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The Energetics of Acoustic Signaling in Anurans and Insects[1]

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SYNOPSIS. This review focuses on the energetics of advertisement calls in frogs and insects (mostly ensiferans). I also review a number of methodological questions relating to the most appropriate ways to normalize metabolic rates for calling animals and to calculate efficiency of sound production.

Although the mechanism of sound production is very different in these groups (vocalization *vs.* stridulation), net metabolic costs normalized to mass are similar among species producing the most conspicuous calls. Features of the call that interact to determine energetic cost include repetition rate, call duration, and intensity (sound pressure level). Anurans tend to produce louder (more intense) calls while ensiferans tend to produce sound during a greater proportion of the calling bout. All evidence suggests that advertisement calls are produced aerobically and the aerobic costs are similar or exceed the aerobic (but not necessarily total costs) of terrestrial locomotion.

The pattern of radiated sound tends to be constant within a species and can be predicted to some degree from characteristics of an animal's acoustic radiator. Efficiency of sound production (acoustic power/ net metabolic power) is low (0.05 to 6%) and variable when compared to locomotion (~10–20%). From the present sample it appears that frogs are more efficient than ensiferans, but as more katydids are studied this trend may not hold. Of the factors that have been identified as determining efficiency the most important are the match between the size of the radiator and wavelength radiated, the absorption properties of the environment immediately around the animal, and the presence or absence of structures such as baffles and acoustic burrows.

INTRODUCTION

Male advertisement calls (also termed calling calls) are produced for the purpose of attracting females, often from a considerable distance. In many cases they are loud and repeated at a high rate over a long time span. The other side to their obviously beneficial role in securing a mate is that these calls involve costs to the caller. Costs include: (i) the actual time spent calling (*vs.* searching or feeding); (ii) increased risk of predation, especially to phonotactic predators (for example see Ryan 1985b); and (iii) the energetic expenditure made while calling (as compared to doing nothing). In this paper I will review our understanding of the energetic costs of producing advertisement calls. My approach is comparative and will focus entirely on the two groups that historically have been the favorite subjects for these investigations: anurans and insects (particularly Ensiferan Orthopterans (crickets and katydids) and cicadas (Homoptera)). Not only are the males of many species in these groups among nature's most conspicuous callers, but they seem to be more amenable to producing advertisement calls under laboratory conditions than are members of other groups such as mammals or birds.

The physiological study of the energetics of advertisement calls has developed around the following questions:

1. How costly is calling in terms of energy, *i.e.*, what is the metabolic power input (P_I)

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for calling? Is calling exclusively aerobic or are there significant anaerobic components?

2. How efficiently do animals convert metabolic to acoustic energy? To answer this question one must be able to determine the acoustic power output (P_O) during calling.

3. Which structural and biochemical factors are the main determinants of efficiency and do these vary among individuals?

4. Are there behavioral ways for males to increase the efficiency of sound production or to change the pattern of radiation?

5. Are there individual differences in power input, power output, and efficiency? If so, what causes these and are they correlated with fitness?

Ryan (1988) presented an excellent review of many of these topics, especially in terms of addressing the constraining effects of energy and sexual selection on call design. Bennet-Clark (1989) provided a superb overview of biophysics of sound radiation in insects. My purpose is to complement these treatments by reviewing recent studies and in particular by focusing on the comparative physiological and biophysical aspects of sound production. This paper consists of an overview of the mechanisms of sound production followed by a discussion of the metabolic costs (including the factors which determine these costs and possible physiological constraints on behavior) and finishes with an examination of the factors which determine the efficiency with which metabolic energy is converted into sound. Included in the sections on metabolic cost and on efficiency of sound production are a number of methodological comments.

MECHANISMS OF SOUND PRODUCTION

We can analyze the process of sound production and transduction in an animal or mechanical device by breaking the process into a series of functional elements; these are depicted in Figure 1 (Young, 1990). The analogous elements in an animal may or may not be as distinct as indicated by the boxes in the figure. What is common to all animals is that muscles act as the generator of the mechanical energy that will eventually set a radiator into vibration. Transducers are the mechanical devices that convert the movement of the muscle into the vibration of the radiator (*e.g.*, the file and plectum of an ensiferan); radiators excite the medium into vibration (*e.g.*, the harp and associated cells of cricket wings), impedance matching devices (*e.g.*, baffles or acoustic burrows) increase the efficiency at the radiator and also perhaps alter the directional qualities of the radiation; they may or may not be present. For comparison, in an electrical-audio system the generator is an electrical signal generator, an electromagnet and diaphragm act as the transducer, the diaphragm is also the radiator, and a cone set in a baffle acts as an impedance matching device.

Anuran vocalization

Sound production in anurans *vs.* ensiferans is as different as that in a violin *vs.* a horn. Anurans rely on high velocity movement of a mass of air to induce surfaces to vibrate; sounds produced in this manner are termed vocalizations. In anuran vocalization, air is forced through the larynx where it sets the vocal cords and arytenoid cartilages into vibration (Martin, 1971; Gans, 1973; Dudley and Rand, 1991). Other muscles are involved including those that help to control: (i) the compliance of the laryngeal elements, (ii) the shape of various prelaryngeal cavities (shape may serve to amplify or attenuate specific frequencies and also helps determine the acoustic load on the larynx), and (iii) those that act as valves to control air flow (Martin, 1971; Gans, 1973). A single trunk muscle contraction event is responsible for one call, although the call may be modulated considerably, probably by the action of all of the muscles mentioned above (Gans, 1973; Dudley and Rand, 1991). The muscles that force the air from the lungs across the larynx probably incur the principle metabolic cost of calling and may account for as much as 2 to 16% of a male's mass compared to less than 1% in conspecific females (Taigen *et al.*, 1985; Prestwich *et al.*, 1989). In the species that have been studied, these muscles are known to be highly aerobic in contrast to those of the limbs which show much greater reliance on anaerobic metabolism (Taigen *et al.*, 1985; Marsh and Taigen, 1987; Prestwich *et al.*, 1989).

The frequencies at which the fundamental sound producing elements (vocal cords and arytenoids) vibrate is controlled by (i) their mass and compliance; (ii) the velocity of air flow and (iii) the influence of nearby resonances in the buccal cavity, lungs; and perhaps the vocal sac (Martin, 1971; Gans, 1973; Dudley and Rand, 1991; Purgue, 1993; Rand and Dudley, 1993). The vocal sac is a particularly interesting structure and probably has a number of functions including a role as a visual stimulus (Dudley and Rand, 1991). The sac is inflated during calling; this varies from ranids in many of which the inflation is slight to species where the sac is much larger than the rest of the head (*e.g.*, in the leptodactylid *Physalaemus pustulosis*). One important function of the sac is to store the air expelled by the lungs during production of a call and then to elastically return it to the lungs for re-use in the next cycle (Gans, 1973; R. Marsh personal communication). It is likely that this arrangement may allow for much higher calling rates and may also reduce energetic costs when compared to an alternative situation where new air would need to be drawn in to inflate the lungs.

