ENERGY AND COMMUNICATION IN THREE SPECIES OF HYLID FROGS: POWER INPUT, POWER OUTPUT AND EFFICIENCY

BY KENNETH N. PRESTWICH[1,2], KRISTIN E. BRUGGER[2,*]
AND MARY TOPPING[1]

[1]*Department of Biology, College of the Holy Cross, Worcester, MA 01610, USA*
and [2]*Department of Zoology, University of Florida, Gainesville, FL 32611, USA*

Summary

1. Rates of oxygen consumption for calling, rest and locomotion were measured for three species of treefrogs from the south-east United States: *Hyla cinerea* (Schneider), *H. gratiosa* LeConte and *H. squirella* Bosc.

2. Anaerobic metabolism was slight during calling but large during forced hopping in *H. squirella*. It is assumed that calling in all three species is primarily aerobic.

3. For all species, oxygen consumption during calling rivalled or exceeded that for locomotion in a closed chamber. Calling apparently is at least as costly as closed-chamber locomotion, if anaerobic contributions to hopping are ignored.

4. The mass-specific costs of producing calls are similar in most species of hylids whose calling energetics have been studied.

5. As in other species of hylids, abdominal trunk muscle masses in male *H. squirella* and *H. gratiosa* were large – approximately 10 % of the total body mass.

6. Complete sound fields (with measures of variation) were mapped for each species. Each species is an essentially omnidirectional radiator with only a slight flattening of the field behind the head.

7. Efficiencies of sound production (acoustic power/metabolic power) were calculated for each species and compared with values from other frogs, insects and loudspeakers. Efficiencies in hylids vary between 0·8 and 4·9 %.

8. Factors that contribute to determining the efficiency of sound production are reviewed. Small animals such as frogs and insects must either use low-efficiency radiators or use high-frequency sounds that do not propagate over great distances. It is possible that low-efficiency transducers maximize the area over which an animal is heard per unit of energy expended.

* Present address: Department of Wildlife and Range Sciences, and US Fish and Wildlife Service, University of Florida, Gainesville, FL 32611, USA.

Introduction

Considerable attention has been focused on the energetics of communication in general (Alcock, 1979; Greenfield & Shaw, 1983) and acoustic communications in particular (Bennet-Clark, 1970; Heath & Josephson, 1970; MacNally & Young, 1981; Prestwich & Walker, 1981; Bucher *et al.* 1982; Ryan *et al.* 1983; Taigen & Wells, 1985; Ryan, 1985*a,b*; Taigen *et al.* 1985; Wells & Taigen, 1986; Lighton, 1987; Forrest, 1986; Kavanagh, 1987; Prestwich, 1988). These studies have established that the metabolic costs of producing loud, frequently repeated calls are very high and exceed the costs of terrestrial locomotion in insects and probably also in frogs. However, for the few cases where appropriate data exist (MacNally & Young, 1981; Ryan, 1985*a*; Kavanagh, 1987; Prestwich, 1988), the acoustic power outputs of these animals are relatively low compared to the metabolic power input. Thus, their efficiencies of sound production are low, generally being less than 1 %.

It is the purpose of the studies described in this paper to examine four questions. (i) What are the metabolic power inputs, acoustic power outputs and the efficiencies of sound production in three species of hylid frogs that possess very different calls? (ii) What are the relative costs of calling *versus* maximal locomotion in these species? (iii) Are there differences in efficiency of sound production in hylid frogs? (iv) If so, what are the causes of these differences?

In an attempt to answer these questions we studied three species of hylid (tree) frogs that are common in north Florida: the green treefrog, *Hyla cinerea* (Schneider), the barking treefrog, *H. gratiosa* LeConte, and the squirrel treefrog, *H. squirella* Bosc. These species differ in terms of size (1·4–14 g), preferred habitat, calls and breeding behaviour. *H. cinerea* and *H. gratiosa* often breed at the same place and time and occasionally hybridize (Oldham & Gerhardt, 1975; Gerhardt, 1981): this generally does not happen with *H. squirella*, since its breeding habits are different. According to a recent taxonomic revision by Hedges (1986), electrophoretic data suggest that these three species are more closely related to each other than to other hylids.

Materials and methods

Animals

All animals were collected in Alachua County, Florida. Work on *H. gratiosa* occurred during the last 3 weeks of June, *H. cinerea* was studied between July and mid-August and *H. squirella* throughout the summer whenever it bred.

Fatigue experiments

Since we determined $\dot{V}_{O_2}$ for exercise in a turning respiratory chamber (see below), we were interested in learning if the time to fatigue was similar in this chamber to that observed in animals that were exercised in less confining circumstances. Squirrel treefrogs were forced to hop on a wet floor until they refused to right themselves after repeated prodding. The take-off and landing

point for each hop were marked and the distances were measured. Immediately upon reaching exhaustion, one group of frogs was frozen in liquid nitrogen. Later these were analysed for lactate (see below).

Lactate accumulation

Whole-body lactate was determined to see if it was possible that a significant portion of the cost of calling was paid anaerobically. Squirrel treefrogs were used.

There were three experimental groups: rest, hopped to exhaustion (see above) and calling. Frogs that had remained motionless for at least 30 min in a large beaker in the laboratory were quickly frozen in liquid nitrogen. Calling males were captured from a natural chorus after they had called for at least 30 min and were frozen in liquid nitrogen. Less than 5 s passed between capture and freezing.

The frozen frogs were cut into two sections: the rear legs and the remainder of the body (referred to as the trunk). Each of these sections was homogenized at 4°C in $0.5 \, mol \, l^{-1} \, HClO_4$, the homogenate was centrifuged at $10000 \, g$ and the supernatant was analysed for L-lactate according to the method of Gutman & Wahlefeld (1974).

Measurement of oxygen consumption

$\dot{V}_{O_2}$ measurements were made by injection of 15 ml gas samples into an Amtek Applied Electrochemistry model S-3A O_2 analyser. Each metabolic chamber consisted of a canning jar, lid and closing ring. The lid was fitted with two ports for drawing or introducing gas. The tightness of the seal for these chambers could easily be checked by drawing 20–50 ml of gas (depending on the jar size) and seeing if the lid bulged inward and remained that way.

Air samples were drawn using a pair of 20 ml syringes attached to a three-way stopcock. The remaining port was attached to a length of Tygon tubing (2 mm i.d.). To obtain a sample, the stopcock was opened to one of the syringes and a sample of air was pumped back and forth to ensure mixing. Next, the plunger was drawn back and held for a moment and the stopcock was closed. The plunger was slowly pushed forward until slight resistance was felt. This procedure brought the pressure up to or above atmospheric pressure. Then a second sample was withdrawn from the other syringe using the same procedure. This was the procedure that was followed at the end of a measurement period. The only variations were as follows. (a) Initial measurements were taken after air equalling five times the volume of the chamber had been flushed through the system and the sample was then drawn through a 3 m length (9.5 ml volume) of sampling tube. The second port was left opened while these samples were drawn. (b) Final samples taken in the field were drawn from a very short, low-volume (<1 ml) Tygon line attached to the other of the two ports; this procedure ensured a sample of chamber air. (c) Laboratory measurements of resting and locomotory $\dot{V}_{O_2}$ used short Tygon lines from the sampling port.

The gas samples (approx. 18 ml) were injected into the O_2 analyser *via* a two-way stopcock into a 3 m Tygon line (2 mm i.d.). The injection point was 5 cm

upstream from two low-volume canisters containing soda lime to remove CO_2 and silica gel to remove H_2O. Thus, when the sample was rapidly injected, it displaced the gas in the upstream Tygon and filled this dead space with essentially undiluted syringe gas. The flow rate was set at approx. $15 \, \text{ml min}^{-1}$. Oxygen fractions were read from a chart recorder connected to the O_2 analyser. The effectiveness of this set-up was demonstrated by analysis of several different gas samples of known composition. All $\dot{V}_{O_2}$ data are reported at STPD.

Oxygen consumption during calling

Data for *H. gratiosa* were obtained in the field. Animals were captured from a chorus and placed in a 946 ml canning jar containing about 40 ml of pond water. The jar was closed with a nylon net held in place with the canning lid ring. The frogs were kept in an ant-secure area overnight at the edge of the pond. One hour before sunset the next evening, 300 ml of O_2-saturated pond water was added to each bottle so that the frogs could float while calling. The bottles were then capped with a canning lid that contained two air-tight ports described above. The lid was closed and tested for leaks and the jars were placed in the pond at its margin and anchored in the vegetation. The jars were not floating, but the pond did act as an effective water bath. The purpose of this arrangement was to simulate the normal calling situation of this frog as much as possible. During the next hour, large amounts of air were pushed through each chamber at regular intervals. At sunset, each jar was flushed with fresh air for the last time, and sealed as two 15 ml samples were drawn. Initial sample oxygen fractions (F_{O_2}) were never lower than 0·2080. Some of the captive animals started calling at about the same time that free-ranging animals formed a chorus. Final samples were drawn 1–1·5 h later. The lowest observed final F_{O_2} was 0·1782.

Calling rates were determined either by recording the calls using an internal microphone (Taigen & Wells, 1985) or, more commonly, by listening to a calling animal and recording the calling rate. This did not allow for the recording of call duration. The animals and the sealed gas samples were immediately brought to the laboratory where the gas samples were analysed and the animals were weighed, measured and released.

