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Energy, Calling, and Selection[1]

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SYNOPSIS. Acoustic signals often mediate the mating process and are under selection through the action of female choice. Acoustic signalling requires relatively large amounts of energy input, but metabolic energy is coupled to acoustic energy inefficiently. Although not necessarily a cause and effect relationship, females often prefer signals with more energy. Females may prefer more intense calls, more complicated calls, or calls produced at a greater repetition rate. I discuss various evolutionary changes that could increase acoustic energy received by the female and examine how these changes are influenced by other factors inherent to communication systems: signal radiation, species recognition, sexual selection, the physiology of the receptor system, and environmental bioacoustics. I conclude that these factors constrain the ability of the animal to maximize energy received by the female. I then consider how two hypotheses, the good genes hypothesis and the runaway sexual selection hypothesis, attempt to explain the evolution of female choice for signals with greater energy content.

INTRODUCTION

An important issue in energetic constraints on animal behavior is how both the amount of energy available and the ability to utilize that energy to support behavior influence an individual's fitness. An important and obvious component of fitness is mating success. Mating is a social phenomenon mediated to some extent by social signals; signals that usually advertise the presence of the male to the female, or signals involved in male-male interactions related to mating.

I will address the relationship between energy, acoustic signals used in mate attraction, and selection. Most of the appropriate data are from studies of frogs and some are from studies of insects. Acoustic communication offers advantages in studies of animal behavior for several reasons. First, acoustic signals can be easily recorded, quantified, and described. Second, rates of oxygen consumption during singing or calling are relatively easily measured, thus allowing an accurate estimate of energetic costs. Third, correlations between aspects of a male's acoustic signal and his mating success can be measured and, most importantly, these correlations can serve as hypotheses that can be tested experimentally with phonotaxis experiments. This latter, and in my opinion crucial, advantage seems to have been forgotten in the rush for multivariate analyses of male traits influencing mating success (*e.g.*, Arnold, 1983). As valuable as these statistical tools might be, they are strengthened when they lead to experimentally testable hypotheses.

The most important advantage of considering acoustic communication in the context of this symposium is the direct link between energy and fitness. As I will document below, calling and singing are energetically both very demanding and very inefficient behaviors, and many studies have shown a positive correlation, although not necessarily a cause and effect relationship, between the amount of acoustic energy received by the female and the male's attractiveness to the female. Thus the energy content of the signal is under selection. Of prime importance, then, is the amount of energy invested in the signal, the efficiency with which metabolic energy is converted to acoustic energy, the rate of energy loss as the signal travels through the environment to the female, and the transformation of the acoustic energy to neural excitation in the female's auditory system (Fig. 1).

I will consider the influence of each of these factors on signal structure and suggest that maximizing the amount of acous-

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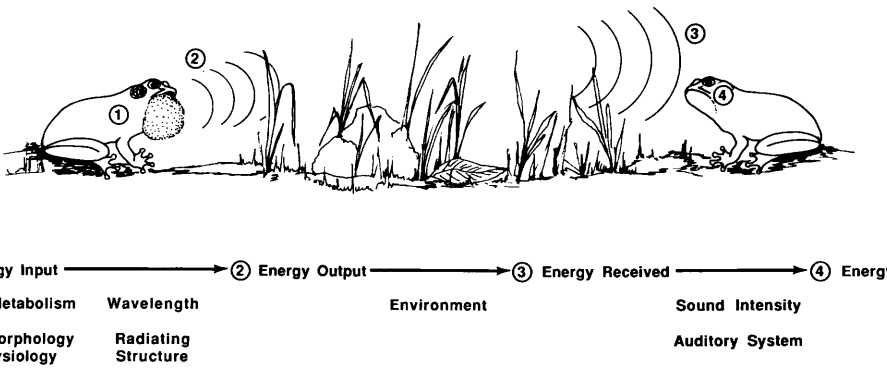

FIG. 1. An illustration of major factors influencing the amount of acoustic energy perceived by the female.

tic energy that reaches the female is a complex task due to a variety of constraints and opposing selective forces. I will then discuss how evidence of selection on the amount of energy in the signal bears on two competing hypotheses that attempt to explain the evolution of female preferences for calls with more energy. My emphasis is clearly not one restricted to physiological ecology, but instead integrates physiology, behavior, and evolution. lution.

THE ENERGETIC COST OF ACOUSTIC SIGNALLING

The amount of energy generated to support acoustic signalling has been estimated by several techniques such as measuring the rate of thoracic heating and cooling during singing in insects (*e.g.*, Bennet-Clark, 1970; Heath and Josephson, 1970) and by comparing fluid energy losses in the syrinx to resulting acoustic energy in the calls of birds (Brackenbury, 1977). A more satisfying estimate of energy utilization is derived from direct measures of the rate of oxygen consumption ($\dot{V}O_2$) during singing or calling. Although measuring oxygen consumption in animals is an important *modus operandi* in physiological ecology (*e.g.*, Walsberg, 1986), these measures usually are used to estimate metabolic rate ($\dot{V}O_{2\ rest}$) or the maximum rate of oxygen consumption ($\dot{V}O_{2\ max}$).

