrograph such as the Sona-Graph (Kay Elemetrics), with the direct production of a tracing of both spectral and temporal properties on electro-sensitive facsimile paper (as a sonogram or audio-spectrogram). The sonograms were of only limited resolution for temporal and spectral features (frequency range 85 - 8000 Hz, dynamic range about 10 dB), but the additional spectrum (termed a section by Kay) was satisfactory for the display of the frequency structure in a 10 ms selection of the recorded signal (frequency range 85 -8000 Hz, resolution 45 Hz, amplitude range 35 dB). The use of the Sona-Graph was favoured by the early workers in the emerging field of bio-acoustics because of the convenience of preparing the images and the relative ease of interpretation of them - for the instrument had originally been designed for visualising human speech (Potter 1945). Baker (2001) has outlined the history of development of the audio-spectrograph, and its application to the study of bird song. Potter (1950) presented the first spectrograms of calls of frogs, namely of ten North American species that were derived from disc recordings made in the field by Kellogg and Allen (1948), along with some brief general comments on the acoustical nature of each type of call. Blair and Pettus (1954) provided the first detailed description of the advertisement call of a frog, namely of the Colorado River Toad (*Bufo alvarius*), and they included a figure with two sonograms and their associated sections that were produced on a Sona-Graph. Blair (1955a) published the first quantitative study of advertisement calls, with values derived from analysis of recordings on a Sona-Graph, in which he described geographical variation in two species of narrow-mouth frogs (*Microhyla = Gastrophryne*). I had direct access to this instrument while at the University of Texas, and so was then able to become familiar with its operation.

Figure 4. The author with Philips GM 3156 cathode ray oscilloscope and attached Southern Instruments M 726 continuously recording 35 mm camera with M 729 motor unit. Also shown is a Pyrox Magictape TR-ST1 tape recorder for playback and A. J. Williams SR4 resonant reed frequency meter to indicate the AC mains frequency as a check for calibration of the film speed. Photograph taken ca 1954.

Cathode ray oscilloscopes were in wide use in research laboratories by the early 1950's and suitable continuously recording cameras were also then available. This apparatus was readily adapted to acoustic analysis, and the resulting oscillograms (waveforms) were especially suitable for the display of temporal features such as envelope shape, amplitude modulation and pulse structure, but other than for carrier frequency were impractical for the determination of spectral composition. The inclusion of an accurate time marker as a second trace on the photographic record allowed accurate measurement of the temporal aspects of the signal. Audio-spectrographs were expensive during the 1950's, and there were very few in Australia; hence I started my acoustic analysis by using an oscilloscope and recording camera which the Department of Zoology was able to obtain for my use because of the lower cost. Our first publication on the calls of frogs and which included oscillograms (but lacking a time base on the tracings) was published in 1955 (Littlejohn and Lee 1955). While an oscilloscope and recording camera were obtained soon after I had taken up a lectureship in Zoology at the University of Melbourne October 1959, our first Sona-Graph (Kay 6061-A) was not acquired until some five years later. These two analogue procedures for acoustic analysis remained in use in our laboratory until the first instrument for digital analysis, a processing digital oscilloscope (Norland 3001), became available in 1982. We progressively converted to using digital equipment with the acquisition of a digital Sona-Graph (Kay DSP 5500) in 1988 and digital tape recorders (Sony TCD-D7) in 1995. Waveforms and audio-spectrograms were both readily produced and measured on the same digital system of analysis, and with great flexibility when microcomputers and associated sound cards and audio software became available in the late 1980s and early 1990s (Littlejohn 1998).