The procedure was similar for *H. squirella*, except that a smaller container was used (approx. 450 ml with 10 ml of pond water) and the animals were collected and measured the same night since we could not predict from one day to the next whether a chorus would form (Brugger, 1984). Only about one frog in 12 would call after being captured, and we were careful to use individuals that began to call soon after capture and did not struggle within the chamber.

$\dot{V}_{O_2}$ values for calling in *H. cinerea* were measured in the laboratory using frogs captured from large choruses earlier that same evening. A tape recording of a chorus was played to these animals and it seemed to stimulate calling and vocal interactions. Very few individuals called but those that did had their $\dot{V}_{O_2}$ measured as described above, except that 450 ml containers with 20 ml of pond water were used.

In both *H. squirella* and *H. cinerea*, there were animals that called relatively little over an hour. However, these calls were given at the typical rate and duration for animals in a chorus. Thus, the reports for numbers of calls per hour are for individuals that only called during a short time period, not for individuals that gave a few calls, widely spaced in time.

Oxygen consumption for rest and locomotion

Resting metabolic rates were taken under conditions designed to reflect resting rates in the field, not standard rates. Thus, we captured animals from a chorus and completed all our observations the next evening between 2 h before and 2 h after sunset. All animals defecated during their brief captivity, indicating that they had fed recently. For these measurements, the animals were placed in a Precision Instruments dual-programme illuminated incubator set for sunset at the same time as in the field and at a temperature equal to that at which calling cost was measured.

Measurements of exercise $\dot{V}_{O_2}$ were obtained by hand-turning the chamber so that the frog was forced to locomote maximally. We found that the temperatures tended to rise by 1–3 °C. To avoid this problem, the chambers were turned while partially submerged in a water bath. Final samples were drawn when the animals reached exhaustion, which was defined as the time when the animals would no longer right themselves.

Measurement of call spectra and sound fields

Recording of calls

Most calls were recorded using an AKG model CK-9 microphone and Marantz PMD 340 tape recorder. Sonograms were produced using a Multigon Uniscan II digital sonograph. Oscillograms were obtained using an Apple IIe computer equipped with an RC Electronics eight-bit digital oscilloscope and further spectral analysis of the calls was made using the RC Electronics spectral analysis (fast-Fourier transformation) software; the sampling rate was 28 kHz.

Calibration of the sound pressure level meter for short calls

All calls were measured using a C-weighted scale. This scale gives an essentially flat response between 70 and 5000 Hz (Peterson, 1980). Since nearly all the acoustic energy radiated by the frogs used in this study falls within this range (see Table 4), the estimates of acoustic power obtained from the SPL meter were not biased by the frequency spectrum used by a particular species. The SPL meter was calibrated before and after use.

In measuring efficiency of sound production, root mean square (rms) acoustic power should be used since it and $\dot{V}_{O_2}$ (metabolic power input) are both averages (Bennet-Clark, 1970; MacNally & Young, 1981; Kavanagh, 1987). (Oxygen consumption data represent the sum of all energy expenditures made during calling, not the instantaneous peak powers developed by the muscles during call production.) There are two methods for obtaining rms acoustic power. Perhaps

the most accurate method involves carefuly recording a call and then obtaining an oscillogram. Since the power at any point on the oscillogram is proportional to the voltage squared, the mean of the squared waveform voltages over time yields an average power output.

Since the equipment needed for this type of measure was unavailable, we used a GenRad model 1565 sound pressure level (SPL) meter. This meter obtains rms SPLs by using one of two different RC circuits; these circuits differ in terms of their time constants. The meter finds an exponential (running) average SPL, where the most recent data are weighted more heavily than older data in obtaining the rms value; the smaller the time constant, the more quickly the older data are suppressed in obtaining the rms SPL (Peterson, 1980). Thus, the time constant is a measure of the response time of the averaging circuit to the signal. The time constant used in this study was 125 ms and is referred to as 'fast' rms.

Unless a call measured by an RC circuit has a duration of 3–4 times the time constant, the circuit will give a reading that is lower than the actual SPL of the signal. The shorter the signal, the more severe this effect. The relationship between a sound's duration, the meter's time constant and the actual sound pressure is given as:

$$p_m = p_r(1 - e^{-t/RC}) , \qquad (1)$$

where p_m is the rms pressure of a short-duration call (in Pa), as reported by the meter, p_r is the actual rms pressure of the call (in Pa), t is the duration of the call (in s), and RC is the time constant (in s). It can be seen from this equation that only if the value of t approaches 3–4 times the time constant does the pressure recorded by the meter (p_m) approximate to the actual SPL of the sound. The pressure levels used in equation 1 can be converted into dB using the familar equation:

$$L_p = 20 \log \frac{p}{0·00002} , \qquad (2)$$

where p is the sound pressure (in Pa), L_p is the SPL (in dB), and 0·00002 Pa is the reference sound pressure.

Call duration for the hylids used in this study varied between about 140 and 200 ms. Thus, indicated fast-rms SPLs would all be underestimates. Therefore, it was necessary to obtain a duration-dependent correction factor for each species' call in order to know the actual rms SPL of the call. Calls of constant amplitude and variable duration were synthesized using an Apple IIgs computer. Each call consisted of a rise or attack phase of 10 ms, a full-amplitude plateau phase (varied between 20 and 1000 ms) and a decay phase of 10 ms. The amplitude and duration characteristics of these 'calls' were checked using an Apple IIe computer equipped with an RC Electronics eight-bit digital oscilloscope. The SPL of each synthetic call was measured at least 10 times and the results averaged. The range of variation of replicated calls was less than 0·4 dB; most replicates were identical.

These results (Fig. 1) are in excellent agreement with the predicted values. At relatively long call durations (>500 ms), the rms sound pressure levels were

constant. With shorter calls, the measured rms values decreased approximately as predicted. For the range of durations applicable to our study (140–200 ms), the measured SPLs deviated less than 0·7 dB from the values predicted using equation 1; this corresponds to at most a 15 % error between measured powers of our model calls and the power predicted from equation 1.

With this correction established, it was also important to determine whether intra-call variations in amplitude were accurately averaged by the SPL meter. The frog calls showed an initial period of high amplitude followed by a decrease of 3–10 dB (see Figs 6, 7). Calls with total durations of 140, 180 and 200 ms were synthesized as above. Modulated versions of these calls were produced by reducing the last one- or two-thirds of the call to a power level that was half (−3 dB) or a quarter (−6 dB) that of the peak level. Thus, these calls were similar in general appearance to those of the treefrogs (see oscillograms, Figs 6 and 7). For example, a call consisting of a peak plateau of amplitude A and duration t followed by a second plateau with amplitude half that of the first plateau (6 dB below A) and of duration 2t would be predicted to be approximately 3·5 dB below an unmodulated sound of amplitude A and duration 3t. The results of these experiments were all within ±0·5 dB of the expected SPL value; most were within 0·2 dB (±11 dB and ±4·5 % of expected power levels).

In summary, these results indicate that the GenRad 1565B SPL meter can be used to measure the rms SPL of 140–200 ms duration frog calls accurately, provided that a correction is made according to the call duration (Fig. 1). With
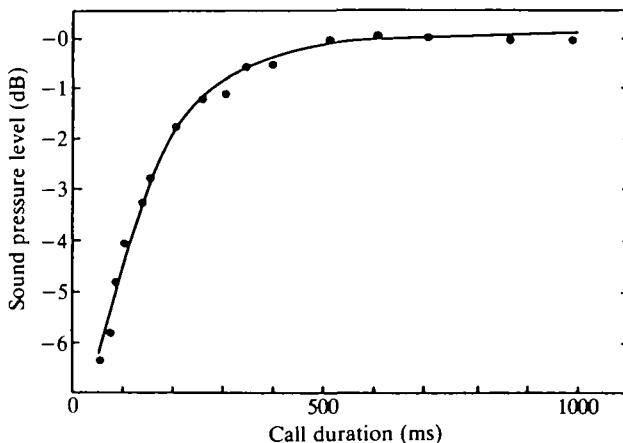

Fig. 1. The effect of call duration on the fast rms SPL reading for the GenRad 1565 SPL meter. Sound pressure levels of synthetic calls with equal and constant amplitude but of different duration were measured to quantify the effects of the meter's time constant and tendency to average calls with silent periods. Data are plotted in terms of SPL (in dB) below the SPL of long calls of equal amplitude as a function of call duration. The line is fitted by eye. Data conform to theoretical predictions (equation 1) within 15 %. This graph provides correction factors for the short calls of the hylids used in this study.

proper calibration, this method should be useful in other studies involving power output.

Mapping of sound fields

In the case of *H. gratiosa*, the sound field was mapped by placing a floating hemisphere of 0·75 m radius (to avoid near-field effects) made of light-gauge aluminium wire over a frog as it called in the pond. The hemisphere was centred over the frog and readings were taken at 25 points that were separated by 45° in the horizontal plane and 30° intervals in the vertical planes (see Fig. 9). Measurements were made on *Hyla squirella* in a similar manner, except that a 0·5 m wire hemisphere was used.

Hyla cinerea calls from vegetation, and therefore a complete sphere was measured. A thin metal rod that extended 0·5 m from the end of the SPL meter microphone was used to gauge distance to the frog. Measurements were made by moving the SPL meter through a total of 42 points. Obviously, it was not possible to obtain as exact recordings of distances and angles as in *H. gratiosa* or *H. squirella*, but there was so little deviation in SPL that this did not affect the overall picture of the sound fields (see Results). Only animals that were at least 1·4 m above the ground and that were on thin branches of vegetation were used.

