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Energetic cost of communication

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Summary

Communication signals may be energetically expensive or inexpensive to produce, depending on the function of the signal and the competitive nature of the communication system. Males of sexually selected species may produce high-energy advertisement signals, both to enhance detectability and to signal their size and body condition. Accordingly, the proportion of the energy budget allocated to signal production ranges from almost nothing for many signals to somewhere in excess of 50% for acoustic signals in short-lived sexually selected species. Recent data from gymnotiform electric fish reveal mechanisms that regulate energy allocated to sexual advertisement signals through dynamical remodeling of the excitable membranes in the electric organ. Further, males of the short-lived sexually selected species, *Brachyhypopomus gauderio*, trade off among different metabolic compartments, allocating energy to signal production while reducing energy used in other metabolic functions. Female *B. gauderio*, by contrast, do not trade off energy between signaling and other functions. To fuel energetically expensive signal production, we expect a continuum of strategies to be adopted by animals of different life history strategies. Future studies should explore the relation between life history and energy allocation trade-offs.

Key words: *Brachyhypopomus,* communication, electric fish, energetics, Gymnotiformes, life history, trade-off.

Introduction

The structure and function of animal communication signals, like all traits, can be subject to physiological constraints and limits. Energetic costs of signals have interested those who work on the interface between evolution, behavior and physiology because signal costs can be measured more readily than many other socially relevant behaviors. Across the suite of signal forms, the amount of energy that animals allocate to communication signals depends on a suite of physical and life history factors (Fig. 1). For instance, passive visual signals, such as colorful plumage or iridescent scales (Endler and Thery, 1996; Rutowski et al., 2010), should require the least energy investment on the part of the signaler, because the sun provides the energy in the signal, although pigment accumulation or growth of diffracting structures may entail other nutritional or developmental costs (Andersson, 2000; Fitzpatrick, 1998; McGraw, 2006). Conversely, during bouts of active broadcast, mate-attraction signals can exceed the rest of the animal's energy budget. Where the interests of signaler and receiver are strategically aligned (Searcy and Nowicki, 2005), communication should be cooperative and signals should be as efficient as possible (signals to alert relatives of predators may be an exception, because the stakes are so high). By contrast, when interests of signaler and receiver differ, as occurs under sexual competition, the signaler may be under pressure to allocate considerable energy to signals. In such cases, high-energy signaling can be promoted through either of two mechanisms: efficacy or conspicuous consumption. Signals of efficacy are those in which a stronger signal is more effective for physical or physiological reasons, rather than for social or informational reasons (Maynard-Smith and Harper, 2003). Louder signals can be effective because they command a larger active space (detectable area), aiding in territorial defense or advertisement to distant conspecifics (Brenowitz, 1986). Alternatively, louder signals may be effective at close range because they render the signaler more impressive to prospective mates or rivals by providing more stimulation to the receiver's sensory system (Brenowitz, 1989). Researchers have shown that increasing signal amplitude can substitute for tuning the signal to

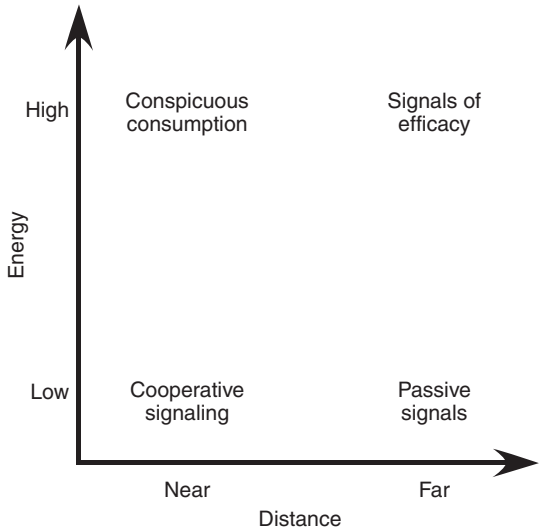

Fig. 1. Close-range and long-range communication signals may be either high- or low-energy, depending on their function. At close range, high-energy signals may indicate energy availability through conspicuous consumption, indicating the quality of the signaler. Conversely, high-energy signals may render the signal more efficacious by increasing the transmission distance or by increasing the degree of sensory stimulation at any range. Low-energy signals include visual signals and cooperative signals, where the interests of the signaler and the receiver are strategically aligned.