Structure of advertisement calls

The following features of advertisement calls may be derived from the above procedures of objective analysis: (1) call a single note, or a train of rapidly repeated notes; (2) calls or notes of simple structure (e.g., a sustained tone), or amplitude modulated to result in a train of pulses with a distinctive pulse repetition rate; (3) note envelope of near-uniform amplitude or with a gradual increase or decrease in amplitude (i.e., a positive or negative ramp); (4) pulses with characteristic shapes based on times of rise and decay and depth of amplitude modulation; (5) notes of similar structure (monophasic), or of two distinct forms (diphasic); (6) frequency spectrum with one of the following properties: a narrow or broad continuous band of frequencies with one peak (dominant frequency), or a set of frequencies that are harmonically related to a fundamental and with one of these being the dominant frequency, or a carrier frequency with sidebands above and below it resulting from amplitude modulation of a carrier frequency at the pulse repetition rate - which determines the interval between these frequencies (this carrier frequency is often the dominant frequency); and (7) dominant frequency may rise or fall throughout a call or note so that the signal is frequency modulated. Features (1) to (5) are best displayed and measured on oscillograms (waveforms), and features (6) and (7) on sonograms.

Two other physical properties of advertisement calls to consider are those associated with their propagation. The first is the sound pressure level which is measured in decibels (dB) at a stated distance from the source, usually 15 or 25 cm for small frogs. Because of the short rise times and rates of amplitude modulation, the maximum (peak; integrating time < 50 µs) reading of sound pressure level is the only meaningful value to obtain for the calls of frogs (peak sound pressure level = PSPL; 0 db re 20 µPa). Such levels can be quite high for small frogs (< 30 mm); for example, with mean values adjusted to 25 cm: 101 dB PSPL for the Victorian Smooth Froglet (Littlejohn & Harrison, 1985), and 106 dB PSPL for the Common Froglet, *Crinia* [previously *Ranidella*] *signifera* (Littlejohn, Harrison & Mac Nally, 1985). The other property is the pattern of radiation from the source as depicted by a polar diagram. In most of the Australian species that we have studied, the elastic vocal sac under the throat is inflated like a balloon while advertisement calls are being produced and should approximate an omnidirectional source. This property would result in the most effective broadcasting pattern for establishing acoustic contact with intended receivers in that the full 360 degrees of radiation would be covered.

Factors affecting variation in advertisement calls

Frogs are ectotherms (i.e., "cold-blooded"), so that their body temperatures are influenced by the ambient thermal environment (e.g., either water or wet-bulb air temperature – see earlier comments on effective temperature), and subsequently their level of metabolism. Some features, such as durations and repetition rates of calls, notes and pulses, are based on the metabolic rate - which affects muscle function and neural transmission. Hence values of those components from calls recorded at different body or effective temperatures may require adjustment before they can be compared. A correction factor is then derived from the significant slope for values of a call characteristic plotted against effective temperature in linear regression analysis. The values can then be adjusted to a common temperature for comparison, or the residuals of the regression may be directly compared. Some characteristics, such as pulse rate and call duration, are highly correlated with effective temperature; whereas others, such as dominant frequency and number of pulses per note, may not be affected by this extrinsic variable. The dominant frequency of the advertisement call, however, is inversely proportional to the size of the frog – which is usually indicated by body length. Thus the calls of smaller frogs will have higher dominant frequencies than those of larger frogs, and this value must also be adjusted before comparison if significantly correlated with body size.

Because of the constraints of body size, differences in dominant frequency of the call will usually only occur between species when the sizes of adult males differ. Closely related species of frogs are usually about the same size, so that they may have similar dominant frequencies. Hence the advertisement calls of closely related species that call at the same place and time should differ in temporal structure, especially duration or pulse repetition rate – with means usually differing by a factor of two or more and ranges of variation are separated by a gap (Littlejohn 2001). The advertisement calls of three species of froglets (*Crinia parinsignifera*, *C. signifera* and *C. sloanei*) that breed at the same time and place in the Riverina have overlapping dominant frequencies but differ markedly in duration, pulse number and the resulting pulse repetition rate (Figure 5).

