J. exp. Biol. **116**, 47–52 (1985)
Printed in Great Britain

ENERGETIC EFFICIENCY OF VOCALIZATION BY THE FROG *PHYSALAEMUS PUSTULOSUS*

BY MICHAEL J. RYAN*

Museum of Vertebrate Zoology, University of California, Berkeley, California 94720, U.S.A.

Accepted 4 September 1984

SUMMARY

1. Male *Physalaemus pustulosus* consume, on average, 1·2 μl of oxygen in the production of a single call, which is equivalent to an energy input per call of 0·024 J.

2. The total power of complex calls, which can have a varying number of components, ranged from 0·36 to 0·46 mW. The total acoustic energy contained in these complex calls ranged from 0·12 to 0·30 mJ.

3. The energetic efficiency of the vocalizations ranged from 0·5 to 1·2%, which is similar to the range estimated for some other animals.

4. The low energetic efficiency of vocalization by these frogs is due, in part, to the fact that the wavelengths of the call are too long, relative to the size of the frog, to be radiated efficiently.

5. Although shorter wavelengths (higher frequencies) are radiated by the frog at relatively greater intensities, longer wavelengths (lower frequencies) attenuate less rapidly in the environment. It is suggested that selection generated by the acoustics of the environment favours calls with lower frequencies, but the morphology of the animal sets a lower limit to which frequencies can evolve.

INTRODUCTION

Acoustic signals are widespread in the animal kingdom, and their biological importance has been demonstrated conclusively. The process that gives rise to acoustic signals involves the transformation of metabolic energy to acoustic energy. Recent research has suggested that the amount of energy utilized in the production of acoustic displays might be an important constraint on male reproductive behaviour (Arak, 1983; Bradbury, 1983; Ryan, Bartholomew & Rand, 1983; Woolbright, 1983) and, in some cases, the amount of acoustic energy in the signal has an important influence on the male's ability to attract mates (Rand & Ryan, 1982; Sullivan, 1982; Arak, 1983; Ryan, 1985). Therefore, it is of considerable interest to know the efficiency with which animals convert metabolic energy to acoustic energy.

In principle, estimates of the energetic efficiency of sound production are straightforward: the amount of energy contained in the acoustic signal is compared to the

* Present address: Department of Zoology, University of Texas, Austin, Texas 78712, U.S.A.
Key words: Vocalizations, energetics, Anuran.

amount used to produce the signal. However, because of the difficulty in determining energy expenditures associated with acoustic signalling, this comparison has only been made with insects (Prestwick & Walker, 1981; MacNally & Young, 1981). Brackenbury (1977) has estimated the energetic efficiency of crowing in a chicken by comparing the total fluid energy losses in the syrinx with the resulting acoustic energy. This is the only estimate of the energetic efficiency of acoustic signal production available for a vertebrate.

The purpose of this paper is to estimate the energetic efficiency of vocalization by a frog, *Physalaemus pustulosus* (Leptodactylidae). These data will provide a better understanding of the energetic constraints on the reproductive and communication behaviour of a vertebrate species for which there already exists a significant amount of information on other aspects of these behaviour patterns (e.g. Ryan, 1980, 1983; Ryan, Tuttle & Rand, 1982; Ryan *et al.* 1983; and reviewed in Ryan, 1985), and will shed some light on the general role of morphological and physiological constraints in the evolution of animal vocalizations.

The call

P. pustulosus produces a vocalization that consists of two components, a 'whine' and a 'chuck'. In a typical call, the whine is 400 ms in duration, and its dominant frequency sweeps from 900 to 400 Hz. There is some energy in the second and third harmonics of the fundamental. The chuck is 40 ms long, has a fundamental frequency of 230 Hz, and has energy in 12–14 harmonics of the fundamental. Calls contain a whine and from 0–6 chucks. All males can produce complex calls (i.e. calls with chucks), and call complexity increases with the number of males vocalizing at the breeding site (Rand & Ryan, 1982).

MATERIALS AND METHODS

Estimates are available for the amount of oxygen consumed, above that needed for maintenance, by a male *P. pustulosus* during vocalization (Bucher, Ryan & Bartholomew, 1982). Ryan *et al.* (1983) showed that anaerobiosis does not contribute significantly to the energetic support of vocalizations, and this contribution is ignored in the following calculations. Therefore, assuming that the consumption of 1 ml oxygen yields 20·10 J, I estimated the energy utilized for the production of a single call.