There is debate as to whether the vocal sac acts as the principle sound radiator (Martin, 1971; Gans, 1973; Ryan, 1988) and if it serves as a resonator. Capranica and Moffat (1983) and Rand and Dudley (1993) have argued that the sac does not act as a cavity resonator. Both groups placed calling frogs in air where helium was partially substituted for other gases. The lower density of He-enriched air results in a higher sound velocity and this shifts the resonance frequency upward in cavity resonators such as Helmholtz oscillators. Failure to observe such a shift led Rand and Dudley to conclude that the vocal sac was not a cavity oscillator in the leptodactylid species they studied. On the other hand, Purgue (1993) has presented evidence that the vocal sac of bullfrogs does act as a tuned resonance and that this is consistent with its dimensions, elastic properties, and internal pressure. He argued that vocal sacs should not be expected to behave in the manner of a rigid-walled resonator, such as a Helmholtz oscillator, and that changes in the density of air filling such a cavity would not be expected to cause large changes in its resonance properties. Further work is needed before the roles of the sac as a resonator and radiator is definitively settled.

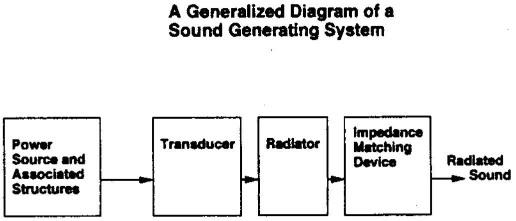

FIG. 1. A generalized schematic showing the functional elements of a sound production system. See text for description.

The vocalization system can be summarized using the scheme presented in Figure 1. The primary power input is via the abdominal trunk muscles. These force air through the laryngeal vocal apparatus which acts as the transducer; however, its operation is influenced and heavily modified by a series of resonating cavities (which probably includes the vocal pouch) and radiation is through the general surface of the head and perhaps the entire body (Ryan, 1988) with the vocal pouches probably being the main radiator, at least in species where the pouch is relatively large.

Stridulation in ensiferans

By contrast, ensiferans rely on friction between specialized surfaces on the forewings (tegmina); this process is termed stridulation. Each forewing contains a series of cells that are framed by wing veins. A portion of the cubital vein on both tegmina has its ventral surface modified into a series of teeth and is termed the file. The upper posterior surface of each wing, near the anal node, is thickened and is termed the plectum or scraper. In singing, the tegmina are raised from the body at an angle that is characteristic of a species and that partially depends on the type of call being produced. One tegmen lies slightly over the other. The tegminal (flight) musculature closes and opens the wings through a small arc that is equal to or shorter than the length of the file. During the closing phase, the plectum of the lower wing is drawn against the teeth of the file on the tegmen above it. As the plectum is gathered and released by each tooth, the resulting vibrations (which are in phase) are transferred to the cells of each of the tegmina. Single tegminal cells or groups of cells (depending on the species) vibrate and produce airborne sounds; these may be either pure tones (usually the case in crickets where the wing cells form resonant structures) or mixes of many frequencies (often the case in katydids). The properties of these radiating cells influence the rate at which the file moves past the scraper. (Bailey, 1970; Sismondo, 1979; Elliott and Koch, 1985; Kock *et al.*, 1988; Bennet-Clark, 1987, 1989). Each cycle of opening and closing the wing produces a pulse of sound followed by a silent period; this pulse is termed a syllable. In addition to changes in frequency or syllable duration, different calls can be produced by varying the temporal sequence of syllable production. A similar system is used by some grasshoppers (non-ensiferan orthopterans) except that here specialized structures on the hind leg are rubbed against the wings.

In terms of the functional elements shown in Figure 1, in stridulation the metabolic power is from the muscle's work of swinging the mass of the tegmina through a small arc (shorter than the file and much less than used in flight) against the friction of the file (Bennet-Clark, 1970; Prestwich and Walker, 1981); this friction is in part is determined by the acoustic properties of the wing (Elliott and Koch, 1985; Koch *et al.*, 1988). The transducer consists of the file, scraper and associated vibrating areas of the tegmina, and the radiator is the vibrating wing cells. In addition, the animal may also modify the acoustic environment around the tegmina by using baffles (Prozesky-Schulze *et al.*, 1975), acoustic burrows (Bennet-Clark, 1970), or reflectors (Forrest, 1982).

The energetics of calling has also been studied in some cicadas. Cicadas use a non-stridulatory device, the abdominal tymbal organs, to generate sound. Sound is produced when a muscle contracts and deforms the skeleton inward, as the muscle relaxes, the skeleton elastically recoils; this buckling and return induces sound waves (Pringle, 1954). The tymbals are coupled acoustically to abdominal air sacs which act as resonators and amplify the sound which is radiated either through the entire abdomen or out of the tympanal (ear) openings (Fletcher and Hill, 1978; Simmons and Young, 1978; Young, 1990). In this paper, I will refer to the train of sound waves produced by each tymbal muscle contraction as a syllable.

METABOLIC POWER INPUT (P_I) FOR CALLING

The roles of anaerobic and aerobic metabolism in calling

The energetic cost of sound production is the increment in metabolism caused by the muscles used in calling and also those muscles used to support the calling muscles, particularly those associated with the circulation and respiration. The energy may be obtained from aerobic or/and anaerobic pathways. Anaerobic metabolism does not seem to have a significant role in calling in either insects or frogs. Given the highly aerobic nature of insect flight muscle there is no reason to believe that anaerobic metabolism should have a significant role. *Anurogryllus arboreus* is the only calling insect that has been studied: 20 minutes of calling resulted in no significant change in the thoracic muscle concentrations of l- or d-lactate (Prestwich, unpublished). In anurans the picture is more complicated because calling animals often have elevated levels of l-lactate. However, based on data for four species (two hylids, a leptodactylid and a hyperolid), it seems unlikely that significant anaerobic accumulations occur in the abdominal trunk muscles of calling frogs (Ryan *et al.*, 1983; Taigen and Wells, 1985; Prestwich *et al.*, 1989; Grafe *et al.*, 1992). The source of any lactate accumulations most likely is the rear leg musculature and is associated with locomotion during or prior to calling. In summary, only aerobic processes seem to be significant in calling and they have been the main focus of all studies of the metabolic costs of calling.

Measurement of aerobic metabolic power

Commonly used means to measure aerobic metabolism (such as respiratory gases) all give the average metabolic power. They do not measure the peak power developed by muscles but instead average energy usage during all phases of muscle contraction and relaxation. This point is significant because it means that comparisons between metabolic power input only should be made with average (not peak) acoustic power output (Prestwich *et al.,* 1989, and see Fig. 2).

The preferred method of measuring aerobic metabolism is to determine both $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ during a respiratory steady-state. This allows for the calculation of the respiratory quotient (RQ); knowledge of the RQ allows close estimation of the actual energy yielded when a particular amount of O_2 is consumed or CO_2 is produced (Elliot and Davidson, 1975). If only one respiratory gas can be determined, it is common to assume a RQ that is intermediate (representing a mixed metabolism of fats and carbohydrates); if $\dot{V}_{O_2}$ is measured and this assumption is employed, the largest error is about 3.5 to 4.5%. Alternately, one can assume a RQ value based on a value for related species engaged in similar activities. Published measurements for RQs of calling animals are 0.73 for an African reed frog *Hyperolius marmoratus broadleyi* (Grafe *et al.,* 1992) and for crickets, 0.8 in *Anurogryllus muticus* and near 1.0 in both *Teleogryllus oceanicus* and *T. commodus* (Lee and Loher, 1993). Recently Prestwich (unpublished) has determined the values for two other crickets, 0.86 in *Anurogryllus arboreus* and 0.81 a mole cricket, *Scapteriscus borellii.* Finally, in cases where CO_2 is the only gas measured, it is important to determine whether or not the animals are utilizing significant anaerobic metabolism. It is quite possible to have a situation in calling anurans where the animal is moving while calling and engaged in significant anaerobic metabolism. In this case, $\dot{V}_{CO_2}$ (and therefore P_i) would be overestimated due to decreases in blood pH.

