

SHORT COMMUNICATION

Energetic cost of calling: general constraints and species-specific differences

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Abstract

The energetic cost of acoustic signalling varies tremendously among species. Understanding factors responsible for this heterogeneity is important for understanding the costs and benefits of signalling. Here, we present a general model, based on well-established principles of bioenergetics, which predicts the energetic cost of call production across species. We test model predictions using an extensive database of resting and calling metabolic rates of insects, amphibians and birds. Results are largely supportive of model predictions. Calling metabolic rates scale predictably with body mass and temperature such that calling and resting metabolic rates are directly proportional to each other. The cost of acoustic signalling is ~ 8 times higher than resting metabolic rate in ectotherms, and ~ 2 times higher in birds. Differences in the increase in metabolic rate during calling are explained by the relative size of species' sound-producing muscles. Combined with published work, we quantify call efficiency and discuss model implications.

Introduction

The concept of evolutionary fitness provides a unifying basis for the study of behavioural ecology in general and animal communication in particular. Nevertheless, defining the concept of fitness is challenging (e.g., Arnold & Wade, 1984a,b). Some biologists have suggested that it may be helpful to quantify individual fitness in energetic terms (Brown *et al.*, 1993). Indeed, Boltzmann (1872) argued 'the struggle for existence is a struggle for free energy available for work'. In the study of animal communication, the energetic cost of producing a signal can take many forms, from the neuromuscular control of signal production to the investment and maintenance of specialized structures to produce sounds (Bradbury & Vehrencamp, 1998). All such costs are ultimately constrained by an organism's metabolic rate, or the rate at which an animal utilizes energy for survival, growth and reproduction (Brown *et al.*, 2004).

Among the various forms of animal communication, acoustic signalling is the most pervasive. It can be seen, to varying degrees, in every major taxonomic group and across virtually all environments. While there is general agreement that acoustic signalling is energetically costly (e.g., Taigen *et al.*, 1985; Halliday, 1987; Prestwich *et al.*, 1989) and that these costs vary considerably among species (Prestwich *et al.*, 1989; Wells, 2007), a general quantitative model describing these costs has remained elusive. Such a model would increase our understanding of the fitness costs and benefits of acoustic signalling and provide a baseline for interspecific comparisons.

We propose a model of the energetic cost of acoustic signal production, based on principles of bioenergetics, which yields general, quantitative predictions on the cost of calling for diverse species from different environments. The model builds on the well-established relationship of individual metabolic rate to body size and temperature, and more recent work showing that spectral and temporal call features of acoustic signals, including call frequency, duration and rate, show about the same body-size and temperature-dependencies as metabolic rate (Gillooly & Ophir, 2010). We first evaluate the model by compiling and analysing published data that report both

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metabolic rates at rest and during call production. Evaluating the model using these data allows us to quantify the average energetic cost of signal production in insects, amphibians and birds. We then assess the extent to which observed differences in the relative cost of signal production within and across these taxonomic groups are explained by the relative size of sound-producing muscles among species. This follows from a previously proposed hypothesis that total metabolic demand is governed by the size of the muscles producing the sound (Wells, 2007). Finally, we combine our results with recently published work on call power to calculate average call efficiency for amphibians, insects and birds.

Model development and predictions

The model presented here links the energetic cost of signal production to the body-size and temperature-dependence of whole-organism metabolic rate. To begin, we assume that whole-organism resting metabolic rate, B , scales with body mass, M (g), to the $3/4$ power and exhibits an exponential temperature-dependence described by the term $e^{-E/kT}$. Thus:

$$B = b_0 M^{3/4} \cdot e^{-E/kT_B} \quad (1)$$

where b_0 ($W/g^{3/4}$) is a normalization constant independent of body size and temperature, and varies among taxonomic groups. The Boltzmann–Arrhenius factor, $e^{-E/kT}$, describes the exponential temperature-dependence of the biochemical reactions that govern metabolism, whereby E is the average activation energy of the respiratory complex (~ 0.65 eV), k is Boltzmann's constant ($8.62 \cdot 10^{-5}$ eV K^{-1}), and T_B is absolute temperature at rest in Kelvin (K) (Gillooly *et al.*, 2001). The $3/4$ power scaling for whole-organism metabolic rate assumed by the model describes only the central tendency among species and does not explain variation about this average. Still, this central tendency is strongly supported empirically (Kleiber, 1932; Hemmingsen, 1960; Gillooly *et al.*, 2001; Savage *et al.*, 2004), and consistent with different theoretical predictions (West *et al.*, 1997; Banavar *et al.*, 1999). We extend this model to predict calling metabolic rates by assuming that the energetic cost of calling shows the same size and temperature-dependence as resting metabolic rate such that calling metabolic rate (C , in W) is described by the following equation:

$$C = c_0 M^{3/4} \cdot e^{-E/kT_C} \quad (2)$$

where T_C is absolute temperature when calling, and c_0 ($W/g^{3/4}$) is a normalization constant that is independent of body size and temperature and varies among taxonomic groups. Together, eqns 1 and 2 indicate that temperature-corrected calling metabolic rate will be directly proportional to temperature-corrected resting

metabolic rate as they both exhibit the same body size dependencies, such that:

$$C \cdot e^{E/kT_C} \propto B \cdot e^{E/kT_B} \quad (3)$$

Furthermore, in most cases, where the temperatures at rest and during calling are the same, C will simply differ from eqn 1 by a constant.

Our theoretical framework leads to four predictions with respect to calling metabolic rate and its relationship to resting metabolic rate, body size and temperature. First, following eqn 2, we predict that a plot of the natural logarithm of temperature-corrected calling metabolic rate (i.e., $\ln(C \cdot e^{E/kT_C})$) versus the natural logarithm of body mass should yield a linear relationship with a slope of $3/4$, reflecting the constraints of individual metabolic rate on the energetics of call production. Second, following eqn 2 we predict that a plot of the natural logarithm of mass-corrected calling rate (i.e., $\ln(C \cdot M^{-3/4})$) versus $1/kT$ should yield a linear relationship with a slope of about -0.65 , reflecting the average temperature-dependence for resting metabolic rates (Gillooly *et al.*, 2001). Third, given the common body size dependence of Eqs. 1 and 2, we predict that a plot of the natural logarithm of temperature-corrected calling metabolic rate versus the natural logarithm of temperature-corrected resting metabolic rate should yield a linear relationship with a slope of 1 reflecting the proposed proportionality between calling and resting metabolic rates (see eqn 3). Finally, fourth, we predict that the fold-increase in metabolic rate from resting to calling among species (i.e., metabolic scope; CMR/RMR) will be directly related to the relative size of sound-producing muscle among species, as proposed by Wells (2007).

Material and methods

We test predictions 1–3 using published data on calling and resting metabolic rates from 38 species (13 birds, 14 insects, and 11 frogs). We test prediction 4 using data for 12 species for which reports of sound-producing muscle mass, and calling and resting metabolic rates were available (Appendix S1). To the best of our knowledge, we have included all published data reporting calling and resting metabolic rates and those reporting sound-producing muscle mass. Most calls considered here were for purposes of courtship.

Species ranged in size from 0.06 g for the cricket *Oecanthus quadripunctatus* to 428 g for the bird *Corvus mellori* (Appendix S1). Body temperatures of ectotherms were assumed to be equivalent to ambient temperature (range: 9.9–29 °C) during both resting and calling, except in those few cases where calling body temperatures were reported as being significantly higher than those at rest (e.g., katydids and cicadas; $n = 3$). Body temperatures of birds were assumed to be a constant 40 °C. Because the normalization constants, b_0 , are different for endotherms

and ectotherms (Hemmingsen, 1960; Gillooly *et al.*, 2001), we separated birds from insects and amphibians in most analyses. Note that the nonindependence of calling and resting temperature estimates allowed us only to assess the temperature-dependence of calling metabolic rates in prediction 2.

All studies used in our analyses estimated metabolic rates, either during calling or at rest just prior to calling, by measuring oxygen consumption rates, which were then converted to watts (W) using the standard conversion factor of $20.1 \text{ J mL}^{-1} \text{ O}_2$. Generally, oxygen consumption was measured by passing air through a plastic chamber, and a gas meter was used to measure the flow rate of ambient air into and out of the chamber. The rate of oxygen consumption was then calculated by taking the difference between the fractional O_2 content of the ambient air and the excurrent air. For more details about specific methodologies of individual studies, see references listed in Appendix S1.