Ryan (1985) provided measures of the peak sound pressure level of complex calls of five *P. pustulosus* males. At least 20 calls of each male were measured with a General Radio model 1982 sound pressure level meter set at peak reading. Measurements were made directly in front of the male at a distance of 0·5 m. The median peak sound pressure was 90 dB SPL (re. 2×10^{-5} N m^{-2}), the median for individuals ranged from 88 to 91 dB SPL. Examination of oscillographs of various calls with chucks shows that peak voltage occurs during the chuck. Sound pressure level can be converted to power (dB SPL = 10 antilog (W1/Wo), where Wo is 10^{-12} W). Therefore, the peak voltage of the call, which corresponded to a peak sound pressure of 90 dB SPL, has a power of

1 mW. I used an Apple II computer and digitizer to determine the mean voltage of the calls with 1, 2, 3 and 4 chucks presented in Fig. 1. Although there is variation in the waveform, and thus the energy content, of calls within and among males, the calls

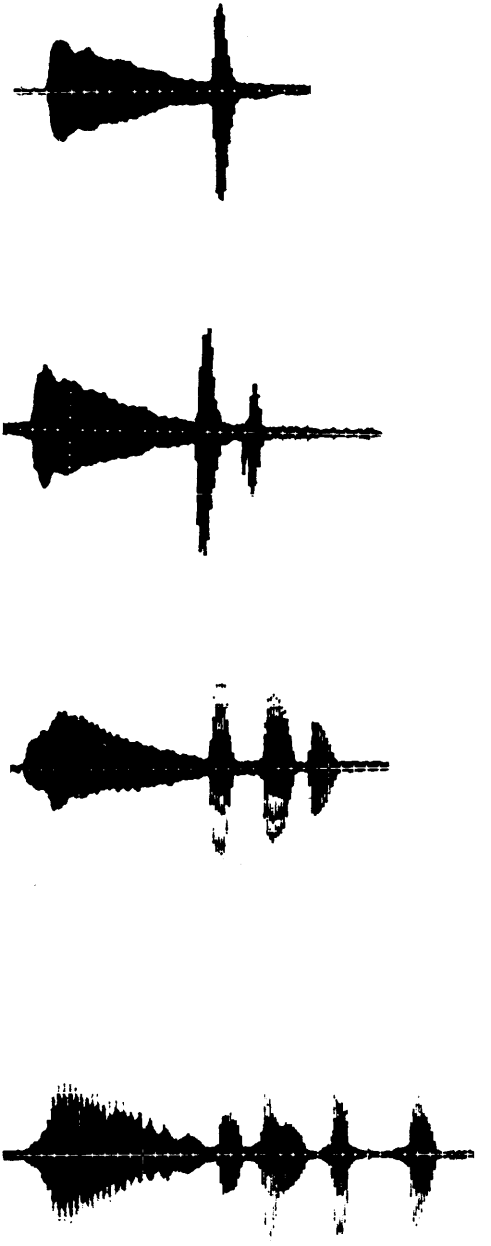

Fig. 1. Oscillograms of the advertisement calls of *Physalaemus pustulosus* containing various numbers of chucks (1–4) used to determine energy output. Call durations are presented in Table 1.

presented in Fig. 1 are typical. They do not necessarily represent statistical means. Since power and volts are both linear measures, I used average volts to estimate the average power of each call (peak voltage/average voltage = 1 mW/average power).

The total power of the call is a product of the power at the point of measurement and the area over which the call is radiated. I assumed that the frog is an omnidirectional source (this is true of some frogs but others radiate more energy from the front, Gerhardt, 1975), and that water, the substrate from which the frog calls, is a totally reflective surface. Therefore, the call is radiated over a hemisphere with an area of $2\pi r^2$, where, in this case, $r = 0{\cdot}5$ m. The violation of the first assumption (i.e. if the intensity of the call is greater in front of the frog than in other directions) would result in an overestimate of the power of the calls. This method used to estimate the total power of the call gives the same results as an alternative method provided by MacNally & Young (1981).

Power is the rate at which energy is expended. Since $W = J\,s^{-1}$, the total energy of the call is estimated by the product of the total power and the call duration. The energetic efficiency of vocalization is simply: (energy output/energy input) × 100 %.