Although they exist, measures of oxygen consumption during natural activities are less common, especially in vertebrates. The reason for this dearth of data on natural behavior is not lack of interest by researchers but lack of cooperation by subjects. Few animals will perform biologically relevant behaviors in the confines of a respirometer. One behavior that can be measured in a respirometer is acoustic signalling in insects and anurans. This is fortunate because, as just discussed, acoustic signalling is crucial to mating and therefore of obvious and significant evolutionary importance.

Currently, there are relatively few studies that have directly measured $\dot{V}O_2$ during calling or singing (Table 1). Even so, some generalizations can be made. First, $\dot{V}O_{2\ call}$ is high for all species measured, and on a per gram basis is higher for insects than frogs. However, frogs have lower resting metabolic rates than insects; the ranges of factorial scopes for singing and calling ($\dot{V}O_{2\ call}/\dot{V}O_{2\ rest}$) that are available for insects and frogs are similar (Table 1).

A second generalization about the energetic cost of calling is that $\dot{V}O_{2\ call}$ and the factorial scopes for calling also can be high relative to other behaviors, including estimates of maximum rates of oxygen consumption estimated from forced locomotory activity. In katydids, the rate of oxygen consumption per gram of active muscle is within range of that found for wing muscles in other insects (Stevens and Josephson, 1977). This similarity might be expected since wing muscles can be involved both in flight and in stridulation that gives rise to sound production. In anurans, there appears to be a striking difference between the amount of energy

TABLE 1. *Rates of oxygen consumption during calling and resting, and factorial scope for calling in six insect and three frog species.*

Species	$\dot{V}O_{2\,call}$[a]	$\dot{V}O_{2\,rest}$[a]	Scope[b]	Reference
Cystoma saundersii	6.28	0.34	18.5	MacNally and Young, 1981
Anurogryllus arboreus	3.82	0.30	12.7	Prestwich and Walker, 1981
Oceanthus celerinictus	3.47	0.46	7.5	Prestwich and Walker, 1981
Oecanthus quadripunctatus	4.4	0.63	7.0	Prestwich and Walker, 1981
Euconocephalus nasutus	18.4	0.62	29.7	Stevens and Josephson, 1977
Neoconocephalus robustus	15.8	0.8	19.7	Stevens and Josephson, 1977
Physalaemus pustulosus	1.0	0.18	5.5	Bucher *et al.*, 1982
Hyla versicolor	1.70	0.08	21.2	Taigen and Wells, 1985
Hyla crucifer	1.51	0.12	12.6	Taigen *et al.*, 1985

[a] $\dot{V}O_2$ is in ml/g·hr.
[b] Scope is factorial scope for calling which is ($\dot{V}O_{2\,call}/\dot{V}O_{2\,rest}$).

needed to support calling relative to other behaviors. Bucher *et al.* (1982) showed that the factorial scope for calling in *Physalaemus pustulosus* was similar to the factorial scope for maximum locomotory activity in many other anurans. The most striking example of high energetic costs for calling, however, comes from the study by Taigen and Wells (1985) on the treefrog *Hyla versicolor.* The factorial scope for calling in this species is 21.2—the highest rate of oxygen consumption and the largest factorial scope for activity of all ectothermic vertebrates studied to date (Table 1). Of further interest in this species is the observation that rates of oxygen consumption during vigorous forced activity, what normally would be considered maximum aerobic capacity ($\dot{V}O_{2\,max}$), was only 62% of peak $\dot{V}O_{2\,call}$ (but see Walsberg, 1986). These estimates of the amount of energy needed to support vocal behavior in frogs were surprising and, as emphasized by Bennett (1986), indicate that our intuition might not serve us well in estimating the energetic costs associated with various behaviors.

A third generalization of calling energetics is that calling is supported primarily by aerobically generated ATPs. Ryan *et al.* (1983) showed that there was no significant difference in whole-body lactate levels between calling males and noncalling males in *P. pustulosus.* Taigen and Wells (1985) showed that in *H. versicolor* there were no significant differences in whole-body lactate levels between samples of males that were collected early in the evening *versus* males collected later in the evening. Pough and Gatten (1984) did report significantly elevated lactate levels in calling spring peepers (*Hyla crucifer*) compared to resting frogs. However, Gatten (1985) cautions that these levels might have resulted from movements associated with calling; even if real, these data indicate only minor anaerobic support of calling.