Results and discussion

Data are largely supportive of predictions. Following Prediction 1, the natural logarithm of temperature-corrected calling metabolic rate is linearly related to the natural logarithm of body mass. For all taxonomic groups, the slopes of the fitted lines are statistically indistinguishable from the predicted slope of $3/4$ (ectotherms: 0.74, CI = 0.55 to 0.92; endotherms: 0.74,

CI = 0.64–0.84) (Fig. 1a, b, in red). The relationships account for 67% of the variation in calling metabolic rate among ectotherms, and 96% of the variation among endotherms. Moreover, in both cases, the body-size dependence observed for temperature-corrected calling metabolic rate are not significantly different than those observed for resting metabolic rate, with slopes of 0.67 (CI = 0.55–0.79) for ectotherms and 0.74 (CI = 0.61–0.87) for endotherms (Fig. 1a, b, in blue). Following Prediction 2, the natural logarithm of mass-corrected calling metabolic rate is linearly related to inverse absolute temperature ($1/kT$), with a slope (-0.76 , CI = -1.10 to -0.42 , $r^2 = 0.40$) that is statistically indistinguishable from the predicted slope of -0.65 (Fig. 1c). Following Prediction 3, the natural logarithm of temperature-corrected calling metabolic rate is nearly linearly related to the natural logarithm of temperature-corrected resting metabolic rate in both groups such that the observed slopes are statistically indistinguishable from the predicted slope of 1.0 (Fig. 2; ectotherms = 1.05, CI = 0.83–1.27; endotherms = 0.97, CI = 0.83–1.10). Resting metabolic rate explains 76% and 96% of the variation in calling metabolic rates among ectotherms and endotherms, respectively. Finally, in agreement with Prediction 4, metabolic scope increases with the relative size of sound-producing muscle among species ($r^2 = 0.63$; Fig. 3).

These results show that the energetic cost of call production across species is directly proportional to

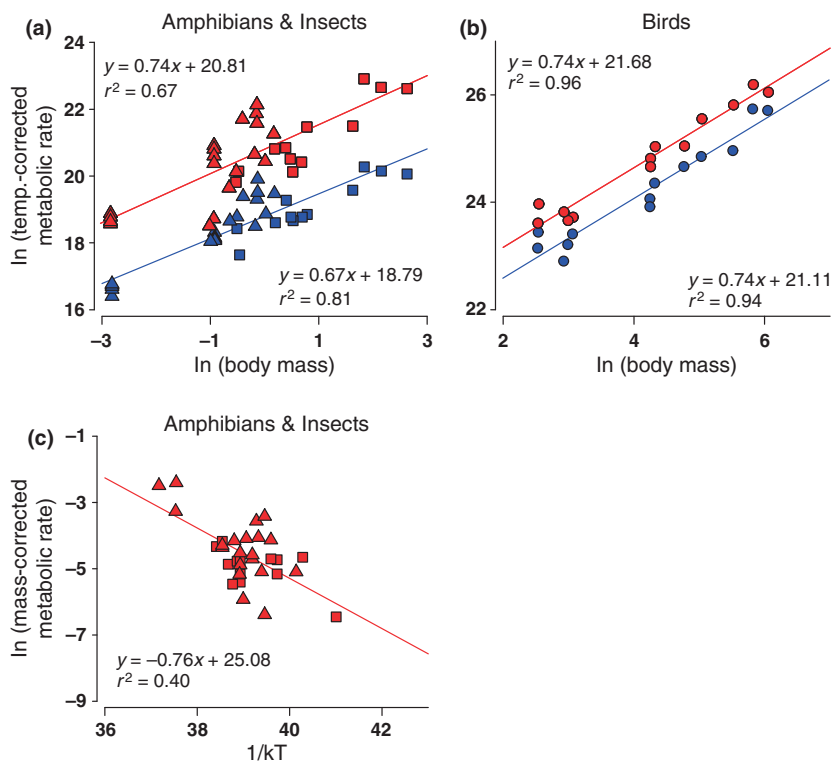


Fig. 1 Prediction 1 (panels A and B) – Effects of body size on temperature-corrected resting (blue; eqn 1) and calling (red; eqn 2) metabolic rates (in Watts) for (a) amphibians (boxes; $n = 11$) and insects (triangles; $n = 20$), and (b) birds (circles; $n = 13$). Prediction 2 (panel C) – Effects of temperature on mass-corrected calling metabolic rate for amphibians and insects (eqn 2). Note that eqns 1 and 2 predict slopes of 0.75 for both panels A and B, and -0.65 for panel C, based on the constraints of body size and temperature on individual metabolism. Body size and temperature corrections were performed on metabolic rates based on the formulas in eqns 1 and 2, as described in the Appendix S1.