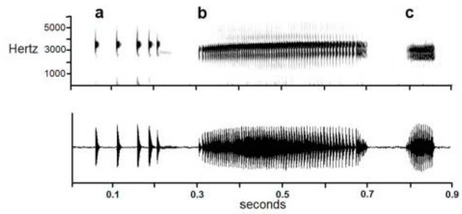

Figure 5. Sonograms (upper panel) and waveforms (lower panel) of the same advertisement call of each of three species of froglets recorded calling together at a pond near Tocumwal, New South Wales (effective temperatures: ca 11 ºC); (a) Common Froglet (*Crinia signifera*), (b) Plains Froglet (*C. parinsignifera*), and (c) Sloane's Froglet (*C. sloanei*). Note that the ungraduated abscissa for the waveform represents relative linear amplitude.

Experimental documentation of function of advertisement calls

These studies began at the University of Texas in 1958 with laboratory experiments in which breeding females of Strecker's Chorus Frog (*Pseudacris streckeri*) were released into a temperature-controlled enclosure and presented with two previously recorded advertisement calls as stimuli. One of the acoustic stimuli was from a male of the same species as the female being tested (i.e., a conspecific call) and the other was from a related species, the Spotted Chorus Frog (*P. clarki*) which breeds at the same time and place (i.e., a heterospecific call). The calls, which were recorded at effective temperatures within the range of the temperature-controlled enclosure (19.5 ± 2 ºC), were replayed through two small loudspeakers placed at opposite ends of the enclosure. These two-choice discrimination tests demonstrated that females showed deliberate orientative behaviour and moved towards the loudspeaker that was the source of the conspecific call (= positive phonotaxis) - which they either approached closely or directly contacted the loudspeaker (Littlejohn and Michaud 1959). This specificity of positive phonotaxis by breeding females was subsequently shown for several other species of North American frogs.

In later tests, at the University of Melbourne (starting in 1967), we began a program of call discrimination experiments on two closely related species of tree frogs - Ewing's Tree Frog (*Litoria* [previously *Hyla*] *ewingii*) and Verreaux's Tree Frog (*L. verreauxii*) - collected from localities where they occurred together in the Melbourne area. We first determined that the females of these two species displayed positive phonotaxis only to the advertisement call of the same species (Figure 6). The calls are of similar basic structure, with overlapping ranges of dominant frequencies, but differing strikingly in pulse repetition rate by about a factor of two for population means. The next step was to prepare synthetic calls that differed only in pulse repetition rate (and inevitably the associated number of pulses). The stimuli were prepared on the basis of the mean values for the two species adjusted to 10 ºC, for samples recorded in the area of common geographic range in south Central Victoria and slightly higher pulse repetition rates, namely 80 p s^{-1} for *L. ewingii* and 157 p s^{-1} for *L. verreauxii*. These calls were then used as the stimuli in the discrimination trials, and the results showed that this difference in pulse repetition rate was sufficient for specificity of response by breeding females (Loftus-Hills and Littlejohn 1971). Other studies on North American species have greatly expanded and refined the analysis of the functional significance of components of the advertisement call in eliciting positive phonotaxis in frogs (see Gerhardt and Huber 2002, Wells 2007).

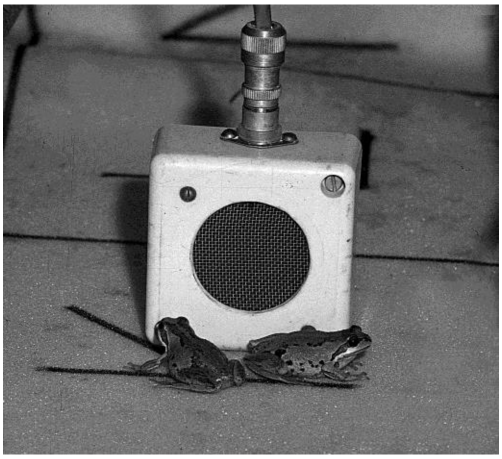

Figure 6. Two breeding females (body length about 30 mm) of Verreauxii's Tree Frog (*Litoria verreauxii*) that have been attracted to a loudspeaker from which the recorded advertisement call of a male of the same species is being played.