ENERGETIC EFFICIENCY OF CALLING

A fourth generalization about the energetics of acoustic communication is that much of the substantial metabolic energy invested in calling is lost and not incorporated into the signal. That is, the efficiency with which metabolic energy is coupled to acoustic energy is low. MacNally and Young (1981) estimated the energetic efficiency of singing in the bladder cicada *Cystoma saundersii* to be 0.8%. Vocalizations in humans are thought to be produced with an efficiency of 1% (Wood, 1962). Brackenbury (1977) compared the fluid energy losses in the syrinx to the total acoustic energy to estimate the efficiency of crowing in a chicken as 1.6%. The frog, *P. pustulosus,* produces a call with a whine and from 0–6 chucks (Fig. 2). Although the power of the call increases with the number of chucks, the energetic cost of calling does not. Therefore, the energetic efficiency increases with the number of chucks but only ranges from 0.5% to 1.2%.

One reason for the low energetic efficiency of coupling metabolic to acoustic energy results from a fundamental mismatch between the wavelengths of the sig-

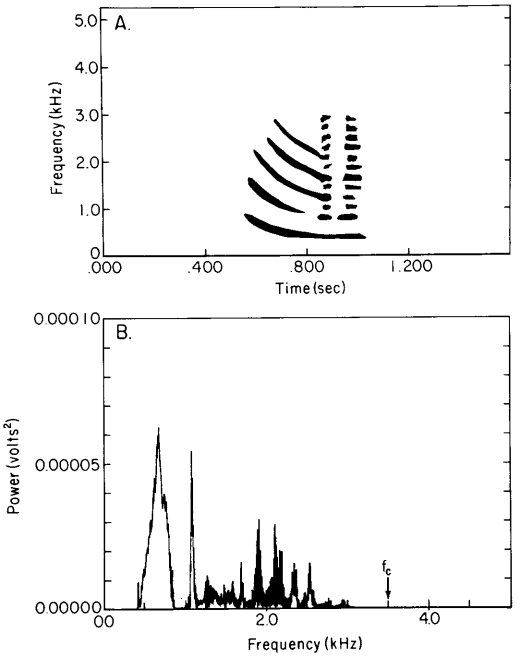

FIG. 2. (A) A sonogram of the mating call of *Physalaemus pustulosus*, containing a whine and two chucks. (B) A power spectrum of the call above. f_c is the cutoff frequency.

nal and the size of the structures radiating or resonating those signals. This mismatch has been discussed by several authors (MacNally and Young, 1981; Wiley and Richards, 1982; Ryan, 1985*a*, 1986*b*, 1988) and appears to be especially true for vertebrates that are characterized by relatively low frequency signals. (Michelson and Nocke [1974] show greater congruence between song frequency and the properties of sound resonating structures in insects.)

An example of this mismatch is apparent in frogs. In most anurans, it is thought that the vocal sac is a radiator rather than a resonator. This has been demonstrated in two ways. Martin (1972) punctured the vocal sac of the toad *Bufo cognatus*. The call produced under these conditions was lower in amplitude and slightly detuned, but the spectral components, especially the dominant frequency, were unchanged. An ingenious experiment further demonstrating this fact is reported by Capranica and Moffat (1983). Male spring peepers, *H. crucifer*, were forced to call in a bag of helium. The resonant frequency of a resonating structure is determined by the relationship between the size of the resonator and the wavelength. The frequency of sound is a product of the speed of sound and the wavelength, and the speed of sound is *ca.* three times faster in helium than in air. Thus the calling medium does not influence the wavelength that will be resonated, but it will affect the frequency of that wavelength. The frequency should be higher by a factor of three in helium if the sound is being resonated. This was not the case; the dominant frequency of the *H. crucifer* call is the same in air and helium.

The addition of a radiator to a sound producing system will increase the efficiency with which sound is coupled to the environment. The magnitude of the increase is dependent upon the size of the radiator, which determines its cutoff frequency ($fc = c/2\pi r$, where c is the speed of sound and r is the radius of the radiator [Beranek, 1954]). At lower frequencies (and longer wavelengths) the efficiency is drastically reduced. For example, in the call of *P. pustulosus* most of the energy in the call is contributed by the whine which has a duration *ca.* 400 msec and most of its energy in the frequencies between 400 Hz and 1,000 Hz. The chuck is much shorter in duration, *ca.* 26 msec, and has a broader frequency range—most of its energy is in frequencies between 200 Hz and 3,000 Hz (Fig. 2). This frog averages 3 cm in snout-to-vent length. If the entire frog, rather than only the vocal sac, radiated the call, this frog would have a cutoff frequency of 3,500 Hz. This is a conservative (low frequency) estimate, but even under these conditions, more than 99% of all the energy in the call is below the cutoff frequency (Fig. 2). In order to couple all of the energy at maximum efficiency, the frog would need to be 26 cm long.

DOES SELECTION INFLUENCE CALLING ENERGETICS?