RESULTS

Bucher *et al.* (1982) showed that the amount of oxygen consumed during calling was highly dependent on the number of calls produced, but was not significantly influenced by the number of chucks produced. Therefore, estimates of the amount of energy expended to produce a call do not vary with the number of chucks. However, they do vary with the calling rate, which ranged from 1·3 to 22·6 calls min^{-1}. Males calling at a greater rate consume less oxygen per call, ranging from 0·5 to 1·9 μl. To estimate energy input, I used the mid-range value of 1·2 μl of oxygen consumed per call, which yields an energy input equivalent of 0·024 J.

The average power of calls with 1, 2, 3 and 4 chucks was 0·23, 0·24, 0·29 and 0·28 mW, respectively. The area of the hemisphere over which the call was radiated was 1·57 m^2, giving total powers which ranged from 0·36 to 0·46 mW (Table 1). Both call duration and the total amount of energy in the call increased with the number of chucks. Total energy ranged from 0·12 to 0·30 mJ (Table 1).

Since the energy input per call did not increase with the number of chucks, and since calls with more chucks contained more energy, metabolic energy was coupled to

Table 1. *Total power, energy and energetic efficiency for calls of* Physalaemus pustulosus *with various numbers of chucks*

Call	Total power (mW)	Call duration (s)	Total energy (mJ)	Energetic efficiency (%)
Whine + 1 chuck	0·36	0·34	0·12	0·5
Whine + 2 chucks	0·37	0·40	0·15	0·6
Whine + 3 chucks	0·46	0·54	0·25	1·0
Whine + 4 chucks	0·44	0·69	0·30	1·2

Energetic efficiencies assume an energy input of 0·024 J/call.

acoustic energy more efficiently in calls with more chucks. The energetic efficiencies ranged from 0·5 to 1·2 %.

DISCUSSION

The production of vocalizations by *P. pustulosus* is a very inefficient process. This appears to be true for the generation of animal acoustic signals in general, regardless of the physical structures involved. Brackenbury (1977) estimated that the efficiency of crowing in a chicken is 1·6 %. MacNally & Young (1981) estimated that the energetic efficiency of sound production in the cicada, *Cystosoma saundersii*, is 0·8 %. Reviewing the available data, they suggested it was unlikely that any insects have efficiencies greater than 10 %. Wood (1962), without presenting data, stated that the efficiency of the human voice is 1 %.

In part, the coupling of metabolic energy to acoustic energy is inefficient because animals often produce sounds with wavelengths that are long relative to the size of the radiating structures, and longer wavelengths are radiated less efficiently. For example, the whine component of the *P. pustulosus* call has a dominant frequency that is modulated from 900 to 400 Hz. Ryan (1985) used standard equations to calculate the cut-off frequency for a radiator (Beranek, 1954). The cut-off frequency defines the efficiency with which a spherical radiator transmits sounds of different frequencies. Energy in frequencies above the cut-off frequency is transmitted with maximum efficiency, while below this cut-off frequency the radiation efficiency is drastically reduced. It is not known which parts of the frog radiate sound, although the vocal sac probably is of primary importance (Martin, 1972). If we assume that the entire frog radiates the sound, this gives the lowest cut-off frequency, which for *P. pustulosus* is 3500 Hz. Clearly, most of the energy in the call is not radiated at maximum efficiency. This species probably is capable of producing calls with higher frequencies. *P. pustulosus* should be able to maintain the tension on the vocal cords, which results in the higher frequencies at the onset of the whine (Drewry, Heyer & Rand, 1982), for the entire call. Also, for its size, *P. pustulosus* has a call with much lower frequencies than any other closely related species examined (Ryan, 1985). This suggests that there has been an evolutionary change to call frequencies that are transmitted less efficiently.

Although higher frequencies are radiated at relatively greater intensities by the frog, lower frequencies generally attenuate less rapidly in the environment (Michelson, 1978; Wiley & Richards, 1978). Since the energy content at the receiver, not at the source, is under selection (Rand & Ryan, 1982; Sullivan, 1982; Arak, 1983; Ryan, 1985), the acoustical properties of morphology and environment are in conflict (see also MacNally & Young, 1981). Selection generated by the environment favours calls with low frequencies but the morphology of the animal sets a lower limit to which frequencies can evolve.

I am grateful to E. Brenowitz, E. Lewis and S. Rand for discussions and to G. Bartholomew, T. Bucher, S. Rand, K. Troyer and D. Wake for comments on the manuscript. Financial support was provided by a fellowship from the Miller Institute for Basic Research in Science.

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