For all three species, measurements were made with as little interfering vegetation as possible. For a given individual, 4–8 SPL readings were taken per point. If these SPL data varied by more than 1·5 dB, they were averaged by first converting to power using the relationship:

$$L_w = 10^{(L_p - 120)/10} , \qquad (3)$$

where L_w is the power level (in watts), and L_p is the SPL (re: 20 μPa). This is a rearrangement of the familiar acoustic power equation where the reference level (0 dB) is defined as 1×10^{-12} W. The power levels for each point were then averaged and reconverted to dB. Generally, most replicate readings were so close to each other (less than 1·5 dB difference) that given the precision of our recording instruments it was not necessary to go through this procedure; the dB values were simply averaged (Peterson, 1980).

The sound fields shown in Figs 9–11 were generated by obtaining the distance from the frog to the 70 dB isobar for each point. We established that, for the conditions under which we measured these sound fields, the inverse square law of attenuation was followed. That is, SPL decreased by 6 dB each time distance doubled. Thus, we calculated the length of a vector passing from the frog through the measurement point to the 70 dB isobar using:

$$R = r_1 \times 2^{(L_{pi} - L_{p,iso})/6} , \qquad (4)$$

where R is the length of the vector from the frog to the isobar, r_1 is the distance from the frog to where the SPL was measured, L_{pi} is the SPL in dB at the measuring point and $L_{p,iso}$ is the SPL at the isobar (70 dB for this study). After these distances had been calculated for each point of each frog's sound field, the

values for all individuals were averaged to give the mean length of a vector from the frog to the 70 dB isobar and the standard error of the mean (S.E.M.) of the length of this vector was calculated. Thus, the S.E.M. values reported for each data point on Figs 9–11 are for the vector for the indicated point; they are not resolved into separate x, y and z components. Finally, the mean species sound fields were drawn from these data using simple trigonometry to determine the x, y and z values of all known isobar surface points relative to the frog.

Estimations of acoustic power output

The total power per call is simply the product of intensity ($W m^{-2}$) and area (m^2). Since we had calculated the dimensions of a 70 dB sound field, the power contained in this field is simply:

$$W = S \times 10^{(L_{p,iso} - 120)/10} , \tag{5}$$

where W is power in watts, S is the surface area (in m^2) of an isobar, and $L_{p,iso}$ is the SPL (in dB) of this isobar (70 in this study). Our results (Figs 9–11) showed that the sound fields were slightly flattened hemispheres or spheres. Thus, we assumed that the sound fields were either hemispherical or spherical. To calculate the area of the 70 dB isobar, we found the centre of the sound field (very near to the centre of the animal), determined the average radius, and then calculated the area.

Biologically, the acoustic output per hour is more meaningful than the output per second (since call rates vary and since metabolism was not determined for such short time intervals). It can be obtained by multiplying the result of equation 3 by the total time the animal is actually calling per hour. This is known as the calling effort (Taigen & Wells, 1985) and is equal to the product of calling rate and call duration. For our calculations, we used mean values of these parameters for frogs calling freely in a chorus. Thus:

$$P_o = W \times CR \times D , \tag{6}$$

where P_o is the power output (in $J h^{-1}$), W is the work per second (watts, see equation 5), CR is the calling rate (calls h^{-1}), and D is the mean call duration (s $call^{-1}$).

Calculations of efficiency

Efficiency (E) is defined as:

$$E = (\text{acoustic power}) \times (\text{metabolic power input})^{-1} \times 100 . \tag{7}$$

Metabolic power can be estimated as the *net* cost of calling when producing a given power output. Net metabolism is calling $\dot{V}_{O_2}$ minus resting $\dot{V}_{O_2}$. This treatment assumes that maintenance costs remain constant in going from rest to calling. To convert these values to units of power, we assumed a respiratory quotient (RQ) of 0·85, which reflects a mix of carbohydrate and fat metabolism. Two measurements from our laboratory of RQ (0·78, 0·88) during calling suggest that this is close to

the true value. Further support for this assumption is lent by the work of Wells & Taigen (1986) on *H. versicolor*. Thus, we assume $1 \, \text{ml} \, O_2 \, g^{-1} h^{-1} = 20 \cdot 54 \, J \, g^{-1} h^{-1}$.

Vocal sac dimensions

Vocal sac dimensions were estimated from a series of photographs of calling individuals of known size. Several photographs were used for each individual to obtain the best estimate of the size, and the estimates of several individuals were averaged to obtain the species mean.

Abdominal muscle mass

The abdominal muscles are responsible for forcing the air used in a call across the vocal apparatus and thus their development reflects the ability of an animal to call (Taigen *et al.* 1985). We possessed a large number of alcohol-preserved amplexed pairs of *H. squirella*. These animals had been weighed while alive. We dissected out the abdominal musculature of both sexes, placed it in saline for a while, blotted it dry, and then weighed the tissue. Masses obtained in this manner fell in the same range as those measured from three freshly killed individuals. Also, five *H. gratiosa* that were killed accidentally were dissected and weighed as above. Results were expressed as a percentage of fresh body mass.

Statistics

All results are expressed as means ± standard errors of the mean. The level for statistical significance was set at $P < 0.05$.

Results

Table 1 gives values for $\dot{V}_{O_2}$ in non-starved, freshly collected individuals at rest and during maximal locomotion at the same temperatures at which $\dot{V}_{O_2}$ for calling was measured. It should be borne in mind that the exercise $\dot{V}_{O_2}$ values were taken in a closed container.

Table 1. *Oxygen consumption in three species of treefrogs at rest and during maximal locomotion in a turning chamber*

Species	Condition	N	Mass (g)	Temperature (°C)	$\dot{V}_{O_2}$ ($\mu l \, O_2 \, g^{-1} h^{-1}$)
Hyla cinerea	Rest	10	$5 \cdot 1 \pm 0 \cdot 2$	27	135 ± 17
	Loc. max.*	10	$5 \cdot 1 \pm 0 \cdot 2$	27	1020 ± 57
H. gratiosa	Rest	9	$13 \cdot 9 \pm 0 \cdot 9$	29	95 ± 10
	Loc. max.*	10	$13 \cdot 8 \pm 0 \cdot 9$	29	1250 ± 52
H. squirella	Rest	9	$2 \cdot 2 \pm 0 \cdot 1$	27	165 ± 12
	Loc. max.*	9	$2 \cdot 2 \pm 0 \cdot 1$	28	1790 ± 49

Standard errors of the mean (s.e.m.) are given as ± values after each mean.
*Loc. max. refers to maximal locomotion. Mean time to exhaustion (min:s) ± s.e.m.: *H. cinerea*: $18:10 \pm 1:40$; *H. gratiosa*: $19:30 \pm 1:30$; *H. squirella*: $19:42 \pm 1:15$.
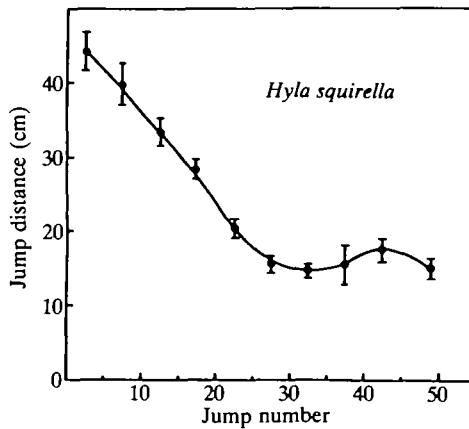
Fig. 2. Fatigue as a result of forced hopping on a wet floor for *Hyla squirella*. Most of the animals would not right themselves after an average of 4 min 15 s ($\pm$ 12 s.e.m., $N = 12$). Similar curves are seen in *H. crucifer*. Bars indicate $\pm$s.e.m.

Fig. 2 presents the results of the forced hopping experiment. The time required for fatigue in the free-ranging animals used in this experiment (approx. 4 min 15 s) was much less than that required to exhaust animals in rotating metabolic chambers (19 min 42 s in *H. squirella*, Table 1). $\dot{V}_{O_2}$ values for resting and maximally active, hopping frogs are given in Table 1.

Table 2 shows the lactate accumulations in the whole body, legs and remainder of the body (trunk) for *H. squirella*. Lactate concentration increased significantly over resting values in the legs and whole body as a result of forced exercise. Trunk lactate levels did not increase significantly when calling but did during forced hopping (ANOVA, Fisher's LSD; all significant differences with at least $P < 0.03$). Thus, it appears that anaerobic metabolism was not a significant factor in sustained calling whereas it was in sustained, maximal hopping.

The slopes of the regression lines for the cost of calling are all significantly different from 0 (for all lines, $P < 0.0002$, ANOVA) (Figs 3–5). There are no statistically significant differences between the slopes of these lines ($P = 0.12$, ANCOVA). In *H. cinerea* and *H. gratiosa*, the y-intercepts of the regression lines fall within two standard errors of the resting $\dot{V}_{O_2}$ (Table 1), whereas in *H. squirella* the intercept is considerably larger than the resting $\dot{V}_{O_2}$. The cause of this difference (if it is real) is not known. In all three species, calling animals generally changed position little, with the exception of *H. gratiosa*, which typically swims occasionally from one calling site to another.