Up to this point, I have suggested that animals invest a large amount of energy in the support of calling, and that much of this investment is lost in the transforma-

TABLE 2. *Influence of acoustic energy on female mate preference in anurans.*

Species	Call parameter	Source
Hyla versicolor	Intensity	Fellers, 1979
Hyla cinerea	Intensity	Gerhardt, 1981
Bufo calamita	Intensity	Arak, 1983
Hyla crucifer	Intensity	Forester and Czarnowsky, 1985
Physalaemus pustulosus	Components	Rand and Ryan, 1982
Hyla microcephala	Components	Schwartz, 1986
Hyla ebraccata	Components	Wells and Schwartz, 1984
Geocrinia victoriana	Components	Littlejohn and Harrison, 1985
Hyla crucifer	Rate	Forester and Czarnowsky, 1985
Hyla microcephala	Rate	Schwartz, 1986
Bufo woodhousei	Rate	Sullivan, 1983
Hyla regilla	Rate	Whitney and Krebs, 1975
Hyla regilla	Duration	Whitney and Krebs, 1975

tion from metabolic to acoustic energy. This would represent an interesting departure from optimality if evidence suggested selection favoring males that emitted more call energy.

Variation in the total amount of acoustic energy produced by a calling male has two major sources: the amount of energy in a single call, and the total number of calls produced. The most simple model of female choice is a passive model in which females are attracted randomly to conspecific mating calls. In such a system, an increase in the intensity or the duration of calling would increase the "domain of attraction" of the signaller (Parker, 1982) and thus be favored by sexual selection.

Data also suggest selection on variation in acoustic energy output through the action of active female choice. In a number of species females are attracted to calls that are more intense; the greater the amount of energy in the call, the greater the intensity (Table 2). In other species, females are attracted preferentially to those types of calls that contain more energy because they contain more components or syllables (Table 2). Calling rate also influences female mate choice; females prefer males that produce more calls per unit time, and the greater the number of calls the greater the total acoustic energy produced by the male (Table 2).

Although none of the above data demonstrate that females select certain males because they emit more acoustic energy per se, increased energy output is correlated with increased call attractiveness, and thus surely is correlated with any trait the female might be choosing in the above examples (more intense calls, more complex calls, greater calling rates). As such, total acoustic energy will at least be under indirect selection by female choice due to its phenotypic correlation with other traits.

SELECTION ON ENERGY COUPLING

Given the importance of the amount of acoustic energy emitted for mate attraction, the low efficiency of the coupling of metabolic to acoustic energy seems puzzling. This is especially so because such coupling could be greatly increased by reducing the mismatch between the wavelength of the call and the radiating structures through the use of shorter wavelengths (higher frequencies). However, there are potentially four factors that will constrain this means of increasing the efficiency of acoustic coupling: species recognition, sexual selection, environmental bioacoustics, and the sensitivity of the receptor. The manner in which these factors can complexly interact to either decrease or enhance the potential advantage of increased transformation efficiency can be illustrated with data from *H. crucifer*.

The call of *H. crucifer* is shown in Figure 3A. It is almost a pure tone with a dominant frequency around 2,900 Hz and a duration of about 120 msec. A hypothet-

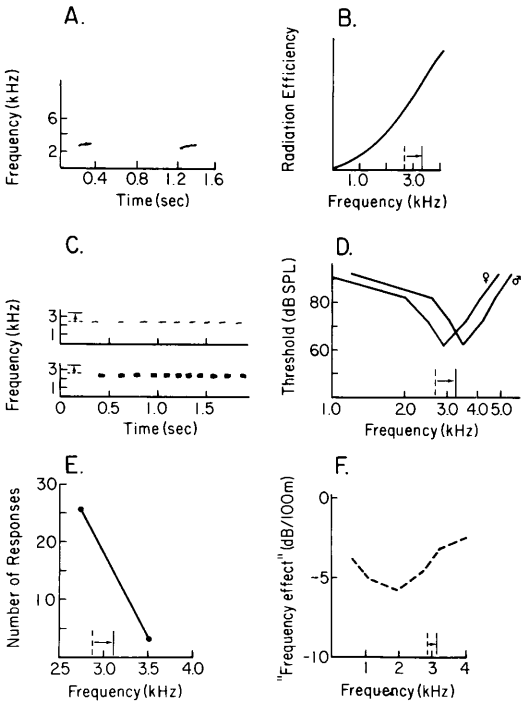

FIG. 3. (A) A sonogram of the mating call of *Hyla crucifer*. (B) A radiation efficiency curve for *H. crucifer*. (C) Sonograms of the mating calls of two congeners that are sympatric with *H. crucifer*, *H. avivoca* (top) and *H. femoralis* (bottom; redrawn from Gerhardt, 1974). (D) A tuning curve of VIIIth nerve fibers thought to originate from the basilar papilla in *H. crucifer* (W. Wilczynski, personal communication). (E) The number of positive phonotactic responses by female *H. crucifer* elicited in response to calls of different frequencies. The line between the points suggests that how preference might change as a function of frequency (data from Forester and Czarnowsky, 1985). (F) The effect of frequency on the amount of excess attenuation (*i.e.*, attenuation above that expected due to the spherical spreading of sound). A more positive frequency effect signifies greater excess attenuation (redrawn from Marten and Marler, 1977).

ical radiation efficiency curve is illustrated in Figure 3B, which is based on the demonstration by Capranica and Moffat (1983) that the spring peeper uses a radiator and not a resonator to couple the call to the environment, and on the conservative assumption that the entire body of the frog is used to radiate the call. Also shown are the calls of two treefrogs of the *H. versicolor* species group (Fig. 3C). These species are sympatric with *H. crucifer* throughout much of its range, and thus form an important part of the acoustic environment in which *H. crucifer* must communicate.