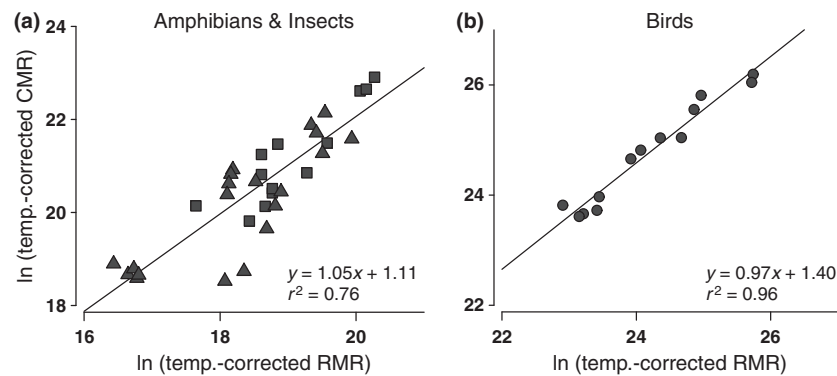


Fig. 2 Prediction 3 – Relationship between temperature-corrected calling and resting metabolic rates (in Watts). The natural logarithm of temperature-corrected calling metabolic rate (CMR) versus the natural logarithm of temperature-corrected resting metabolic rate (RMR; eqn 3) for (a) amphibians (boxes) and insects (triangles), and (b) birds (circles). Note that eqn 3 predicts a slope of 1.0 for both panels A and B. Temperature corrections were performed on metabolic rates based on the formulas in eqns 1 and 2, as described in the Appendix S1.

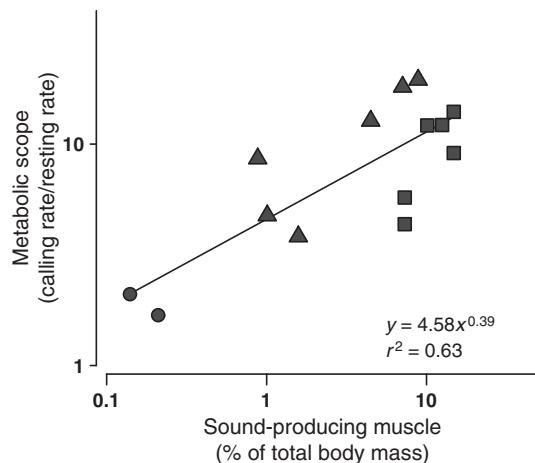


Fig. 3 Prediction 4 – Relationship between metabolic scope and the percentage of total body mass that is comprised of sound-producing muscle (sound-producing muscle (g)/total body mass (g) · 100) for amphibians (boxes), insects (triangles), and birds (circles). Metabolic scope is defined as the factorial increase from resting to calling metabolic rate.

resting metabolic rate, and thus varies predictably with both body size and temperature. Calling metabolic rate increases as a power law function with body mass, with an exponent of about 0.75, and increases exponentially with temperature such that a 10 °C increase in temperature leads to an approximately 2.5 fold increase in calling metabolic rate. Differences in the intercepts in Fig. 1a, b indicate that, among all species, the cost of calling is substantial. Birds show the lowest cost of calling, but even among this group, the observed two-fold increase in metabolic rate during calling is about the same as that described for egg production (King, 1973).

Across all groups, metabolic scope is quite variable, ranging from the two-fold difference observed in birds to

an average difference of eight-fold in ectotherms – even after correcting for temperature. Much of this difference is explained by the relative size of the sound-producing muscle that is active during calling (Fig. 3). For instance, whereas on average the call muscles of the frogs and insects considered here are about 10% and 4% of their total body mass respectively, a bird's syrinx is only about 0.2% of its total body mass.