In males of both *H. squirella* and *H. gratiosa*, abdominal muscles make up a large portion of the total mass (Table 3). In *H. squirella*, a *t*-test on log-arcsine transformed data revealed a highly significant difference between the percentage of total body mass that was abdominal muscle in the two sexes ($P < 0.001$).

Sonographs typical for each species are shown in Figs 6–8. Summaries of the data including dominant frequencies, calling rates and durations are given in

Table 2. *Mean lactate concentrations (with* S.E.M.*) in* Hyla squirella *under resting conditions, after having called in a natural chorus for at least 30 min and after forced locomotion to exhaustion*

	Activity		
	Resting (N = 5)	Calling (N = 8)	Exhausted (N = 7)
Mass (g)			
Legs	0·70 (0·12)	0·60 (0·09)	0·68 (0·14)
Trunk	1·75 (0·11)	1·87 (0·41)	1·48 (0·02)
Whole body	2·45 (0·11)	2·47 (0·46)	2·16 (0·20)
Whole tissue lactic acid* (μmol g^{-1})			
Legs	5·94 (0·99)	9·24 (1·91)	24·04 (6·01)
Trunk	1·35 (0·43)	2·12 (0·77)	4·93 (0·62)
Whole body	2·67 (0·45)	4·45 (0·20)	10·65 (1·45)

* Lactate concentrations for each type of activity are given for the whole animal, rear legs only (legs) and trunk, forelegs and head (trunk). The purpose of this division was to partition lactate that accumulated in the rear legs from that in the rest of the body, including the abdominal trunk muscles which are responsible for calling. Lactate concentrations are significantly elevated over rest in whole frogs and in their legs after exhausting exercise. Leg lactate concentrations in chorusing animals are high but not significantly greater than resting levels. Since lactate concentrations in the trunk are not elevated significantly, it is unlikely that anaerobic metabolism makes a significant contribution to the cost of calling.
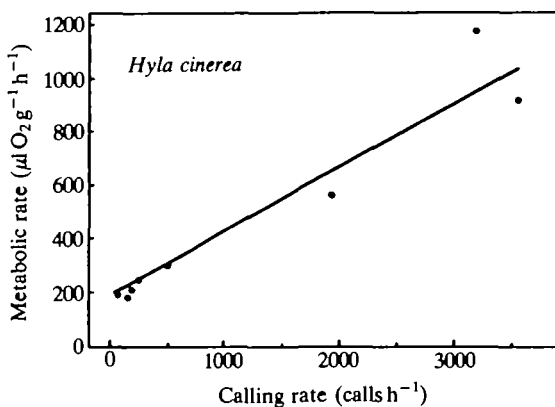

Fig. 3. The cost of calling in *Hyla cinerea* at 27 °C. The five animals that produced less than 1000 calls over an hour actually produced those calls over a short span of time and at a rate typical of animals in a chorus. For instance, the individual that produced 490 calls made 432 of these in 7 min and 30 s. The regression line extrapolates to a value very close to that of resting metabolism. The equation for the line is: $\dot{V}_{O_2} = 0.248R + 158$, where $\dot{V}_{O_2}$ is in μl O$_2$ g^{-1} h^{-1} and R is the calling rate in calls h^{-1}. $r^2 = 0.93$. $N = 10$.

Table 3. *Abdominal trunk muscle mass in* Hyla gratiosa *and* H. squirella

Species	Sex	N	Total body mass (g)	Abdominal and trunk muscle mass* (g)	%TBM†
Hyla gratiosa	M	5	9·9 ± 1·8	0·89 ± 0·14	9·3 ± 0·6
H. squirella	M	27	2·1 ± 0·1	0·18 ± 0·01	8·7 ± 0·27
H. squirella	F	26	3·1 ± 0·2	0·08 ± 0·00	2·7 ± 0·12

*Male abdominal muscle mass in *H. squirella* is much greater than that of females (which do not produce calls). Note, that for most *H. squirella*, the total body masses were taken while the individual was alive and the muscle masses were from the preserved individuals. Owing to rounding errors, the percentage of total mass that is abdominal musculature calculated from this table will not yield results identical to those reported in the last column.

† %TBM = (abdominal muscle mass/total body mass) × 100.

Table 4 (along with data from the literature on other hylids and a leptodactylid). Mean sound pressure levels presented in Table 4 have been corrected using Fig. 1. The corrections for each species are +3·0, 2·2 and 2 dB for *H. crucifer*, *H. gratiosa* and *H. squirella*, respectively. Figs 9–11 show the sound fields for each species. Note that all are essentially omnidirectional radiators. The only area of obvious deviation from hemispherical or spherical shape is directly behind the head.

Calculations of power output, power input and efficiency at maximal observed calling rates are presented in Table 5. Table 6 gives estimations of the sizes of the vocal pouches.
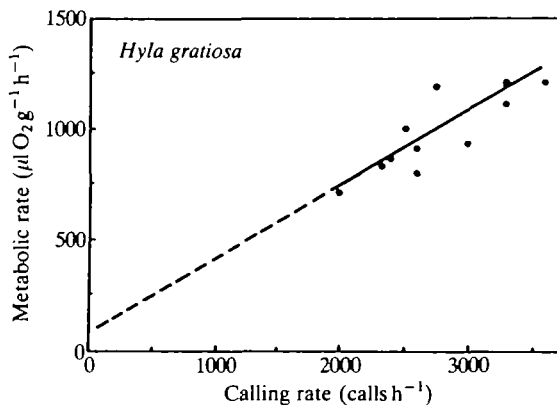

Fig. 4. The cost of calling in *Hyla gratiosa* at 29 °C (range 28–30·5 °C). Part of the scatter in these data is probably due to slight, intermittent swimming activity of these animals when they stopped calling for brief intervals. These are all field-collected data. The regression line extrapolates to a value very close to resting metabolism. The equation for the regression line is: $\dot{V}_{O_2} = 0·3082R + 113$, units as given in Fig. 3. $r^2 = 0·73$, $N = 12$.
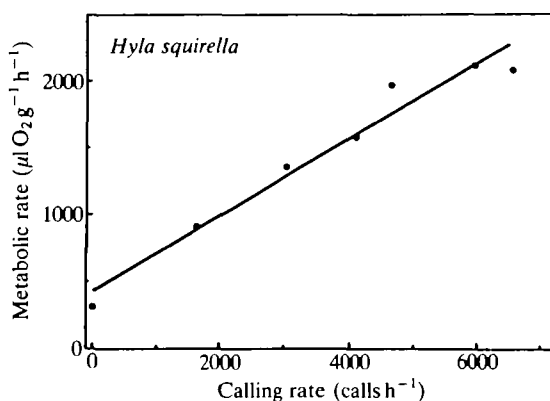
Fig. 5. The cost of calling in *Hyla squirella* at a mean temperature of 28°C (range 27–28·5°C). These data were all collected in the field. Note that, unlike the other two species, the y-intercept of the regression line is well above that of the resting metabolism (Table 1). The regression equation is: $\dot{V}_{O_2} = 0\cdot281R + 411$, with the units the same as given in Fig. 3. $r^2 = 0\cdot96$, $N = 7$.

Discussion

Our data reinforce the contention of Taigen & Wells (1985) and Taigen *et al.* (1985) that calling costs in hylids rival or exceed the cost of locomotion. This contention is dependent on the assumption that $\dot{V}_{O_2}$ for locomotion measured in turning chambers represents maximal locomotory $\dot{V}_{O_2}$. Whether $\dot{V}_{O_2}$ for activity measured in turning chambers is maximal is open to debate. However, we are aware of no measurements that disprove the contention that turning chamber measures are at the maximum of near-maximum $\dot{V}_{O_2}$. Furthermore, although our floor-exercised squirrel treefrogs exhausted faster than those exercised in respiration chambers, this in no way disproves the idea that the animals in the chambers were at peak $\dot{V}_{O_2}$ for locomotion. The differences in time to exhaustion could be due to different intensities of anaerobic metabolism; these are not directly coupled to $\dot{V}_{O_2}$. Finally, the $\dot{V}_{O_2}$ values reported for *H. cinerea* exercised in turning chambers are similar to those reported by Walton (1987) who used a treadmill.

At the calling rates typical of the natural choruses we studied (Table 4), the metabolic rates during calling are 920, 1220 and 2265 μl O$_2$ g^{-1} h^{-1} in *H. cinerea*, *H. gratiosa* and *H. squirella*, respectively (from regression equations for Figs 3–5). These correspond to factorial metabolic scopes during calling of 7, 12 and 16 times resting. For the same species the $\dot{V}_{O_2}$ values for maximal activity were 1020, 1250 and 1790 μl O$_2$ g^{-1} h^{-1}, which correspond to factorial scopes for locomotion of 9, 13 and 11 times resting. Furthermore, since many individuals of these two species call at even higher rates (rates of 3500 for *H. cinerea*, 3900 for *H. gratiosa* and 7200 calls h^{-1} for *H. squirella* are not uncommon at 27°C), the aerobic energy expenditures during calling can be higher than those reported in this study. Clearly, the aerobic costs of calling exceed or are comparable with the aerobic costs of locomotion (Taigen & Wells, 1985; Taigen *et al.* 1985). However, it should

Table 4. *Call parameters for the frogs used in this study and for two other hylids and a leptodactylid*

Species	Calling rate[a] (calls h^{-1})	Duration[a] (s)	L_p[b] (dB)	Dominant frequencies (Hz)[c]
Hyla cinerea[d]	3070	0·14	89·5	Many evenly spaced bands between 900 and 4000 (Fig. 5)
H. gratiosa[d]	3600	0·18	93·2	450 and 1900 (Fig. 6)
H. squirella[d]	6600	0·20	90	1200, 2950–3400 (Fig. 7)
H. crucifer[e]	6000	0·067	95·5	1800, 3600
H. versicolor[f]	1200	0·57, Variable	100	1000, 2000
Physalaemus pustulosis[g]	≈1100	Variable	90	Complex

[a] The values reported here are for high to maximal calling rates; the call durations and SPL levels are those associated with these rates. These values vary with temperature and in at least one species, *Hyla squirella*, in a not totally predictable pattern (Brugger, 1984).