In anurans, there are two distinct inner ear organs that function primarily in the detection of acoustic disturbances: the amphibian papilla (AP) and the basilar papilla (BP). These organs also have distinct frequency ranges to which they respond at threshold: the AP is more sensitive to lower frequencies while the BP is more sensitive to higher frequencies. Wilczynski *et al.* (1984) showed that the call of the spring peeper falls totally within the threshold range of the BP (Fig. 3D). Another interesting feature is the fact that there is sexual dimorphism in the tuning of the call. The BPs of males are tuned to slightly higher frequencies and thus are mismatched to their own calls. This might result from the fact that the BP acts as a simple resonator, its size determines its resonating properties which are correlated with body size. Since males are smaller they have smaller BPs which are tuned to higher frequencies (Fig. 3D).

Forester and Czarnowsky (1985) have demonstrated that in *H. crucifer* larger males have lower frequency calls, and these calls are more attractive to females in phonotaxis experiments. Similar results have been found in *P. pustulosus* (Ryan, 1980, 1983, 1985*b*) and *Uperolia rugosa* (Robertson, 1986). The potential influence of call frequency on female preference is illustrated in Figure 3E. This figure is not meant to represent accurately the dynamic range of female preferences, which is not possible from the data available, but only to illustrate hypothetically how female preference might change with call frequency.

Marten and Marler (1977) showed the amount of excess attenuation (frequency effect) for pure tones of various frequencies in a temperate forest at ground level (Fig. 3F)—these data can be extrapolated easily to spring peepers given the facts that their call is tonal in nature, and the demonstration that playbacks of calls through the environment mimic attenuation effects of natural calls (Ryan, 1986*a*).

Using these data as a simple illustration

demonstrates the myriad of effects with potential selective importance that would result from an increase in the frequency of the call. As shown on the radiation curve (Fig. 3B), the efficiency of acoustic coupling would no doubt be increased if the animal were able to produce higher frequencies. This should result in the call being produced at a higher intensity, ensuring the advantages derived from more intense calls in mate attraction discussed above. There are potential effects that might enhance or offset this advantage.

In many species of anurans spectral cues are one of the factors important in species recognition. Thus the evolutionary consequences of a change in the spectral properties of the call will depend strongly on the structure of calls of sympatric species. If a frequency change results in a call becoming more similar to that of another species there are two consequences. First, males now communicate in a more noisy environment which hinders the ability to attract a female. Second, the male might no longer be recognized as a conspecific by the female if his call becomes too similar to that of a heterospecific. In the example shown here (Fig. 3C), an increase in call frequency reduces conspecific interference.

Another effect derives from the sensory physiology of the receiver. If call frequency were increased to improve the match between wavelength and radiation efficiency, the call would no longer match the tuning of the female's BP. Thus the intensity of the call at the female might increase, but the perceived intensity of the call (*i.e.*, the loudness) might decrease. Interactions among males further complicate matters. There is sexual dimorphism in the tuning of the BP; the male's tuning is mismatched to his call. Brenowitz *et al.* (1984) suggested that male spacing is determined by auditory threshold—males arrange themselves such that they can barely hear their neighbor's call—and that this spacing is a compromise between male interactions and female attraction. An increase in call frequency would bring the call into a better match with the male's BP, thus increasing the nearest neighbor distance and decreasing the chance of having mates attracted to male's call intercepted by parasitic males (Fig. 3D).

Another possible disadvantage of an increase in call frequency derives from sexual selection. Although higher frequency calls might be of greater intensity, these calls might no longer be preferred by females (Fig. 3E). The phenomenon of female preference of lower frequency calls might be a manifestation of a better match between call frequency and BP tuning, *i.e.*, the disadvantages derived from a mismatch between the call and the female's BP and that due to female preference for lower frequency calls might not be independent effects.