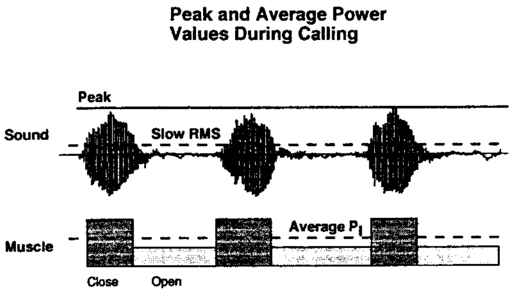

FIG. 2. A cartoon illustrating peak and average acoustic and metabolic power. This specific example is for a cricket but it is of general applicability. Top: Sound is produced in a series of pulses termed syllables; each syllable consists of periods of sound and silence: in ensiferans these correspond closely to the periods of tegminal closure (sound) and opening (silence). Bottom: Muscle movements that produced the sound. Here the height of the bar indicates the energy generated by the muscle. The closing muscles must generate more force since the file and scraper are engaged in this portion of the cycle. Note that this is a simplistic representation—actual course of force *vs.* time is more complex. When metabolic power is measured, it is done at the site of the respiratory exchanger and it represents an average of the action of both sets of muscles and also supporting systems (such as the respiration and circulation). Thus, to compare power input with acoustic output, one must use average (rms) measures of acoustic power.

One other significant issue is whether to report total or net metabolic rate for calling. The net metabolic rate is defined as the increment in metabolism that occurs over resting levels; it is assumed that maintenance costs remain constant and that therefore the increment represents additional metabolic cost associated with the activity (primarily the activity of muscles and associated increases in circulatory and respiratory costs). While this seems a reasonable assumption, it is nevertheless an assumption. Most investigators report both values and use the net value as the actual cost of calling (see below).

Normalization of metabolic power to characteristics of the call

Since animals typically give differing numbers of calls and even calls with differ-

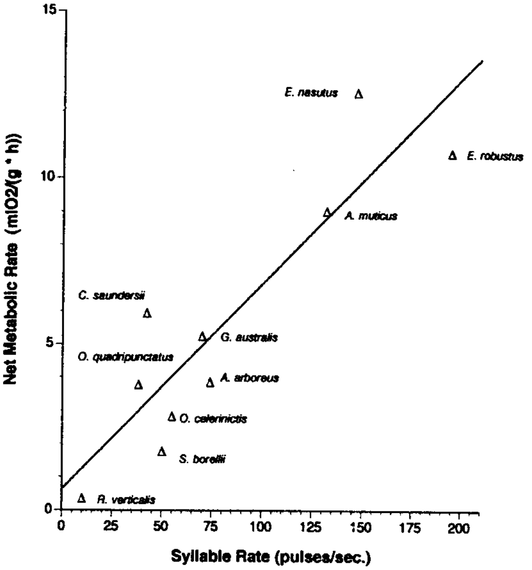

FIG. 3. The metabolic cost of calling in insects. Species average values for net metabolic rate are plotted against syllable rate (sound pulses per second). The equation for the least squares fit regression is: net $\dot{V}_{O_2}$ (mlO2/(gh)) = 0.062 * syllable rate + 0.62, r^2= 0.81, N = 10.

ent characteristics over the time when their metabolic rate is being measured, it is important to take this into account when determining the cost of calling. The simplest approach is to assume that all the calls are alike in terms of their duration and intensity, or at least that they average out the same, and then to regress net power input during calling on either calling time or total number of calls produced (MacNally and Young, 1981; Prestwich and Walker, 1981; Bucher *et al.*, 1982; Kavanagh, 1987; Prestwich *et al.*, 1989; Grafe *et al.*, 1992; Bailey *et al.*, 1993). The slope of the regression line is the average power input per call or average power input per unit calling time.

An alternative method that is especially useful when the duration of calls and intercall intervals vary between individuals is to utilize the *calling effort* (Taigen and Wells, 1985) which is defined as the total time that the animal actually produces sound per hour. Usually it is calculated simply as the product of the average duration and average calling rate for a particular measurement session. Regression gives power input per second of calling, similar to that in the first method except that differences in the average durations of individual's calls are now taken into account.

However, both calling effort and the total number of calls are incomplete measures of behavior—both ignore differences in call intensity. Thus, it might seem ideal to regress power input on power output since power output takes intensity, repetition rate and call duration into account. However, if animals differ in the efficiency with which they produce sound (this will affect intensity), an improved fit will not be obtained by regressing on acoustic power (the slope of such a regression is the reciprocal of efficiency). If the goal is to obtain an equation that is most useful in predicting costs of calling, the most appropriate independent variable will depend on the particular species under study: it is best to regress metabolic data on number of calls (if the calls are similar in duration and intensity over time), on calling effort (if the duration of calls vary but intensities are similar, see discussion below), or on power output if intensities vary but efficiencies are the same.

COMPARISONS OF METABOLIC COSTS OF CALLING

Relationships between characteristics of the call and metabolism

Net metabolic power input (P_i) measurements are presented for calling insects and frogs in Figures 3 and 4 and in Table 1. Perfect comparisons between the groups are difficult because of differences in body size, call structure (many short syllables in insects *vs.* long calls in frogs), and calling effort. Nevertheless several trends emerge. Not surprisingly, within each group the energetic cost of calling increases with calling rate (Figs. 3 and 4). Interestingly, if net P_i for calling is regressed on calling effort, the slope for the insect regression becomes non-significant. The reason for this result is clear—most species that have been studied are trillers and one energetically relevant inter-specific difference is wing stroke rate. For most of these species the closing phase (when the sound is produced) occupies a bit more than half of the entire wing stroke cycle (*e.g.*, see Prestwich and Walker, 1981). Thus, regardless of the wing stroke rate, these species may have similar calling efforts. But the species with the highest wing stroke rates and therefore the highest tegminal velocity, have the highest power consumptions since power is proportional to the square of velocity. So, in this case, calling effort will not be a good predictor of P_i and it may be that regressions of P_i on syllable rate are best for making comparisons among stridulating insects.

In frogs calling effort can be useful because in many species the duration of contraction of the calling muscles is variable. Furthermore, the relationship between the duration of the call and velocity of muscle contraction is far from being as constant as it is in ensiferans. Long, complex calls are produced by long contractions and short calls are probably produced by short duration contractions (see diagrams in Dudley and Rand [1991] that show the relationship between air flow (contraction) and different length calls). This differs from the situation in insects only in the fact that insects do not usually vary the duration of their tegminal muscle contraction during a particular type of call and thus there is a simple correspondence between call rate and metabolic demand. By contrast, if frogs vary the duration of their call (as many species do) and if long and short calls are both counted as single calls, obviously individuals with short duration calls will have lower costs than those with long duration and the same calling rate. Calling effort will better explain the variation in metabolism and is the preferred measure (Taigen and Wells, 1985; Wells and Taigen, 1989). This is especially true in species that produce complex calls such as *Physalaemus pustulosis* (see Ryan, 1985*b*), *Hyla versicolor* (Taigen and Wells, 1985) and *H. microcephala* (Wells and Taigen, 1988). On the other hand, species which produce single, relatively constant duration calls such, as *H. cinerea, H. gratiosa, H. squirella* and *Pseudacris crucifer,* can be adequately described by regressions on calling rate (Taigen *et al.*, 1985; Prestwich *et al.*, 1989).