[b] Measurements taken directly in front of the frog, at a 30° angle. SPL is normalized to 0·5 m. All the sound pressure level values (L_p) (except for *P. pustulosis*) are corrected for call duration, according to Fig. 1 (see Materials and methods).

[c] This is a somewhat subjective assessment of the frequencies containing most acoustic energy; energy levels of each spectral component were found using either a sonogram or a spectral analysis program.

[d] This study.

[e] T. L. Taigen & K. D. Wells (unpublished results); Blair (1958). The SPL value provided by Taigen & Wells is a fast rms recording with a time constant similar to that of the SPL meter we used. The reported SPL value was 90 dB. The SPL value given in the table is corrected according to Fig. 1; the reported fast rms SPL was 90 dB.

[f] This species produces a call that could be described as a short, variable-length trill. The call is lengthened when females are present, Wells & Taigen (1986). Spectral data, Blair (1958). There was no need to correct the rms SPL reading since the call is so long.

[g] Bucher *et al.* (1982); Ryan (1985*a,b*). The call in this species is very complex consisting of a 'whine' lasting about 400 ms during which the main frequency changes from 900 to 400 Hz followed by various numbers of 'chucks' which are spectrally complex. Thus, the total length of the call is variable (Ryan, 1985*a,b*).

be remembered that, given the apparently low involvement of anaerobic metabolism in calling (Table 3, also see Ryan *et al.* 1983) compared to its important contribution to hopping, the overall cost of locomotion may be higher than that of calling, although certainly not by much.

Unlike in *Physalaemus*, there does not appear to be any convincing evidence for a stimulatory effect (Bucher *et al.* 1982) of chorusing on the $\dot{V}_{O_2}$ of resting hylids. In *H. gratiosa* and *H. cinerea*, the regression line for calling extrapolates to the y-axis (no calling) at a value that is essentially the same for frogs that are resting but not in a chorus (Figs 3, 4). Similar results have been reported for other hylids (Taigen & Wells, 1985; Taigen *et al.* 1985; Wells & Taigen, 1989). Only in

H. squirella (Fig. 5) is the intercept significantly elevated above resting values;
given the small number of observations, it is quite possible for the regression line's
y-intercept to be slightly biased. Thus, although all regression equations for calling
hylids predict metabolic rates in the absence of calling that are slightly in excess of
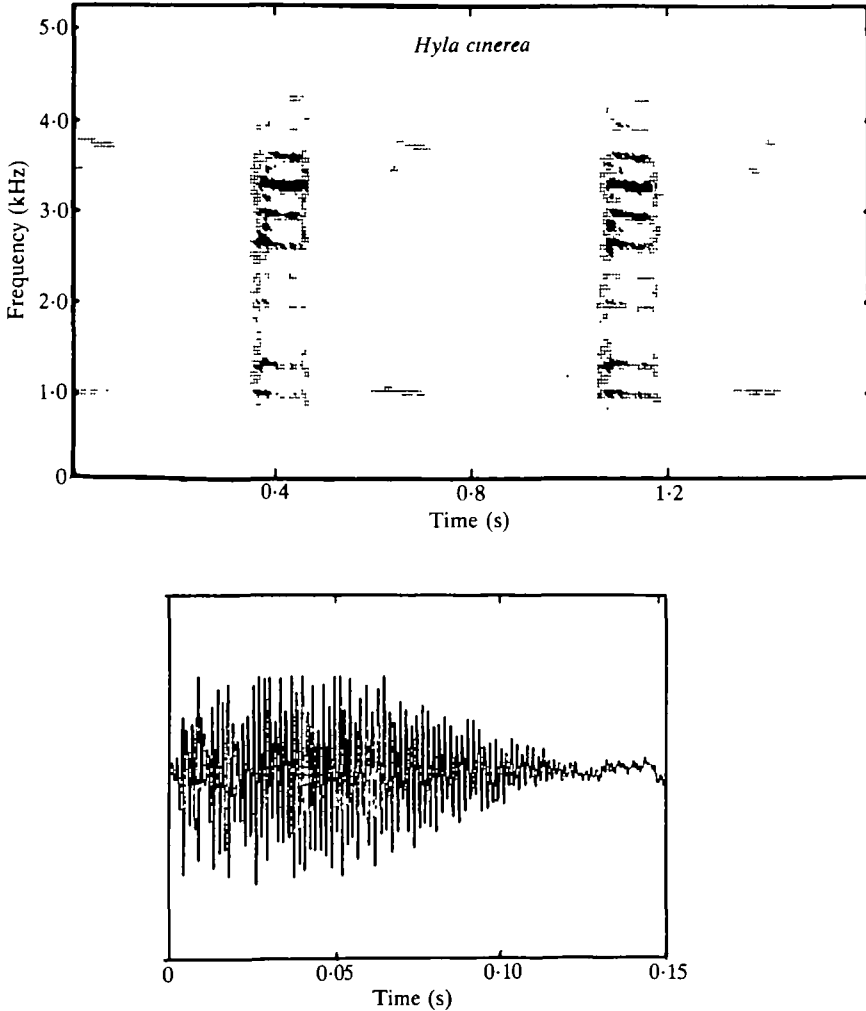measured resting rates of treefrogs not in choruses, these differences are generally

Fig. 6. Sonogram and oscillogram for typical recordings of the calls of *Hyla cinerea*
($T_a = 27\,°C$). Compare this with Figs 7 and 8 for the other two species. *H. cinerea*'s call
contains the greatest number and widest spectrum of emphasized frequencies
(sonogram). Some idea of the frequencies that propagate over the greatest distances
can be obtained from calls of more distant individuals, here seen as less distinct
sonograms. There is also appreciable amplitude attenuation in the latter half of the
call. Power is proportional to the square of the amplitude of the oscillogram. The
fundamental frequency of all three species (Figs 6–8) is close to 100 Hz and is not
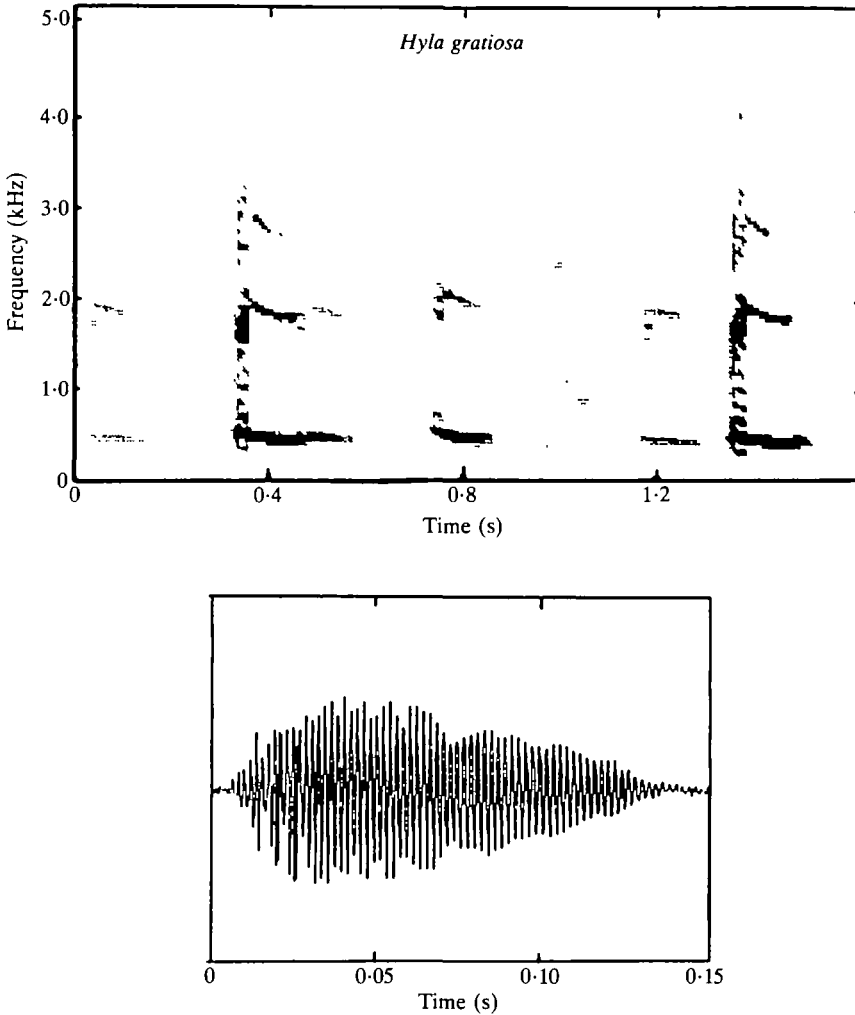evident in these sonographs.