The final factor that might constrain an increase in call frequency is transmission of the call. To increase the intensity of a call as it reaches the female, the call must not only be coupled to the environment efficiently, but it must travel through the environment with minimal excess attenuation. With the exception of some peculiar acoustic phenomena, such as those derived from temperature inversions and ground waves, sound intensity will attenuate minimally as the square of the distance, or at a rate of 6 dB per doubling of distance. Regardless of the environment, higher frequencies will tend to exhibit higher rates of excess attenuation (*i.e.*, attenuation above that expected from spherical spreading alone) due to increased molecular interactions that increase energy loss through heat dissipation. This energy loss is further increased by the environment. As the wavelength of a sound decreases (as the frequency increases) relative to the size of objects imposed in the sound path, environmental attenuation increases; simply, longer wavelengths can travel around some objects that will diffract and reflect smaller wavelengths (Marten and Marler, 1977). Therefore, in many instances an increase in frequency increases the attenuation of the signal with distance; it appears that this would be the case if the frequency of the call of *H. crucifer* were increased (Fig. 3F). At a higher frequency

the signal might be emitted from the animal with greater intensity, but this advantage might be lost as the sound travels to the receiver. There is another potential problem derived from bioacoustics that can affect higher frequencies. Ryan and Brenowitz (1985) showed that in some habitats high frequency sounds produced by insects may have caused a decrease in the dominant frequency of the songs of birds. Insect songs might tend to be too high relative to frog calls to be an important consideration, but this possibility has not been investigated.

Clearly, an animal should be able to increase the amount of acoustic energy received by the female by better matching the wavelength of the call to the radiating structures. But the animal's communication system is part of a larger and more complicated whole, and is influenced by species interactions, sexual selection, sensory physiology, morphology, and environmental bioacoustics. An evolutionary change might accrue advantages at one level but disadvantages at another. It would be tempting to conclude, therefore, that the animal's signal is at the optimum that will maximize the benefits and minimize the costs resulting from these different interactions. This is a difficult proposition to evaluate, but the data collected for the spring peeper by various researchers show that at least in anurans many of the important parameters can be measured.

SELECTION ON ENERGY INPUT

Another general means of increasing the total acoustic energy that reaches the female is to increase the total energy input for calling, either on a per call basis or by increasing the total number of calls. There are data suggesting that selection has acted at the level of the animal's morphology and physiology to do just that. Trewavas (1933) described the hyoid-laryngeal apparatuses of 60 species representing 11 families of anurans; this survey reveals sexual dimorphism in both the size of the larynx and in the mass of the intrinsic musculature associated with the larynx. Eichelberg and Schneider (1973, 1974) examined these muscles in detail in the frog *Hyla arborea* and found that they were rich in glycogen and lipids, and contain large mitochondria compared to other muscles. Taigen *et al.* (1985) present data suggesting adaptation of the trunk muscles involved in calling. They showed that trunk muscles were relatively larger in males than in females. They also showed that relative to limb muscles, trunk muscles exhibit a greater oxidative capacity, as indicated by high citrate synthase activity, and a greater ability to oxidize fat, as indicated by high β-hydroxyacyl-CoA dehydrogenase activity.

DOES PHYSIOLOGY CONSTRAIN BEHAVIOR?

There do appear to be adaptations to increase energy input for calling either in terms of increased input per call or ability to sustain calling over longer periods of time. To consider whether selection might be acting on calling traits, we must first consider whether there is variation in the ability to support calling. This question can be addressed among species and within populations. There are no data available that allow us to evaluate the proposition that species that call more are better adapted to energetically support calling. There are data for other behaviors suggesting this might be true. For example, Taigen *et al.* (1982) suggested that active foragers and nonjumping frogs rely on aerobically generated energy more extensively than do passive foragers and jumping frogs. Bennett and Licht (1974) also suggested a relationship between physiological capacity and behavior in amphibians.

There is substantial variation among species in the amount of time devoted to calling. For example, in Panama some species such as *P. pustulosus* call almost continually from dusk to 2400 hr, sometimes producing in excess of 7,000 calls. Other species, such as *Eleutherodactylus fitzingeri* call only during rainfall, and others, such as *E. bufoniformus* have rarely been heard to call at all. In addressing the question of adaptation at the species level it must be remembered that the animal's physiology evolves under a variety of selective forces and constraints, selection to increase energy

input for calling could be opposed by selection on other characters. The whole animal must be considered. Another important factor that also needs to be considered is phylogeny (Ridley, 1983; Felsenstein, 1985; Huey and Bennett, 1986; Ryan, 1988). The most valuable study of species adaptations for calling would address this question in a group of closely related species for which there is a well-corroborated phylogeny, and that exhibits substantial among-species and little within-species variation in the amount of calling. Ecologists and behaviorists often are discouraged upon completion of a "comparative" study when they learn there is not a phylogeny available for the group they just studied. Rarely, however, is this problem considered before beginning a "comparative" study. If a comparative study is not phylogenetic it is laboring under a misnomer.

Significant variation in calling behavior exists at the population level. Also, there is considerable variation in male mating success in some species, and, as reviewed above, female preference can be related to total acoustic energy received. Are there underlying physiological differences among males that are apparent from differences in calling behavior?