Narins and Capranica (1976, 1978) showed that there is partitioning of function in the two-note (i.e., diphasic) call of the Coqui Tree Frog *Eleuthrodactylus coqui*, in which the two components differ in dominant frequency. They also showed that males and females have selective tuning of the auditory receptors to match either one or other part of the call, and demonstrated that the first note ("co") functions in territorial interactions between males while the second note ("qui") is attractive to conspecific breeding females. The advertisement call of the Victorian Smooth Froglet (*Geocrinia victoriana*) is also strongly diphasic and consists of one, or rarely two or three, longer introductory notes (414 ms) of lower pulse repetition rate (145 p s^{-1}) followed by a series of shorter repeated notes (84 ms) of higher pulse repetition rate (457 p s^{-1}) (mean values from Harrison & Littlejohn 1985). In contrast to the Coqui Tree Frog, both phases in the call of a male of the Smooth Frog are of the same dominant frequency (ca 2730 Hz). Because of the absence of differentiation in frequency, and because such marked diphasy in advertisement calls is uncommon in frogs, we decided to explore the functional significance of the two parts of the call in this species (Littlejohn and Harrison 1985). Thus by careful cutting and splicing, the introductory note and a series of repeated notes were separated, made up into loops of the same overall duration by the addition of blank tape, and transcribed to separate reels of tape. These tapes were then used to provide the alternative stimuli for playback trials. As we already had a long-term field program under way to the south of Colac in south-western Victoria, where we were investigating a hybrid zone between *G. victoriana* and the closely related species the Tasmanian Smooth Froglet (*G. laevis*), we decided to carry out our playback trials there and in the field with equipment and procedures developed during our earlier research. In this area the Smooth Froglets breed in the autumn; males call on land from under cover of litter or at the bases of grass tussocks in situations that will later be flooded with the onset of winter rainfall. The calling site is also where mating occurs and the eggs are laid. Embryos develop on land to the stage of an advanced tadpole within the egg capsule, and then quickly hatch out when covered with water. This reliable seasonal and terrestrial breeding pattern was conducive to field experimentation with electronic equipment. The first step was to assess the responsiveness of breeding females when offered each part of the call as a separate stimulus (both at ca 100 dB PSPL) in a discrimination experiment (Littlejohn & Harrison 1985). The outcome was clear; the females were attracted only to the repeated notes, and showed no interest in the introductory note. We also replayed each of the two phases of the advertisement call separately to males at their calling sites at increasingly higher peak sound pressure levels (Figure 7). The resident subjects responded to the

Figure 7. Field playback setup with microphone (Beyer M 88) and loudspeaker (Kaltro HTM-2 tweeter) directed at a calling male of the Victorian Smooth Froglet which is concealed in the patch of grass in the lower right of the image.

introductory note presented at < 100 dB PSPL by ceasing to produce advertisement calls and then producing only a much longer call derived from the introductory note and with no repeated notes. At 110-120 dB PSPL, the duration of this "long call" increased by about 200% above that of the introductory note in the resident male's call before the playback experiment commenced. The resident also showed aggressive behaviour by emerging from the concealment of its calling site and approaching and contacting the loudspeaker while producing long calls (Figure 8). The long call can thus be classified as an encounter call. Playback of the repeated notes alone had no significant effect on the composition and rate of production of diphasic advertisement calls by the resident male. The effect of playback to a resident male of a complete advertisement call, over the same range of increasing PSPL, was similar to that of the separated introductory note.

Figure 8. A male (body length about 25 mm) of the Victorian Smooth Froglet (*Geocrinia victoriana*) which has left its calling site and approached a loudspeaker from which the recorded advertisement call of a male of the same species is being played at > 100 dB PSPL.