Fig. 7. Sonogram and oscillogram for typical calls of *Hyla gratiosa* ($T_a = 30\,°C$). Note the very low frequency components when compared to the other species. Amplitude decreases steadily in the second half of the call.

slight and could well be due to movement. Bucher *et al.* (1982) reported that non-calling male *Physalaemus* within a chorus showed significantly elevated $\dot{V}_{O_2}$ and referred to this as $\dot{V}_{O_2,stim}$. However, it appears doubtful that a significant $\dot{V}_{O_2,stim}$ exists in hylids.

The slopes of the regression lines for each species we studied are not statistically distinguishable from each other. Nevertheless, the actual calling $\dot{V}_{O_2}$ for *H. squirella* is very high and is essentially equivalent to that of *H. crucifer*: these two species have the highest known mass-specific costs of calling of any frogs. *Hyla cinerea* and *H. gratiosa*, in contrast, have lower costs of calling than other hylids

but higher costs than the leptodactylid *P. pustulosis* (Bucher *et al.* 1982). The reasons for these differences in total calling costs will be dealt with below.

Table 7 shows that the net mass-specific cost per call is similar in most hylids, except for *H. versicolor* which produces a loud call 3–8 times longer than that of any of the other species (Table 4). The similarity of the cost of most hylid calls is
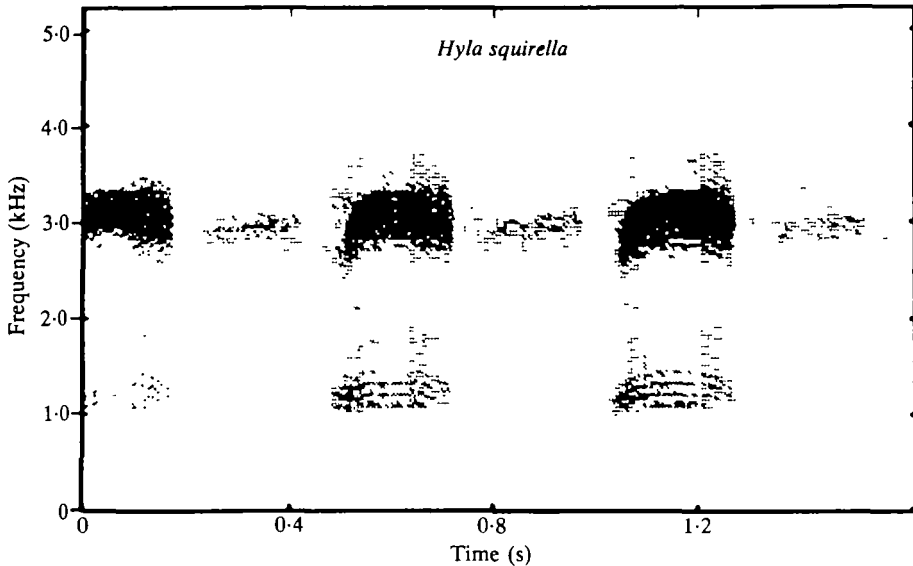

Fig. 8. Sonogram for typical calls by *Hyla squirella* ($T_a = 27\,°C$). This species' call emphasizes a very broad, modulated band of frequencies between about 2900 and 3600 Hz. Note that the call is much longer than in the other two species.

Table 5. *Calculations of the efficiency of sound production for the three species of hylids used in this study*

Species	Mass (g)	P/call[a] (mW)	CE[b] ($s\,h^{-1}$)	P_o[c] ($J\,h^{-1}$)	Net P_i[d] ($J\,h^{-1}$)	Efficiency[e] (%)
Hyla cinerea	5·1	2·85	430	1·23	65	1·89
H. gratiosa	12·5	3·35	648	2·17	286	0·76
H. squirella	2·6	1·57	1320	2·07	94	2·21

[a] Calculated as described in Materials and methods using equations 1, 2 and 3. Note that for green treefrogs the sound field is a sphere.

[b] Calling effort, CE, defined as the product of calling rate and duration (Taigen & Wells, 1985), is the number of seconds per hour that an animal calls. The rates and duration are from Table 4.

[c] Power output, P_o, is the product of acoustic power/call and calling effort.

[d] Power input, P_i, is estimated from $\dot{V}_{O_2}$ predicted by the regression equations in Figs 3–5 minus the resting $\dot{V}_{O_2}$ (Table 1). This was converted from ml O_2 to joules by assuming an RQ of 0·85. To convert this value from a mass-specific to a whole-animal basis, the mass given above was used.

[e] Defined as: (acoustic power output/net metabolic input) × 100.

the result of a complex set of interactions between the different components of muscular work that help determine the characteristics and cost of the call. These include the force, frequency and duration of abdominal trunk muscle contractions (which help determine call loudness, repetition rate and duration). Perhaps the complexity of these interactions is the explanation for the data of Bucher *et al.*

Table 6. *Estimated vocal sac diameters based on photographs of calling frogs*

Species	Minimum and maximum vocal sac diameter (cm)	SVL[a] (cm)	Frequency[b] (Hz)	One-third wavelength[c] (cm)
Hyla cinerea	1·8–4·0	4·1	900	12·1
			3300	3·3
			3800	2·9
H. gratiosa	2·0–5·0	5·9	450	24·2
			1900	5·8
H. squirella	1·2–2·6	3·4	1200	9·1
			3100	3·5

[a] Snout–vent lengths (SVL) are given for size comparisons with the vocal sac and since it is possible that the body itself may also radiate sound (Ryan, 1985*b*).

[b] Because of the number and breadth of the frequency bands used in these species (Figs 6–8), frequencies that are averages for bands containing large amounts of energy have been selected.

[c] For comparison, one-third wavelength values are given for the principal frequencies in the call of each frog. Radiators that are smaller than one-third wavelength tend to be non-directional. Additionally, the relative size of the radiator to the wavelength radiated is one factor involved in determination of the efficiency of the radiator (Beranek, 1954; Kinsler *et al.* 1982; Rossing, 1982).

Table 7. *Net cost of calling in hylids*

Species	Mass (g)	Ambient temperature (°C)	Cost per call[a,c] (μl O_2 g^{-1})	Cost per second of calling[b] (μl O_2 g^{-1} s^{-1})
Hyla cinerea	5·1	27	0·25	1·82
H. crucifer	1·1	23	0·32	4·79
H. gratiosa	12·5	29	0·31	1·74
H. squirella	1·1	28	0·32	1·59
H. versicolor	8·6	20	1·35 (1·11)	2·37 (2·65)

[a] Calculated as (calling $\dot{V}_{O_2}$ minus resting $\dot{V}_{O_2}$)/call rate. For *H. cinerea*, *H. gratiosa* and *H. squirella* regression equations were used to find $\dot{V}_{O_2}$ (Figs 3–5) and respective calling rates were 3500, 3600 and 6000 Hz. For the other species the data in Tables 4 and 8 were used. The values in parentheses for *H. versicolor* are calculated directly from individual data from Taigen & Wells (1985). (*Physalaemus* is not included because of its variable call structure.)

[b] Call durations in Table 4 were used for these calculations.

[c] In spite of different types of calls (Table 4), costs per call are remarkably similar in all species except *Hyla versicolor*, which has a relatively long, loud call. More differences emerge in the cost per second of calling.
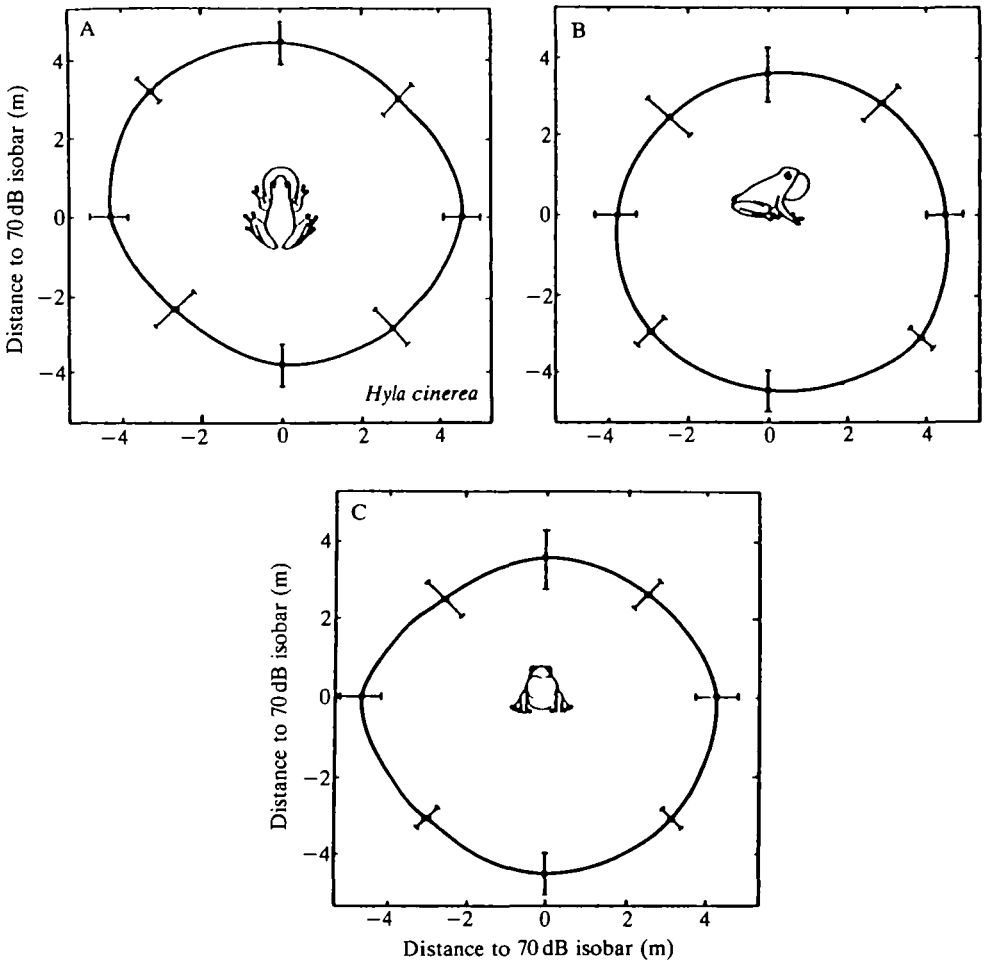
Fig. 9. Mean sound field for *Hyla cinerea* (mean $T_a = 28°C$, $N = 4$). Isobars are for the 70 dB SPL. The field is essentially a sphere with the only noticeable distortion being behind the head. The figures are for the perspectives of directly above the animal's back (A), facing the animal's right side (B) and facing the front of the animal (C). Note that although the average intensity of this sound field is the least of the three species (shown by the short distances to the isobars), P_o is large since it produces a 360° sound field. The frogs depicted in this figure and in Figs 10 and 11 are not intended to be life-size. Error bars are S.E.M. values.