There are suggestive data. Some studies of anurans (Wells, 1978; MacNally, 1981) have shown that male energy reserves are depleted during the breeding season. Energy depletion might result from energy invested in calling or abstention from feeding. Woolbright (1985) argues convincingly that the former effect results in sexual size dimorphism in *Eleutherodactylus coqui.* Regardless of the cause, it is not known if the amount of energy available influences the decision of males to invest in calling as opposed to noncalling satellite behaviors. The way in which energy is mobilized could be as important as total energy expenditure. Wells and Taigen (1986) showed that *H. versicolor* males in dense choruses produced calls that were longer but at half the rate of isolated males. (They suggest that females are likely to prefer longer calls.) Energy expenditures were the same, suggesting that there is an upper physiological limit to calling such that an increase in call duration must be accompanied by a decrease in call rate. They make the intriguing suggestion that males making short calls might be postponing muscle glycogen depletion and thus increasing endurance.

The hypothesis that variation in the amount of calling is related to the ability of males to support behavior has been tested in toads. Sullivan (1982) showed that in the toad *Bufo woodhousei* males varied in call repetition rate, the rank order of males was consistent between nights, and females preferred calls with higher repetition rates. He suggested that call rate is correlated with male vigor, as would be expected under the good genes hypothesis of the evolution of female choice (discussed below). Specifically, if females choose males that are better able to physiologically support behavior, it was argued, and if variation in physiological fitness is heritable, then female choice might have evolved due to the advantages derived from superior physiological fitness accrued to their offspring. Sullivan and Walsberg (1985) tested this hypothesis by estimating the maximum aerobic capacity from measures of $\dot{V}O_2$ during forced activity of males with known calling rates. Their data did not support the hypothesis, as there was no significant relationship between call rate and maximum aerobic capacity.

Wells and Taigen (1984) approached a slightly different question in a similar manner. In *B. americanus,* some males called while others moved around the pond attempting to clasp females. They tested the hypothesis that aerobic capacity limits behavior; specifically, that individual differences in the amount of calling and searching for females are related to aerobic capacity. However, as in Sullivan and Walsberg (1985), Wells and Taigen found no data to support their hypothesis. A possible confounding factor was that searching behavior is more common in noncalling males and this behavior is not necessarily a low energy behavior. Wells and Taigen ranked noncalling and calling males together as a function of the amount of time active, either calling or searching, and again found no significant relationship

between activity and maximum aerobic capacity.

These results are not surprising. As reviewed above, Echilsberg and Schneider (1973, 1974) and Taigen *et al.* (1985) suggested that muscles involved in calling show adaptive differences relative to other muscles. An explicit (Sullivan and Walsberg, 1985) or implicit (Wells and Taigen, 1984) assumption of the above studies is that maximum aerobic capacity is limited by cardiovascular capabilities, thus the whole-body maximum power consumption should be restricted to similar levels regardless of the form of exercise. However, Taigen *et al.* (1985) showed that the trunk muscles involved in calling have adaptations at the level of muscle biochemistry that should increase their power output relative to limb muscles, the latter which are the ones exercised during determinations of $\dot{V}O_{2\ max}$. This, in part, might explain why Taigen and Wells (1985) found that the rate of oxygen consumption during calling is greater than rates of oxygen consumption during forced, maximum locomotory activity—what sometimes is considered to be $\dot{V}O_{2\,max}$. However, Walsberg (1986) reviewed a variety of techniques used to estimate $\dot{V}O_{2\,max}$, and suggested the technique used by Taigen and Wells (1985) might underestimate $\dot{V}O_{2\ max}$ by as much as 30%.

There are now two very separate questions of interest at the population level regarding physiological support of calling behavior. The first question asks if physiological differences among males are responsible for observed differences in calling behavior. The answer to this question must be addressed at the locus of calling, and not by measuring the ability of the animal to sustain locomotory behaviors, or other behaviors not relevant to calling. There are several ways to do this, including measures of muscles mass, enzyme activities, and glycogen stores.

The second question, addressed by Sullivan and Walsberg (1985), asks if calling rate is correlated with general physiological condition of the animal. This is perhaps easier to determine because general physiological condition can be evaluated by measures of whole-animal performance, $\dot{V}O_2$ during various forms of exercise, heart volume, or hematocrit (see also Bennett, 1986; Huey and Bennett, 1986).

A crucial question at this point is whether either the amount of available energy or the ability to utilize energy to support calling behavior constrains the male's ability to partake in mating. There have been few tests of this hypothesis, and at present there is no evidence for such constraints. However, studies must separate clearly questions concerning differences among males in the ability to energetically support calling, from those that ask if the amount of calling is indicative of generally superior physiological condition. Answers to these questions require two different kinds of measurements. As will be discussed below, they also bear quite differently on theories that attempt to explain the evolution of female preferences for calls with greater energy content.