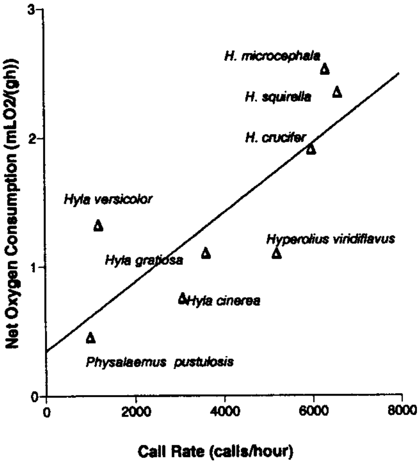

FIG. 4. The metabolic cost of calling in frogs. Species average values for net metabolic rate are plotted against call rate (complete calls per hour). The equation for the least squares fit regression is: net $\dot{V}_{O_2}$ (mlO2/(gh)) = 0.00027 * call rate + 0.344, r^2= 0.65, N = 8. Notice that this plot does not take into account differences in call duration and intensity, both of which can be large.

If the power input data for insects are regressed on power output, a poorer fit results. This probably indicates that efficiency of sound production varies among these species since the slope of such a line is the reciprocal of efficiency. This procedure was not tried for the frogs since there were fewer species where reliable data on power outputs were available; many reports are peak sound pressure levels without oscillograms—the rms values needed to calculate power output (Fig. 2) can not be estimated.

Metabolic scope during calling

The factorial metabolic scopes for calling (the ratio of active to resting metabolism) is similar in the species that have been studied in both groups—insects may expend energy at a rate 2–21 times resting (average ~9) and in anurans, 6 to 21 times resting (average ~ 12, Table 1). Those species with the greatest calling effort and/or intensity (which also correlates with size) have the greatest factorial increases in their aerobic metabolism while calling. Further, these

TABLE 1. *Net metabolic costs of calling in insects and frogs.*

Species	Mass	Syllables/sec[a]	Duration[b]	ml O_2/g/hr	Call/rest[c]	μl O_2/syll.	Ref.[d]
Insects							
Ensiferans							
Trilling crickets							
Anurogryllus arboreus	0.400	74	0.009	3.898	13	0.00588	7
A. muticus	0.400	132	na	9.060	6	0.00763	5
Gryllotalpa australis	1.140	70	na	5.292	13	0.02394	4
Oecanthus celerinictus	0.055	55	0.008	2.879	8	0.00080	7
O. quadripunctatus	0.055	38	0.011	3.816	8	0.00152	7
Scapteriscus borellii	0.826	50	0.012	1.810	4	0.00831	8
Trilling katydids							
Euconocephalus nasutus	na	147	na	12.619	8	na	10
Neoconocephalus robustus	0.880	195	~0.003	10.811	7	0.88000	1
Chirpers							
Requena verticalis	0.371	10	0.015	0.399	2	0.00000	1
Teleogryllus commodus	0.602	variable	na	0.541	4	—	4
Cicadas							
Cystosoma saundersii	1.320	42	na	5.980	21	0.05221	6
Means	0.60	81	0.010	5.2	9	0.10892	
	Mass	Calls/sec	Duration	ml O_2/g/hr	Call/rest	μl O_2/call	Ref.[d]
Frogs							
Hyla cinerea	5.1	0.85	0.14	0.78	8	1.296	9
H. gratiosa	12.5	1.00	0.18	1.12	13	3.889	9
H. microcephala	0.6	1.11	0.075–0.60	1.63	19	0.257	13
H. squirella	2.6	1.83	0.20	2.11	10	0.831	9
H. versicolor	8.6	0.33	0.57, varies	4.20	21	30.100	12
Hyperolius viridiflavus	1.4	1.11	0.070	1.91	7	0.669	3
Pseudacris crucifer	1.1	1.67	0.067	1.92	16	0.352	11
Physalaemus pustulosis	1.7	0.31	0.49, varies	0.91	6	1.40636	2
Means	4.2	1.03	0.22	1.82	12	4.850	
Anuran/insect	6.9	0.01	23	0.4	1.5	44.5	

[a] The number of sound pulses per second; produced by either one tegminal closure or one tymbal buckling cycle.

[b] The time when sound is produced, for ensiferans these figures do not include the silent period when the tegmina are opened.

[c] Factorial metabolic scope The number of times metabolism was raised during calling as compared to rest.

[d] References: 1. Bailey *et al.*, 1993; 2. Bucher *et al.*, 1982; 3. Grafe *et al.*, 1992; 4. Kavanagh,1987; 5. Lee and Loher, 1993; 6. MacNally and Young, 1981; 7. Prestwich and Walker, 1981; 8. Prestwich and Walker, unpublished; 9. Prestwich *et al.*, 1989; 10. Stevens and Josephson, 1977; 11. Taigen *et al.*, 1985; 12. Taigen and Wells, 1985; 13. Wells and Taigen, 1989.

ratios are certainly near the upper limits for both groups since most of the species that have been studied are those that are loudest and call at the highest rates.

These measures may be put into perspective by comparing them with the costs of other activities. Two commonly used measures are cost of terrestrial locomotion and costs of flight. Simple locomotion in crickets typically involves an increase in metabolism of 4 to 6 times (Prestwich, unpublished) although hopping may be complicated by anaerobic metabolism. By contrast, insect flight may involve increases in metabolic rate of between 30 and 200 times. The fact that factorial scopes while calling are high but lower than those for flight are not surprising when one considers the difference in the size of the arcs through which stridulating *vs.* flying wings are moved. In frogs there is often a high reliance on anaerobic metabolism during locomotion; comparisons based on aerobic scopes are misleading since they underestimate total locomotory costs. Nevertheless, such comparisons do indicate that peak aerobic demands in males apparently are made during calling and they can rival or exceed the aerobic cost of locomotion (Taigen *et al.*, 1985; Taigen and Wells, 1985; Prestwich *et al.*, 1989; Wells and Taigen, 1989).

Comparisons of anuran and insect metabolic rates while calling

Table 1 shows that based on the sample of animals studied to date, insects tend to have greater net mass-specific power inputs during calling; they are about 2.5 times those of anurans. This is due to the generally larger calling efforts of the insects that have been studied (they produce sound for a greater proportion of the time than do the frogs). Given that many insects have lower calling efforts than the species reviewed here, this difference may be an artifact. An additional factor is that the katydids which have the highest metabolic rates among the insects can only achieve these rates by elevating their body temperatures to nearly 40°C (Stevens and Josephson, 1977); body temperatures of other insects and frogs are near 20°C.

On the other hand, if whole animal net power is compared—anurans in the sample are nearly 7 times larger than the average insect and average nearly 2.5 times the energy use when calling. The difference is due to the greater intensity of anuran calls—while they may call for a smaller proportion of the time, their calls are considerably louder. Of the sampled species for which reliable intensity data were available, the intensity of the insect calls tended to be about 10 dB below those of the frogs. When the net power input per call per individual is calculated, costs become even higher in frogs. This figure is partially misleading since it compares the cost of producing single syllables in insects (which tend to be very brief) with producing a call in frogs (which lasts many times longer). However, even if this is corrected for, anuran calls are still more expensive and this is correlated with their greater sound intensity. One caveat—too much should not be made of the relationship between size and power. Multiplication of mass and mass-specific net power data from Table 1 shows several cases where smaller species have greater net metabolic demands.