(1982) showing that cost of calling does not increase in *P. pustulosis* as it adds 1–5 'chucks' to its whining call.

The relative sizes of the abdominal muscles that are responsible for pushing air through the vocal apparatus (Gans, 1973; Martin, 1971) are impressive in both *H. squirella* and *H. gratiosa* (Table 3). However, these masses are not as large as those found in two northern treefrog species, *H. crucifer* (16% of total body mass, Taigen *et al.* 1985) and *H. versicolor* (14%, T. L. Taigen, personal communi

cation). The most obvious feature of the northern treefrogs' muscles is the presence of large fat droplets (T. L. Taigen, personal communication). Since we did no histochemistry, we can only speculate that the difference may be due to relatively lower fat stores in the summer-breeding southern frogs that we studied. Our animals fed throughout the breeding season, unlike those studied by Taigen, Wells & Marsh.

Power output

It is believed that the vocal sac is the major acoustic radiator of the frog (Gans, 1973; Martin, 1971; D. Schreyack, unpublished results). The vocal sac of most hylids is approximately spherical (except for the portion of the sac attached to the head). Thus, it should radiate equally well in all directions (=omnidirectional). Gerhardt (1975) compared the directivity of two hylids and found *H. crucifer* to be omnidirectional whereas the call of *H. chrysoscelis* was directed towards the front of the animal. Ryan (1985*a*) assumed that the sound fields of *P. pustulosis* were omnidirectional but he had no measurements demonstrating this.

Since we knew of no complete sound fields for ánurans, we attempted to measure the most accurate sound fields possible with a hand-held SPL meter. The
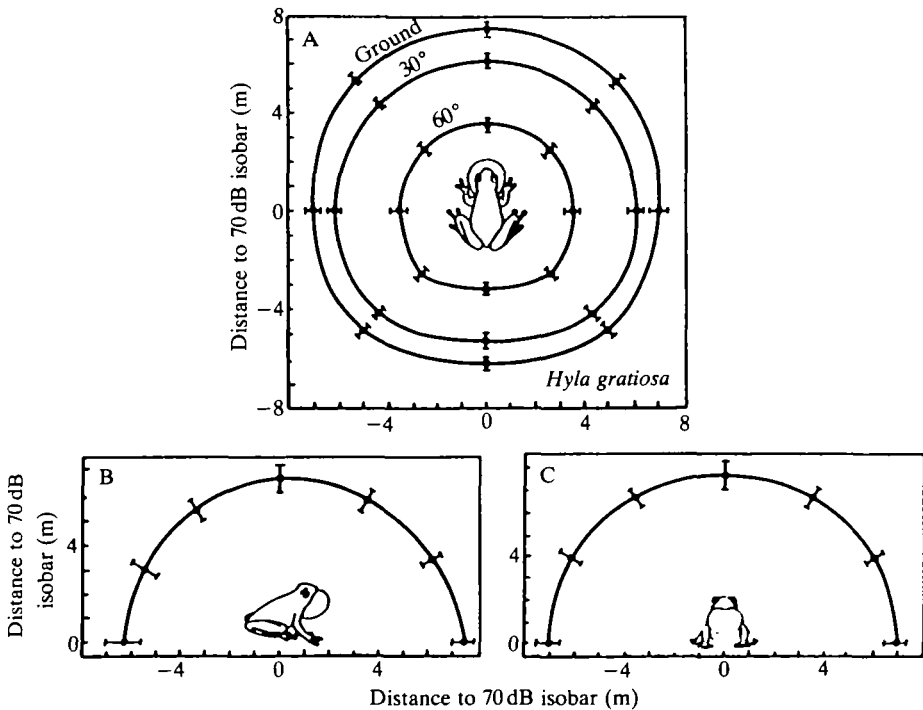

Fig. 10. Mean sound field for *Hyla gratiosa* (mean $T_a = 30 \cdot 2 °C$, $N = 6$). Perspectives are the same as in Fig. 9 and all distances are to the 70 dB SPL isobar. The sound field approximates to a hemisphere with the only distortion from this shape being behind the animal's head. For other comments, see Fig. 9.

results (Figs 9–11) show that, for the species we studied, the sound fields are essentially omnidirectional. The only area of noticeable deviation from a spherical or hemispherical shape is a slight flattening of the field behind the animal's head. Thus, the shape of the field is as would be expected considering that the principal radiator of the frog is a single, large, nearly spherical sac. At full extension, the sac in these species protrudes well beyond the side and frontal margins of the animal's head. If its entire surface is a radiator, then nearly spherical sound waves should result.

By knowing the shape and L_p of the field, it is possible to calculate the power output and the efficiency of sound production. As was mentioned in Materials and methods, we corrected our mean L_p readings using Fig. 1 to account for the effect of the time constant of our SPL meter. Table 5 presents calculations of power output (P_o) and efficiency using these corrected values: for the species we studied, efficiency varies between 0·76 and 2·2 %. Table 8 gives the acoustic efficiencies of some anurans and insects. Anuran species tend to fall above the range of efficiencies for insects using plain radiators (i.e. those not assisted by baffles and special impedance-matching devices, Bennet-Clark, 1970; Forrest, 1982, 1986; Kavanagh, 1987; Prestwich, 1988).

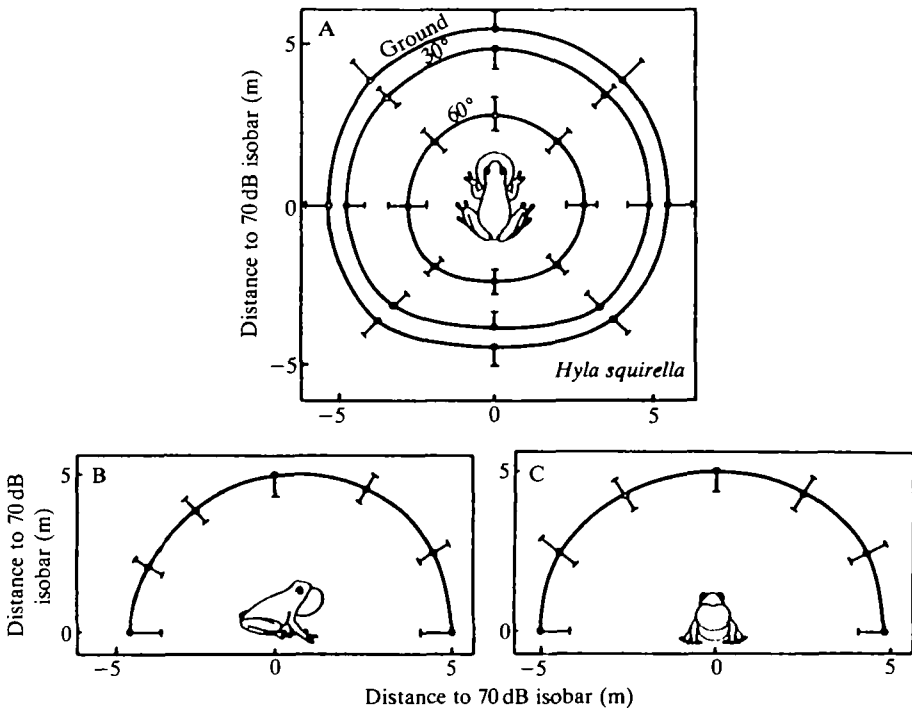It would be interesting to know the causes of the differences in efficiency shown

Fig. 11. Mean sound field for *Hyla squirella* (mean $T_a = 26·8°C$, $N = 7$). Perspectives are the same as in Fig. 9. The field is essentially a hemisphere. (For other comments, see Fig. 9.)