Evolution and Constraints on Calling: Natural Selection and Sexual Selection

The above questions are of relevance to a controversy regarding the evolution of female choice (reviewed in Kirkpatrick, 1987). There appears now to be little argument that female preference for male traits has influenced the evolution of those traits, even if they decrease the male's ability to survive (*e.g.*, Ryan, 1985*b*; Kirkpatrick, 1987). The controversial question is why females have come to evolve certain preferences. There are a variety of nuances and alternatives, but the two major competing hypotheses are known as the good genes hypothesis and the runaway sexual selection hypothesis. The former states that females prefer traits because the male's possession of these traits is indicative of superior genes relative to natural selection. This hypothesis then predicts that the pair's offspring will be endowed with some natural selection advantage; for example, increased foraging abilities, increased competitive ability, or any factor that leads to increased survivorship (Trivers, 1972; Zahavi, 1975; Kodric-Brown and Brown,

1984). The runaway sexual selection hypothesis states that once the female preference is present in the population it increases in frequency because it becomes genetically correlated, through linkage disequilibrium, with the male trait (Fisher, 1958). Thus its increase in the population can occur without the female's offspring receiving any natural selection advantage. Fisher (1958) suggested that females that exhibit the preference initially receive a natural selection advantage, but then its continued evolution is governed by runaway sexual selection. Lande (1981) and Kirkpatrick (1982), however, have suggested that other forces can give rise to linkage between the trait and the preference, and thus it is not necessary to invoke natural selection for initiation of the runaway process.

Anticipating studies that will measure physiological correlates of calling behavior, I consider the results. As suggested above, these studies should measure physiological parameters associated with calling directly, and they also should measure other parameters indicative of physiological fitness in other contexts such as aerobic capacity during forced activity, and behavioral performance such as endurance and sprint speed.

If there were no correlation between any physiological measure and calling behavior, and these results had a low probability of a type II error, this would suggest that other factors such as hormonal status, previous history of the animal, calling site, or a myriad of other socioecological factors might be more important in determining calling behavior than physiological factors.

Another possibility would be that only calling physiology shows a significant relationship to calling behavior. If so, this would tend to agree with the predictions from the hypothesis of runaway sexual selection suggesting that female choice can be based on traits not favored by natural selection. If only calling physiology is related to calling behavior, then it cannot be argued that female preference for these males results in an increase in the vigor or overall survivorship of males. In fact, because of the demonstrated energetic costs (discussed above) and predation costs (Ryan *et al.*, 1981, 1982; Tuttle and Ryan, 1981) associated with calling, female preference for high energy calls probably decreases overall survivorship of males.

A third possibility is that only more general physiological parameters are associated with the amount of calling behavior, but there is no relationship between the amount of calling and the ability to support that particular behavior. This would suggest that males do not differ at the calling locus. Of course, there still might be physiological adaptations for calling, as discussed above, but it would suggest that the variation in calling is not generated at this level. A likely interpretation would be that factors at the level of more general physiology, such as cardiovascular differences, hematocrit, etc., contribute to variation in calling behavior. Interestingly, these results would lead to the same interpretation as that of both general physiology and calling physiology being correlated with calling behavior. This interpretation is discussed below.

The final possibility is that both calling physiology and other physiological and behavioral performance parameters are significantly related to calling behavior. If this were the case, it would suggest that female choice could be responsible for the evolution of both the underlying physiological mechanisms that support calling, and physiological mechanisms that support a wide variety of ecologically relevant behaviors that increase survivorship. Selection would act directly on both factors, or it would act directly on one and have a correlated effect on the other. Regardless, female choice would be promoting factors important in sexual selection and natural selection. However, it must be remembered that showing the effects of female choice on male traits is not necessarily evidence of why female choice exists.

The fact that courtship displays, including mating calls and songs, are expensive has been suggested as evidence supporting the hypothesis of the evolution of female choice by natural selection as opposed to

sexual selection (*e.g.*, Zahavi, 1975; Kodric-Brown and Brown, 1984). The above discussion suggests that this logic is not warranted. Studies of calling energetics and mate choice could reject the natural selection hypothesis in favor of the sexual selection hypothesis, or support the hypothesis of natural selection and sexual selection acting in the same direction. These results cannot support the role of natural selection as an alternative to sexual selection in the evolution of female choice. This appears not to be clear to some researchers.

SUMMARY

Calling is both energetically expensive and inefficient. The amount of acoustic energy received by the female is important in mate choice in several species of anurans; it would be surprising if the same were not true for many if not most of the species of frogs and acoustically signalling insects not yet studied. There is a paradox in that there is selection on acoustic energy output, and output could be greatly increased by better matching the wavelength of the signal to the size of structures that radiate those signals. However, there are a number of other factors impinging on the evolution of call frequency besides increasing the amount of energy that reaches the female. Initially, it seems that acoustic signals used in mate attraction offer the ideal system for investigating energetic constraints on animal behavior because of the demonstrated effect of acoustic energy received by the female on male fitness. But this system does not act in isolation, and this should serve as a caveat to investigations that address energetic requirements and constraints of behavior in isolation from the animal's ecology, social behavior, and morphology. However, the data gathered by several authors on the spring peeper suggest that hopes for an integrative understanding of this issue are not in vain. Furthermore, the high energetic costs of calling have been suggested as supporting the good genes hypotheses in opposition to the sexual selection hypothesis for the evolution of mate choice. Consideration of results that could result from studies of calling energetics and mate choice suggest that logic is not warranted.

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