Effects of temperature on metabolic power

All anurans and most ensiferans are poikilothermic. Generally there is a positive correlation between calling effort and temperature; as a result costs increase with temperature. The only systematic study of this in crickets was that of Prestwich and Walker (1981). They found that most increases in metabolic costs of calling could be accounted for by increases in stridulatory rate that were related to an increase in ambient temperature. In one species, *Anurogryllus arboreus,* this was not the case (costs remained constant although the wing stroke rate and body temperature increased) and they were unable to account for this discrepancy. Taigen *et al.*, 1985 found the expected relationship in a treefrog, *Pseudacris crucifer*: As temperature increased so did note rate and metabolic cost. A different situation exists in some large katydids. These animals regulate their thoracic body temperature during stridulation and need to warm-up prior to beginning stridulation or flight. Thus, as long as the animal is able to maintain its preferred body temperature, the stridulation rate is high and constant and so the relationship between ambient temperature and net metabolic cost for stridulation is complicated (Heath and Josephson, 1970; Stevens and Josephson, 1977).

Other considerations related to energy

Energetic costs also can be compared in terms of total daily energy budget or other costs involved in reproduction. Lighton (1987) discussed the energetic advantages of producing surface waves to attract a mate as compared to the energetic costs of active search. Prestwich and Walker (1981) made rough calculations of a male's daily respiratory energy budget and estimated that between 26 and 56% of their total daily budget might be involved in calling. They also attempted to estimate the loss in body mass due to burning fat or carbohydrate for calling and found the figure to be between 0.5 and 5.6% percent of total dry mass. More recently Bailey *et al.* (1993) and Lee and Loher (1993) have made the suggestion that metabolic costs of calling should be viewed in context with the cost of spermatophore production, which, based on size and material content, may be considerable. However, Lee and Loher also pointed out that in *Anurogryllus muticus,* the main difficulty faced in rapid production of spermatorphores was availability of sperm, not other materials. Grafe *et al.* (1992) compared male and female reed frog energetics and found that females made large energy investments in reproduction (in their eggs) although interestingly they found that male lipid content decreased more over the breeding season than it did in females and they suggested that perhaps this was due to differences in the feeding motivational state of calling males and females.

The question arises as to whether or not energy acts as a constraint on the ability of a male to call. Calling males certainly may use energy at a high rate. Does this influence the total time they may call over a given day or the number of days that they may call? Does it influence the type of call they produce? Taigen and Wells (1985) found that *Hyla versicolor* males produce calls of varying length with longer calls being more attractive to females. Animals that produced many long calls would only tend to do so when other males were present; furthermore, the production of long calls meant that a male could not call for as many hours as a male who produced shorter calls. Similar phenomena correlated with rate and duration have been observed in other species (Ryan, 1985b; Wells and Taigen, 1989). Recent work has suggested that in *H. versicolor* there is a reduction in calling animals' energy expenditures per night over the calling season, but that this could have more to do with fewer competitors than any specific depletion of reserves (Runkle *et al.,* 1994). Investigations into the physiological bases, if any, of these behavior patterns have only recently been undertaken. For instance Lance and Wells (1993) could find no significant differences in size or muscle aerobic capacity between calling and satellite *Pseudacris crucifer.*

One of the more intriguing proposals dealing with energetic constraints is that specific substances are depleted at a high rate and that depletion of these substances, not depletion of total energy stores, is responsible for cessation of activity. It is well known that in many animals highly aerobic muscles require glycogen for contraction, even if they are also burning fat. Wells *et al.* (1994) calculated that in calling *H. versicolor* males ca. 75% of the energy for calling was derived from fat and 25% from glycogen reserves. Two hours of calling reduced the glycogen supplies in the trunk muscles by 50–60%. Taigen and Wells (1985) speculated that one reason that *H. versicolor* males do not produce a greater proportion of long calls (which are more attractive to females) is that these calls selectively deplete glycogen reserves. However, the recent work has not supported this fascinating hypothesis (Wells *et al.* 1994). Schwartz (1994) has attempted to test the hypothesis that glycogen depletion leads to cessation of calling in *H. microcephala.* He found animals that had ceased calling usually had significantly lower abdominal trunk muscle glycogen contents than did those which continued to call, although the fact that some animals stopped calling while still containing high muscle glycogen concentrations implies that other factors (primarily the result of social interactions with other frogs) are involved.

It is far from clear as to whether or not insects might be commonly constrained by lack of energy or specific substrates. It is not uncommon for insects, even when working at high loads, to be able to burn a high proportion of fat to carbohydrate in their muscles, *e.g.,* migrating locusts (Jutsum and Goldsworthy, 1976). It is known that starvation will cause male crickets to cease calling and presumably therefore energy is important. However, it is another question as to how long it might take an insect to obtain sufficient food for an evening's calling. Many ensiferans are generalists in their food habits and presumably do not need to spend long periods of time searching; thus it may be that energy intake is not an important constraint in these species. Finally, there is the fascinating subject of insects that do not feed as adults—at present none of these have been studied as to how the males partition energy available for different reproduction-related behaviors.

ACOUSTIC POWER OUTPUT

Determination of sound fields and acoustic power output

The determination of acoustic power output in principle is a simple problem; all one needs to do is to determine the area of a surface surrounding the calling animal that has a constant acoustic intensity (I—(power/area)). This surface is termed the sound field. Most devices for determining intensity rely on sound pressure level (SPL) and therefore a sound field is defined as having a constant SPL (it is isobaric). The product of the area of the sound field and its intensity gives the acoustic power.

In practice there are many pitfalls to be avoided when determining SPL levels and in mapping sound fields. These have been discussed extensively elsewhere and include general principles of use of SPL meters (Peterson, 1980) and correct determination of average acoustic power in species that produce intermittent or complex calls (Kavanagh, 1987; Prestwich *et al.*, 1989; Forrest, 1991; Bailey *et al.*, 1993). Accurate power output measurements that are comparable with metabolic power data are often not easy to obtain and the neophyte can easily be seduced by the ease of using SPL meters into making serious errors (I write from experience).

Sound field characteristics and their determinants

Animal's sound fields come in many shapes (Bennet-Clark, 1970, 1987, 1991; Paul and Walker, 1978; Kavanagh, 1987; MacNally and Young, 1989; Prestwich *et al.*, 1989; Forrest, 1991; Bailey *et al.*, 1993). These shapes are determined in part by (i) the ratio of the radiator size to the wavelengths radiated—as the ratio exceeds about $1/3\lambda$ the signal becomes increasingly directional with the highest pressures being normal to the plane of the radiator, (ii) the shape of the radiator (Olson, 1957; Beranek, 1954), (iii) the position of the radiator with respect to large objects such as the ground which may act as baffles or reflectors (Prozesky-Schulze *et al.*, 1975; Forrest, 1982), (iv) special features such as arrangements of burrow openings that affect the directivity of the call (Bennet-Clark, 1970,1987, 1991). Nevertheless, several generalizations can be made:

1. Frogs with large (relative to their head size), single vocal pouches tend to produce sound fields that approach being hemispherical (or nearly spherical if the animal calls from an elevated perch, Prestwich *et al.*, 1989).
2. Crickets that do not use environmental devices such as baffles or acoustic burrows (see below) tend to produce figure-eight or "dumbbell-shaped" sound fields (Forrest, 1991; Bennet-Clark, 1989). Recall that while the same sides of the two tegmina vibrate in phase, the front and back sides radiate 180° out of phase (one side compresses air while the opposite produces a rarefaction). Thus, both sides radiate sound simultaneously and the wings are termed doublet sources. Since the radiators are small compared to the wavelength radiated, a hemispherical pattern is produced initially, but it is modified as the compressions or rarefactions from each side spread around the edge of the tegmina and interfere destructively thereby reducing radiation along the plane of the tegmina. In addition, there may be further asymmetries if the animal holds its tegmina at an angle that is not perpendicular to the substratum (Bennet-Clark 1989).
3. If an external baffle such as a leaf is used, the sound field is the same general shape as without, but there is less overlap between the two hemispheres and far greater

acoustic energy is radiated (Prozesky-Schulze *et al.*, 1975;

4. The shape of a sound field emanating from an acoustic burrow is determined by the number and symmetry of the openings. Single openings such as in *Scapteriscus borellii* result in hemispheres (Bennet-Clark, 1987; Forrest, 1991), dual openings enhance radiation about a line connecting the openings (*Gryllotalpa vineae,* Bennet-Clark, 1970), and four openings arranged in a box configuration produces a hemisphere (*Gryllotalpa australis,* Kavanagh 1987).

The significance of different shapes has been investigated by a number of authors. The situation where males call from the ground but females arrive by air was first discussed by Bennet-Clark (1970). He presented a theoretical analysis of the advantages of beaming *vs.* omnidirectional hemispheric radiation to account for the shape of the sound field produced by *Gryllotalpa vineae.* Forrest (1982) reiterated this theme in discussing the use of parabolic reflectors by *Anurogryllus muticus.* On the other hand, if the females do not fly to the males a major problem associated with calling from a ground perch is rapid attentuation of the signal. Paul and Walker (1979) showed one way this constraint can be overcome—male *Anurogryllus arboreus* often climb trees and call from the trunks; this greatly increases the area over which the male's call is audible to the female. It is worth noting that some species of treefrogs (*e.g., Hyla cinerea*) often call from tree branches and would achieve this same effect.

THE EFFICIENCY OF SOUND PRODUCTION

Efficiency of sound production can be defined in a general thermodynamic sense as:

1. Efficiency (%)

$$= \frac{\text{Acoustic Power}}{\text{Net Metabolic Power}} \cdot 100$$

An organism's acoustic energy output is made up of three components—call duration, repetition rate and call intensity. Of these, rate and duration (calling effort) are set by behavior while intensity can vary either due to behavior (for instance less muscle recruitment) or as a result of differential ability to transform stored energy into sound; that is, by differences in the efficiency of sound production. Thus, an animal potentially can tailor calls in accordance with social conditions and internal physiological state. However, given the often great metabolic expense of calling, it would be surprising to see animals work at anything less than maximal possible efficiency (Ryan, 1988). This is especially true given that many studies have shown that the intensity of a male's call is crucial in obtaining a mate. Any individual who produced sound less efficiently than his competitors would probably be quieter and, unless he adopted a successful alternative strategy, probably less successful in obtaining mates. Thus, two reasonable predictions (Ryan, 1988) are that there will be little variation in efficiency of sound production in calling males and that efficiencies of sound production will be as high as possible.

Comments on the measurement of efficiency

In most situations it is not possible to make simultaneous measurements of metabolism and acoustic power. This is because the technical requirements for the two are usually incompatible. Metabolic measurements usually require small chambers, while acoustic measurements are best done in a free field at several wavelengths from the subject and in the absence of reflective surfaces (Peterson, 1980). Thus, it is necessary to assume that the animals produce the same calls in both situations. For the subset of animals that will call in metabolic chambers, calling rates and durations are usually the same as in the field, and therefore it is assumed that intensity must also be the same. With the advent of highly sensitive CO_2 analyzers it should be possible to test these assumptions and simultaneously measure metabolism and acoustic power.

It is important to understand that efficiency is an arbitrary measure. Figure 1

TABLE 2. *Acoustic power outputs in insects and anurans.*

Species	Mass (g)	Po[a] (mw)	Syllable rate[b] (sec^{-1})	Energy/call[c] (mJ)
Insects				
Ensiferans				
Trilling crickets				
Anurogryllus arboreus[2]	0.400	0.059	74	0.00079
Gryllotalpa australis[3]	1.140	0.270	70	0.00386
Oecanthus quadripunctatus (w/o baffle)[2]	0.055	0.010	38	0.00027
Oecanthus quadripunctatus (w/baffle)[2]	0.055	0.042	38	0.00111
Scapteriscus borellii[5]	0.826	0.006	50	0.00013
Trilling katydids				
Neoconocephalus robustus[1]	0.880	1.800	170	0.01059
Chirpers				
Requena verticalis[1]	0.370	0.136	10	0.01357
Teleogryllus commodus[3]	0.600	0.002	variable	—
Cystosoma saundersii[4]	1.320	0.350	42	0.00833
Means	0.656	0.327	60	0.00541
	Mass (g)	Po[a] (mw)	Call rate[b] (sec^{-1})	Energy/call[c] (mJ)
Frogs				
Hyla cinerea[6]	5.1	0.342	0.85	0.402
H. gratiosa[6]	12.5	0.603	1.00	0.603
H. squirella[6]	2.6	0.575	1.80	0.319
Physalaemus pustulosis[7]	1.7	0.041	0.20	0.205
Means	5.5	0.390	0.96	0.382
Anuran/insect	8.3	1.2	0.02	70.6

[a] These two columns give the acoustic power output per second of calling or per second of calling normalized to mass.

[b] Syllable rate (insects) refers to an individual pulse of sound produced by one wing closure or tymbal buckling. Call rate is the number of calls (which in the case of *Physalaemus* may be complex) per second.

[c] These two columns give the acoustic energy or mass-specific acoustic energy per syllable (insects) or per call (anurans).

References: 1. Bailey *et al.*, 1993; 2. Forrest, 1991; 3. Kavanagh, 1987; 4. MacNally and Young, 1981; 5. Prestwich and Walker, unpublished; 6. Prestwich *et al.*, 1989; 7. Ryan, 1985*a*; 8. Stevens and Josephson, 1977.

showed that the process of producing sound involves a chain of transformations. At every point of this process energy is lost from the system and therefore the solution to an efficiency calculation will owe as much to the selection of points at which energy is measured as it will to the actual losses of energy. Thus, metabolic power derived from oxidation of foodstuffs is diminished as a result of losses in (i) chemical transfers to ATP, (ii) myofilament movement, (iii) ionic pumping, (iv) via viscous and elastic losses associated with air movement in frogs or thoracic movement in ensiferans, and, (v) motions of the radiator. On the other hand, since we are dealing with sound production, there is generally no doubt that acoustic energy constitutes useful power output. However, in at least some cases vibrations of the substratum are also important (Bell, 1980; Narins, 1990) and perhaps should be considered in the calculation.

There is a difference of opinion in regards to where the power input should be measured. Bailey *et al.* (1993) argued that efficiency should be calculated using the mechanical output of the muscle responsible for sound production instead of the net metabolic power for the entire animal as used by most investigators. When this is done, sound production efficiency in the bushcricket *Requena verticalis* approaches 57% (as compared to about 6% when net metabolic cost is used). The advantage to this approach is that it makes comparisons between different radiators more meaningful. However, it requires assumptions beyond the ones made when estimating metabolic power input (see previous section): one must assume a value of efficiency of conversion of biochemical (metabolic) energy to mechanical energy by the muscle since direct measures are usually not available. Furthermore, such an analysis does not capture the entire picture of what is important to the animal—presumably males which are best able to convert the energy they have available into signals (while operating within the constraints of other needs) will enjoy the greatest reproductive success. The link between muscles and sound is only part of this process. Thus, the measure of efficiency one uses must be selected in light of the question to be answered; net metabolism is useful when comparing efficiencies of individuals while muscle power output is useful when comparing the transducer-radiator portion of the acoustic system (Fig. 1). The following discussion will be restricted to a consideration of efficiencies calculated using net metabolism.