Table 8. *The efficiencies of sound production in animals and loudspeakers*

Subject	Mass (g)	Efficiency[a] (%)
Anurans		
Hyla cinerea[b]	5·1	1·9
H. crucifer[c]	1·1	4·9
H. gratiosa[b]	12·5	0·76
H. squirella[b]	2·3	2·2
H. versicolor[d]	8·6	3·6
Physalaemus pustulosis[e]	1·7	0·5–1·2[f]
Insects		
Anurogryllus arboreus[g]	0·37	0·09
Cystosoma saundersii[h]		0·5
Gryllotalpa australis[i]		1·05
Telogryllus commodus[i]		0·05
Loudspeaker[j]		
Cone loudspeaker		3–5
Exponential horn loudspeaker		40–50

[a] Efficiency data for animals are only for those species where both power input (P_i) and power output (P_o) have actually been measured. Each efficiency is a species average. Since there are no adequate data for intraspecific variation in efficiency, it is not possible to state the likelihood that statistically significant interspecific differences in efficiency exist. Unless otherwise indicated, efficiencies are calculated using data for power outputs (P_o) obtained from Table 5.

[b] This study, ambient temperature (T_a) was 27°C for *H. cinerea* and *H. squirella* and 29°C for *H. gratiosa*.

[c] P_i data from Taigen *et al.* (1985). $T_a = 23$°C. Data to calculate P_o were taken from T. L. Taigen & K. D. Wells (personal communication).

[d] Taigen & Wells (1985); Wells & Taigen (1986). $T_a = 20$°C.

[e] Bucher *et al.* (1982); Ryan (1985a). $T_a = 25$°C.

[f] In calculating this efficiency, Ryan (1985a) estimated the power per call in *Physalaemus pustulosis* using an SPL meter to measure peak (not rms) SPL and then integrated the oscillogram to obtain an average value. The problem with using this method to estimate efficiency is that metabolic power input is measured as average, not peak, power (see Materials and methods). Thus, Ryan's estimates of power output and power input (P_o and P_i) are not really compatible with each other and his calculations overestimate efficiency. As an approximation, it can be stated that since the rms power of a sine wave is 0·707 times the peak power, then a better estimate of efficiency for *Physalaemus* is between 0·4 and 0·9%. However, frog calls are complex audio signals and not sine waves and therefore these estimates are only approximations. In any case, Ryan's value is a very good estimate of efficiency, especially in the light of the complexity and diversity of *Physalaemus'* calls.

[g] Prestwich (1988).

[h] MacNally & Young (1981).

[i] Kavanagh (1987).

[j] Rossing (1982), p. 374.

in Table 8. Losses in metabolic energy that would affect efficiency can be arbitrarily divided into two groups: (i) factors related to the transduction of chemical energy into vibrations before the radiator and (ii) factors related to the radiator itself. The former includes mechanical efficiency of the muscles, frictional losses not associated with useful sound production in moving air from the lungs to the vocal pouch and back, elastic losses along this same air path, including some of those involved in causing vibrations of the vocal folds, and losses in resonating chambers such as the pharynx. Radiator losses include coupling between the radiator and sound within the vocal pouch, the match between the dimensions of the radiator and radiated wavelengths, mechanical properties of the radiator, and the type of baffle (if any) the radiator is set in.

Ryan (1985a,b) based his explanation for low efficiency on cut-off frequency, that is the frequency below which a horn becomes a very inefficient radiator. He used the circumference of the frog or the vocal sac as the mouth circumference term in the cut-off frequency equation for an exponential horn (Beranek, 1954). Exponential horns are essentially acoustic impedance-matching devices (trans-formers). If a reflecting interface such as the tissue of the vocal pouch is placed over the sound path, the matching function of the horn is compromised. (Think of the effect of putting a membrane over a person's or a horn's mouth.) It is more reasonable to regard the surface of the vocal sac as the actual radiator and the vocal cords, pharynx and vocal sac cavity as the mechanical elements that drive the vibrations of the vocal sac's surface. (In this case the driving force is the vibration of the air within the sac.) Therefore, the surface of the sac is akin to the diaphragm of a speaker and the resonating cavities to the electromagnets that move the diaphragm. It is therefore not correct to use the equation treating the vocal sac as an exponential horn. In any case, Ryan is correct is assigning the low efficiency of *Physalaemus* in part to the large mismatch between the principal wavelengths radiated and the relatively small dimensions of the radiator, as has long been known (Beranek, 1954; Michelsen & Nocke, 1974; Pierce, 1981; Kinsler *et al.* 1982).

The immediately obvious differences between insects and frogs are the means of producing sound (in insects, a vibrating membrane that radiates sound directly into the environment with no intervening masses of air) and the size of the radiators relative to the wavelength of the sound produced. The size mismatch phenomenon is a well-known problem in the efficiency of radiating sound (Beranek, 1954; Kinsler *et al.* 1982; Pierce, 1981; Rossing, 1982). The particular insects shown in Table 8 produce sounds that have wavelengths that are more than 10 times the dimension of the radiator (tegmina or tymbal organ) and simply cannot radiate energy efficiently (Bennet-Clark, 1971, 1975), although they may be greatly aided by the use of resonance phenomena in the tegmina (Nocke, 1971; Michelsen & Nocke, 1974) and air sacs in the body (Fletcher & Hill, 1978). The one exception to this low efficiency is the combined use of a burrow containing a resonating chamber and exponential horn impedance-matching device, as in some mole crickets (Bennet-Clark, 1970, 1987; T. G. Forrest, personal communication)

Thus, Kavanagh (1987) measured the efficiency of an Australian mole cricket as 1·05 %.

In contrast, if we ignore possible resonance functions of the vocal pouch and assume that it simply acts as a radiator (Martin, 1971) then, relative to wavelength, anuran radiators are larger than insect radiators (Table 6; Ryan 1985*a*,*b*).

The anuran with a low efficiency compared to other anurans, *H. gratiosa*, is the case that helps illustrate the size-to-wavelength rule. The wavelength of the principal frequency of its call (450 Hz) is a poor match with the size of the radiator (Table 6). Because this animal calls while floating in the water, one may be tempted to think that a large proportion of its acoustic energy is radiated into the water. However, based on photographs, less than 20 % of the fully expanded vocal pouch touches the water. More importantly, the specific acoustic impedance of water is nearly 3600 times greater than that of air. This mismatch results in most sound being reflected by the water (Pierce, 1981). Furthermore, the mismatch between wavelength and radiator dimension is even greater given the longer wavelength of water-borne radiations. Corroborating this, female *H. gratiosa* swim towards males with their ears out of the water. A similar situation exists with *Physalaemus*, which also calls while floating in the water (Ryan 1985*a*,*b*) and also has an apparently low efficiency of sound production (see Table 8).

Why are the efficiencies of sound production lower in anurans than in comparable artificial devices such as cone loudspeakers? As is mentioned above, the efficiency for radiation of sound at some frequency is determined by a large number of interacting factors. Thus, a precise answer will require a careful investigation of the actual radiating system. The lower efficiencies in insects compared to anurans may in large part be due to the radiator-to-wavelength size problem mentioned above (Bennet-Clark, 1971; Ryan, 1985*b*). Frogs come closer to the proper match.

The differences in efficiency between anurans and cone speakers shown in Table 8 may be due to other factors. The diaphragms of such speakers, like a vocal pouch, commonly do not approach the length of radiated waves. However, unlike speakers based on the action of an electromagnet, frogs possess a large number of mechanical and acoustic couplings where energy losses can occur (see above).

Since other authors (Bennet-Clark, 1971; Ryan, 1985*b*) and ourselves have focused so much attention on the relationship between radiator size and wavelength as an important factor in the determination of efficiency, it is reasonable to ask why animals do not better match these factors. The problem is probably one of body size. Small animals, such as insects and frogs, could obtain better matches by the use of large radiators which might make the animal overly conspicuous to predators (Ryan, 1985*b*) or they could use higher frequencies. But the attenuation of high frequencies (>4000 Hz) is greater than that of intermediate frequencies and also high frequencies do not refract around barriers (Marten & Marler, 1977; Wiley & Richards, 1978; Wells & Schwartz, 1982). Thus, an animal might be better off in terms of the area where it can be heard by potential mates using a low frequency even if it is radiated less efficiently (Forrest, 1986). It is even

conceivable that the energy cost per area over which the advertisement can be heard might be less using the longer, less efficiently radiated, wavelengths.

In conclusion, we wish to add one caution relating to studies of the efficiency of sound production. The SPLs used to calculate P_o and efficiency were not obtained using the most ideal instrumentation (see Materials and methods) and it is possible that the values could be out by as much as 15–25 %. Furthermore, all the efficiencies reported here and in the literature are species averages. At present there are few data that allow rigorous investigation into whether there are significant intra- or interspecific differences in efficiency of sound production (Prestwich, 1988). This is because there are few data for P_o and power input (P_i) for the same individuals. Thus, the summary given in Table 8 presents only species means and no estimation of error. In our work we have been deeply impressed with how much the different factors that control P_o for a given individual can vary while it is calling. Furthermore, Forrest (1982, 1986) and Bennet-Clark (1970) have shown large environmental effects on P_o that are potentially independent of P_i and may vary from individual to individual and from time to time in one individual. Thus, until careful intraspecific studies of variation in efficiency have been made, attempts to explain interspecific differences in efficiency should be viewed cautiously. It is necessary to establish whether real differences in efficiency exist before we can accurately describe the interrelationships between an organism's morphology and the design of its calls and, most importantly, whether intraspecific variations in efficiency have any effect on fitness.

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