Our results can be extended to better understand and quantify average call efficiency, which has been broadly discussed but rarely quantified (Prestwich, 1994). We do this by combining the current results with those recently published describing the size and temperature-dependence of call power (Gillooly & Ophir, 2010); to this end, in Fig. 4 we present the fitted lines for a log-log plot of body mass versus temperature-corrected call power from (Gillooly & Ophir, 2010) and temperature-corrected calling metabolic rate from Fig. 1a–b. From these lines, one may quantify the average percent call efficiency in ectotherms and birds, where percent call efficiency is defined as the energy in the call divided by the energy used to produce the call, multiplied by 100. Results of this analysis indicate that, on average, call efficiency is low and approximately invariant with respect to body size. The low efficiency for frogs and insects (2.26%) and birds (0.95%) observed here is in agreement with values previously reported for individual species (e.g., Prestwich, 1994).

We do not mean to imply that size and temperature alone explain all species-specific differences in the results shown in Fig. 1–4. Certainly, many other factors likely contribute to the remaining variation. For example, some of the variation among insects can likely be explained by the fact that flying insects considered here have metabolic rates that are considerably higher than nonflying insects, as previously shown (Reinhold, 1999). Residual variation about the fitted lines may also reflect fitness-enhancing trade-offs in energy expenditure related to call

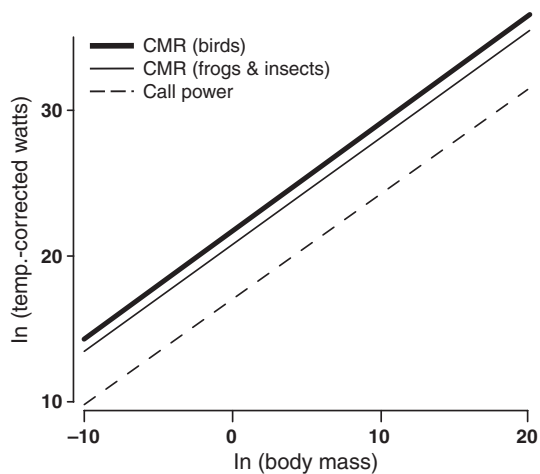


Fig. 4 Effects of body size on calling metabolic rates and sound power. The natural logarithm of temperature-corrected calling metabolic rate (CMR) in Watts (solid lines) for birds (thick line) and frogs and insects (thin line) is compared with the natural logarithm of temperature-corrected sound power in Watts (dashed line; from Gillooly & Ophir, 2010). Both factors are plotted against the natural logarithm of body mass (grams). The equations for the lines of calling metabolic rates are presented in Fig. 1; the equation for the line of sound power (in W) is $y = 0.72x + 17.02$, $n = 48$ (Gillooly & Ophir, 2010). Temperature corrections were performed based on the formulas in eqns 1 and 2, as described in the Appendix S1, and those described in Gillooly & Ophir (2010).

production (Endler, 1992; Prestwich, 1994; Dawkins & Guilford, 1996; Ryan, 1998). In particular, residual variation may be indicative of the influence of selection operating on signals themselves to the extent that signal honesty may be related to the energetic cost of calling (Zahavi, 1975; Grafen, 1990; Maynard Smith & Harper, 1995, 2003; Searcy & Nowicki, 2005; but see Hurd, 1995). In all such cases, these examples show how this model and these results may provide a useful point of departure for quantifying the proximate and ultimate factors that contribute to differences in the energetics of acoustic signalling among species that vary in size or temperature.

The theory and data presented here may provide another small step towards a more general theory of acoustic signalling that is directly linked to individual physiology. Building on the tremendous progress in acoustic communication research focused on closely related species (e.g., Ryan, 1988; Prestwich, 1994; Sanborn, 1997), we recently proposed a series of mathematical models that predict many basic features of diverse animal calls based on the constraints of size, temperature and metabolic rate on muscle dynamics (Gillooly & Ophir, 2010). Here, we extend that theoretical framework by presenting mathematical models, which are similar in form, to predict the energetic cost of calling and call efficiency among different taxonomic

groups. As in our previous study, viewing animal communication through a macro-scale lens points to common constraints and species-specific differences underlying the energetics of call production.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Data shown in Figures 1–3.

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