Efficiency measurements and determinants of efficiency

Bennet-Clark (1970) made estimates of efficiency of sound production using measured acoustic power and estimates of power input based on the mass of the tegminal muscle and published values for insect flight muscle metabolism. These estimates follow the total organism net metabolism convention since the power input of these muscles would make up most of the metabolism of the insect. He estimated 2–4% for a *Gryllus campestris* and about 35% for a mole cricket, *Gryllotalpa vineae*. Since then, actual measurements of both acoustic and metabolic power have been made in both insects and anurans; these measurements are about an order of magnitude lower than Bennet-Clark's first estimates. Table 3 shows that sound production in insects and anurans is not very efficient—all estimates are less than 6% and many are less than 1%. By contrast, most locomotory activities have efficiencies of between 10 and 20%.

One of the reasons for low efficiency has to do with the mismatch between the dimensions of the radiator and the wavelength being broadcast. Ryan (1985b, 1988) and Bailey *et al.* (1993) have presented an analysis of sound production efficiency based on the concept of cut-off frequency; that is, a frequency below which a radiator of a certain radius ceases to be effective. Prestwich *et al.* (1989) criticized this approach on several grounds. Equations that describe the power transfer between different types of radiators and the medium are presented in standard textbooks on acoustics (Beranek, 1954; Olson, 1957). Mickelsen and Nocke (1974) and especially Bennet-Clark (1989) treat the behavior of vibrating tegmina as approximating one of two standard acoustic radiators: a baffled and non-baffled vibrating piston. Frog vocal pouches can be treated as approximating a pulsating sphere without a baffle. Both of these papers present lucid discussions of the effect of radiator dimension on the amount of power emitted and the interested reader is urged to consult them for a detailed discussion. Following Bennet-Clark (1989):

$$2.\quad \text{Radiated Power} \propto \left(\frac{1}{\lambda}\cdot d\right)^2 \cdot r^2 \cdot R_m$$

where λ is the wavelength, d is the amplitude of vibration, r is the radius of the radiator, and R_m is the specific radiation resistance of the source. Thus, an increase in radius or decrease in wavelength will increase radiated power as will greater amplitude of vibration by the radiator.

This proportionality is complicated by the fact that the specific resistance of the radiator, R_m, also depends in a complex manner on wavelength and radiator dimension. If the radius of the radiator is greater than $\frac{1}{3}$ λ specific radiator resistance is roughly constant and about that of the surrounding air. Maximum power is transferred between two adjacent components of a system, for instance a radiator and the air, when the resistances of the components are equal. However, below $\frac{1}{3}$ λ:

TABLE 3. *Net efficiency of sound production and relative radiator size in some anurans and insects.*[a]

Species	Efficiency (%)	Radiator radius/λ
Insects		
Ensiferans		
Anurogryllus arboreus[2,5]	0.05–0.64[c]	0.08
Gryllotalpa australis[3]	1.05	na
O. quadripunctatus[2]	1.8–5.4 (w/baffle)	na
Requena verticalis[1]	6.4	0.16–0.27[d]
Scapteriscus borellii[7]	0.19	0.2–0.35[e]
Teleogryllus commodus[3]	0.05	na
Homoptera		
Cystosoma saundersii[4]	0.82	0.075
Anurans		
Hyla cinerea[6]	1.9	0.17–0.45
Hyla gratiosa[6]	0.8	0.03–0.07
Hyla squirella[6]	2.2	0.11–0.24
Hyla versicolor[6,b]	3.6	na
Pseudacris crucifer[6,b]	4.9	na
Physalaemus pustulosis[8,b]	0.5–1.2	na

[a] The ratios of radiator radius to wavelength for tree frogs is based on the assumption that the vocal pouch is the radiator and gives the ratio for the least and most expanded condition of the pouch relative to the most energetic wavelength.

[b] See notes about the calculation of these efficiencies in Prestwich *et al.*, 1989.

[c] Some exceptional individuals have very low efficiencies, most are clustered near 0.6%.

[d] Calculations based on long dimension of harp and the two principal radiation frequencies.

[e] Based on the two dimensions of the opening of the exponential horn portion of the burrow, for a mole cricket this is the radiator (Bennet-Clark, 1987).

References: 1. Bailey *et al.*, 1993; 2. Forrest, 1991; 3. Kavanagh, 1987; 4. MacNally and Young, 1981; 5. Prestwich, in preparation; 6. Prestwich *et al.*, 1989; 7. Prestwich and Walker, in preparation; 8. Ryan, 1985*a*.

3. $$R_m \propto \left\{\frac{r}{\lambda}\right\}^2$$

and it can be seen that as $\lambda \gg r$, R_m will decrease rapidly and so will the radiated power. Equations for different radiators (for instance ones with different shapes or without baffles) all predict the same general trends: R_m decreases as $r < \frac{1}{3}\lambda$ and for a given radiator to λ below this value, a radiator set in a baffle will have a higher specific radiator resistance (and therefore radiate more power) than one without a baffle (Beranek, 1954; Olson, 1957).

To summarize, radiators maximize their power transfer if (i) their radius approaches ⅓ λ so that their specific resistance matches the surrounding air, (ii) at relative radii above this some gain in power is possible (see eq. 2) but soon the signal becomes more directional as interference occurs towards the margins of the radiator (Beranek, 1954; Bennet-Clark, 1989), (iii) increases in amplitude of radiator vibration increase radiated power, and (iv) in the case of doublet sources (where opposite sides of a radiator vibrate 180° out of phase with each other, *e.g.*, ensiferan wings), baffles increase radiated power by preventing destructive interference. Given that a certain amount of power was delivered to the radiator, any factor(s) which increase the amount of power that is radiated will increase efficiency.

Table 3 shows that for the species where data are available, those which produce sound most efficiently tend to have at least one radiator dimension (ensiferan radiators are not symmetrical) that approaches ⅓λ. Bennet-Clark (1989) pointed out this general trend within the ensifera—crickets use relatively long wavelengths and have large tegmina while katydids use high frequencies or ultrasound and have small tegmina. Whether or not an animal is able to approach ⅓λ is partially determined by its general body size relative to broadcast wavelength. The moderately sized (0.35g) bushcricket

Requena verticalis uses high frequency sounds and is able to get a good match even with small tegmina, while the similarly sized cricket *Anurogryllus arboreus* is 10 times less efficient a sound producer. Although *Anurogryllus* appears to have a mismatch that is 2–3 times worse than the bushcricket, this mismatch is a power function (eqs. 2 and 3). Since many katydids probably have good matches between radiator dimension and principal wavelength, it is reasonable to predict that they will produce sound efficiently compared to gryllids.