Resources of sound communication and design features of calls

It is usual for males of several species of frogs to call at the same time and place. Littlejohn (1965, 1977) has discussed the three ways in which the problems of effective acoustic communication may be reduced or avoided, namely: (1) spectral (frequency) stratification, (2) spatial separation, and (3) temporal partitioning. Because breeding adults of closely related species of about the same body size they are constrained in the frequency band within which long-range acoustic signals such as the advertisement call can be efficiently produced. Even so, some cases of partitioning of frequency bands between frogs of about the same size have been described. For example, although males of the two species of narrow-mouthed toads are about the same body length where they occur together in the southern United States (*Gastrophyne carolinensis*: 22-33 mm, *G. olivacea*: 19-28 mm; Blair 1955b), values of dominant frequencies of their advertisement calls are separated by a gap of about 700 Hz (*G. carolinensis*: 2100-3400 Hz; *G. olivacea*: 4100-4500 Hz; Loftus-Hills & Littlejohn 1992). Where this stratification in frequency does not occur, other ways must be used to avoid or reduce the interference within a restricted common bandwidth of the crowded communication channel (Littlejohn 1977). Thus males of different species may: call within different areas of the breeding site, such as on the banks of a pond or while floating (Littlejohn 1977); or adjust the timing of production of advertisement calls to avoid overlap with those of neighbours. For example, in two south-eastern Australian species that breed on land during the autumn, males of the Southern Toadlet, *Pseudophryne semimarmorata*, insert their very short calls into the silent intervals between the long calls of the Southern Smooth Froglet, *Geocrinia victoriana* (Littlejohn & Martin 1969).

Littlejohn (1977) considered the following components to be important resources for efficient and effective signalling: (1) free channel bandwidth within the most acoustically permeable frequency band in the atmosphere - which is between about 400 and 4000 Hz for most species of frogs; (2) available transmission time within this bandwidth to avoid overlap with the calls of nearby males and consequent “jamming”; (3) broadcasting sites for effective propagation of signals (such as elevated calling stations); (4) sufficient surrounding space to allow effective and clear broadcast of the signal and its reception and assessment by the intended receiver; and (5) where dominant frequencies overlap, an exclusive temporal coding pattern (such as in pulse repetition rate) within the anatomical and physiological capabilities of the sender and the receiver.

What are the characteristics that we might expect the advertisement call to have in order to optimise its efficiency for transmission through the atmosphere and to maximise the reproductive success of the caller in attracting an appropriate mate? The following properties were suggested by Littlejohn (1977). The first requirement would be to achieve the greatest possible range and spread of propagation through being as loud as possible and having an omni-directional pattern of radiation; and a calling male should be readily located by the approaching female. A critical requirement is a distinctive temporal pattern to allow the female to correctly identify the male as being of the same species. Variation in other properties of the call is needed so that a male can indicate his fitness as the best available mate in competition with other calling males of the same species. Finally, the call should also be structured to discourage males of the same species, and of other species with calls having similar dominant frequencies, from vocalising at sites that are close enough to cause acoustic interference or “jamming”. Sustained calling at the highest possible sound pressure level may be important in this latter situation, and if effective, should allow the resident male to maintain an acoustic territory and to maximise the associated reproductive success.

But the advertisement call functions in both modes - in the attraction of breeding females and in the repulsion of males either of the same species competing for mates, or of the same and other species that are competing for the resources of acoustic signalling. Thus the structure of the call may be compromised; the mate-attracting function, however, would seem to have the priority in terms of evolutionary fitness of the caller. In contrast, an encounter call should be non-directional so that the territory holder is difficult for the competitor to locate. Also, the encounter call should not be species-specific but effective against males of other species that could be competing for acoustic space or broadcasting stations - such as elevated sites that would maximise efficiency and range of propagation of the signal.

Conclusions

So it is that frogs, with their emphasis on the acoustic mode, have provided one of the basic model systems for the study of animal communication. As the advances in the technology of sound recording and analysis have been adopted, the scope of the research has been broadened and the precision and depth of questions asked has greatly increased. Some important general principles of animal behaviour, such as in temporal coding patterns and ways of dealing with a crowded communication channel, have also emerged from these studies. The investigations into geographical variation in advertisement calls and associated reproductive behaviour have also provided a clearer understanding of several important aspects of the processes of species formation and of the breakdown of species distinctness through hybridisation (e.g., Gerhardt & Huber 2002). The presence of discontinuity of ranges of variation of advertisement calls has also led to the discovery of many new species of frogs, especially where the external morphology is not markedly differentiated (e.g., *Crinia sloanei*, Littlejohn 1958).

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