A similar set of relationships probably holds true for frogs, but more caution needs to be exercised here in that there is some doubt as to the identity of the radiator. It is often assumed to be the vocal pouch (Martin, 1971; Gans, 1973; Prestwich *et al.*, 1989) but it may also include the lungs or entire body (Ryan, 1988). The cicada *Cystosoma* is interesting because its efficiency of sound production is moderately high while its tymbal organs are small. MacNally and Young (1981) suggested that since the abdomen was filled with air sacs that act as resonators, the entire abdomen is the radiator (as the ratio in Table 3 suggests). It can also be argued that resonance will increase the amplitude of vibration (compared to non-resonant systems) and this would increase efficiency of sound production (eq. 3).

Factors external to the radiator may also have important effects on efficiency of sound production. These include baffles, special acoustic burrows or reflectors, and the nature of the substratum. Baffles are employed by some ensiferans. If the animal calls from a perch where the tegmina are surrounded by a reflective surface, such as a leaf, the sound becomes much louder and less directional (Prozesky-Schulze *et al.*, 1975; Forrest, 1982). Forrest (1991) determined the sound fields for a tree cricket, *Oecanthus quadripunctatus*, with and without baffles and then estimated efficiency of sound production using Prestwich and Walker's (1981) metabolic data (Table 1). He found that the baffle increased the efficiency of sound production by three fold (using the reasonable assumption that power input does not change due to the baffle).

Forrest (1982) reported that a ground dwelling cricket, *Anurogryllus muticus*, constructs a shallow, saucer-like depression beneath its tegmina and calls holding them ¼λ above it. In part this device serves to beam sound upwards, but Bennet-Clark (1989) presented evidence that it may also affect sound production efficiency. Using an artificial source, he found that the SPL directly above the animal increased by 6 dB when the source was placed ¼λ above the reflector (compared to the situation when the source was either nearer than ¼λ to the ground or suspended in a free field). This increase is expected because the reflected wave travels ½/λ and returns to the tegmina in phase with the upper surface of the radiator and therefore adds constructively to the upward radiation.

Probably the most fascinating devices to increase acoustic efficiency are the singing burrows made by many species of mole crickets. Bennet-Clark (1970, 1987) has investigated this system extensively in three species. The singing burrow consists of two components—a wide opening which tapers in an approximately exponential manner (termed the horn) followed by an expanded area called the bulb. The animal sings facing away from the opening of the horn towards the bulb with its tegmina located at the juncture of the horn and bulb. The horn acts as an acoustic transformer and matches the impedance of the tegmina to the air. This maximizes power transfer (Bennet-Clark, 1987) since impedance mismatches result in energy being reflected (in this case back into the burrow). However, by itself, the horn also places an inertial reactive load on the tegmina radiator (due to the mass of the air). Any reactive load reduces useful power transfer by creating pressure and particle velocities that are out of phase; the system is said to be de-tuned. Bennet-Clark showed that the bulb is constructed so as to produce a capacitive reactance that is opposite to the inertial reactance of the horn and thereby tunes the horn. When calling starts, some acoustic energy is initially drained into these reactances instead of being radiated (into the air resistance). However, the energy that drained into the reactances immediately begins cycling between them and no further energy is drained. Instead it is radiated and the tegmina are said to experience a purely resistive load and maximal power is transferred. Bennet-Clark (1987) has shown experimentally (using a tiny doublet source placed in the same spot where the crickets hold their tegmina) that the SPL increases by up to 24 dB above what is measured for the same system in the free field. He also reported that during the process of constructing and tuning a burrow, the SPL of an individual cricket increased by 10–18 dB.

This argues for a high efficiency of sound production in these animals. Bennet-Clark (1970) estimated an efficiency of about 35% for the very loud European mole cricket, *Gryllotalpa vineae.* Kavanagh measured the efficiency of sound production in an Australian mole cricket, *Gryllotalpa australis,* at about 1%; a value that is considerably higher than that reported for most other ground dwelling crickets. Recently, Prestwich and Walker (manuscript in preparation) have measured efficiency in another mole cricket, *Scapteriscus borellii* (the subject of Bennet-Clark's 1987 paper on the efficiency of the acoustic burrow) and found it varied between 0.03 and 0.5% (mean 0.19%), depending largely on soil conditions. The low end of these measurements are in good agreement with estimates by Forrest (1991). It is interesting that crickets calling from this tuned burrow nevertheless have very low efficiencies of sound production. Forrest (1991) has suggested the likely cause of this—all measurements of *Scapteriscus* have been made using the sandy soils it inhabits in Florida. As these soils dry, they probably become good absorbers of acoustic energy; this absorption counteracts many of the advantages of the burrows. The effect is so great that the peak SPL recorded from single individuals has been observed to decrease as much as 25 dB as the soil went from saturated to dry, although power input did not change (Prestwich and Walker, in preparation). I have noted smaller differences but of the same type when *Anurogryllus arboreus* called on wet and dry sand, wood and concrete. Thus, very high efficiencies of sound production in mole crickets may only be possible in soils that are either saturated with water or made of non-absorbing materials such as clays. While model systems are extremely useful in clarifying some of the processes involved (Bennet-Clark, 1987), they are abstractions and must be augmented by measurements using complete systems that include the animal.

CONCLUSIONS

Studies of the energetics of sound production are often technically difficult and require species that will produce natural calls under what is for many of them unusual circumstances (*i.e.,* in small containers). Nevertheless, most studies of power input have indicated that in species which rapidly repeat loud calls the energetic costs rival those of locomotory activities and are important components of an animal's energy budget. It would seem that such activity must be limited energetically, but if so how? There are trade-offs to be made with energy—one behavior can be performed instead of another or stored energy can be utilized for different purposes, for instance, spermatophore production or provisioning (Bailey *et al.,* 1993; Lee and Loher, 1993). Animals can replenish diminished stores, but at present we have no real understanding of the inter-relationship between this and calling. The recent work by Wells, Taigen, Schwartz and their students is promising and needs to be pursued using other species. In particular, this question needs to be addressed in insects.

Animals produce a bewildering number of different types of advertisement calls and we know enough at present to predict which of these should be most energetically expensive by taking into account features of their call and morphology. There are complex interactions between the physical environment, competitive effects (both intra- and interspecific) and energy. What are the selective factors that determine the ways that an animal allocates energy between intensity, duration, repetition rate, and total time calling? Female choice would certainly seem to be a crucial factor here, yet predation and environmental features affecting sound propagation are surely also important factors. Ryan (1988) has made interesting suggestions about call design and in particular has taken a broad view of the factors that should matter. Nevertheless, we still know little about anurans in this regard and even less about insects. And there is a danger in trying to understand these relationships by only studying species that produce the most intense calls and that are most likely to fit into our theories of the role of energy in sexual selection.

Limited data suggest that there are inter-specific differences in the efficiency of sound production (Table 3). To some degree we understand these differences, particularly as they relate to radiator size and enhancements of the calling environment such as baffles and acoustic burrows. But we do not know whether there are intra-specific differences in efficiency of sound production and if so, their causes, heritability, and fitness consequences. For instance, if some males are less efficient at producing sound, do they adopt alternative reproductive strategies? What specifically do differences in the intensity of a male's call indicate?—overall condition, morphological difference, a behavioral choice or some interaction of these? In *Scapteriscus borellii* the principal difference seems to be related to the condition of the burrow and soil moisture (Forrest, 1991; Prestwich and Walker, in preparation). This implies that females may be selecting habitat at least as much as they are selecting a given male. Crickets would seem to be ideal organisms for such studies since they can be easily bred and maintained in the laboratory. Finally, from a physiological perspective, it is of interest to determine how morphological factors influence the efficiency of sound production, especially if we wish to better understand inter- and intra-specific differences in efficiency of sound production.

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