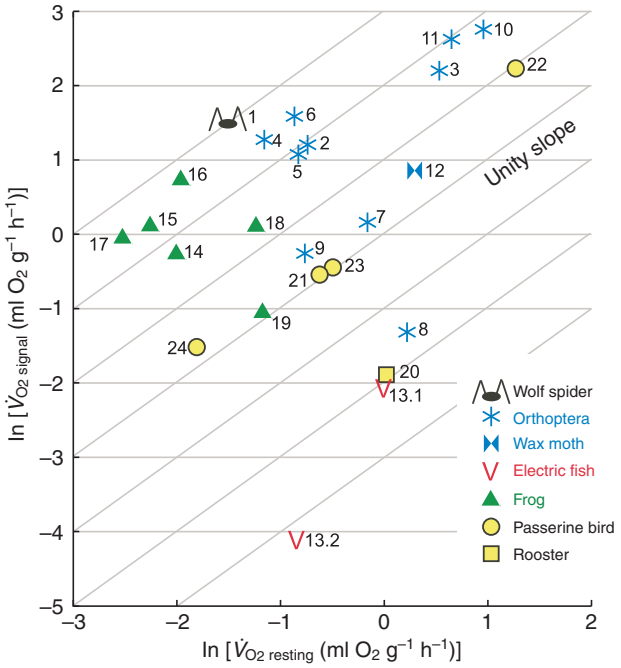

Fig. 2. Energetics of signal production relative to energy at rest, expressed as the natural log of oxygen consumption. Horizontal lines represent equivalent energy expenditure on signals; diagonal lines represent equal proportion of energy allocated to signal and metabolism at rest (equal factorial scope). Comparative data can be viewed two ways, either by the total energy devoted to signaling (*y*-axis only) or as a ratio of energy in the signal versus energy used at rest (diagonal isolines). Considering only mass-specific energy of signaling, Orthoptera have the highest energy consumption, whereas a wolf spider, Orthoptera and frogs use the greatest amount of energy to signal relative to their baseline metabolism. See Table 1 for species numbers.

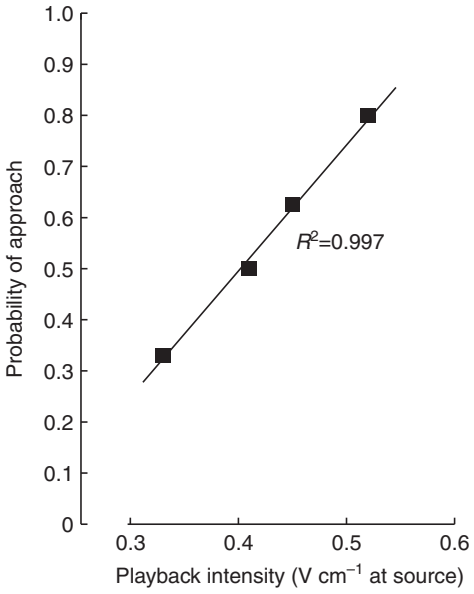

Fig. 3. Stronger signals are more effective in territorial electric fish. In nighttime field trials in a stream in the Venezuelan Llanos, male *Brachyhypopomus diazi* approached a playback electrode playing a conspecific signal over the range of natural intensities recorded for this species. Approach probability was in linear proportion to stimulus intensity. The results shown here are for a single male; data are means of eight 60-s trials per voltage. The interpretation is ambiguous: higher voltages could elicit a greater chance of approach because they signal a greater threat or because they command a larger active space and are more readily detected (P.K.S., unpublished).

the optimal part of the sensory spectrum in determining the attractiveness functions of a signal (Gerhardt, 2005; Ritschard et al., 2010). In such cases, signal intensity can be favored because it increases sensory stimulation, potentially over a range of distances. The concept of conspicuous consumption is that individuals consume resources to show their wealth (Veblen, 1899). Applied to signaling, strong signals may impress receivers because the energy consumed by the signal reflects general energy availability in the signaler, an honest indicator of the signaler's physical condition (Salazar and Stoddard, 2008), in keeping with handicap models (Grafen, 1990; Zahavi, 1975; Zahavi, 1977).

Comparative data

Biologists have carried out an unofficial contest to identify the creature that allocates the greatest amount of energy to its communication signals. Unfortunately, we have no data from the other end of the energy continuum; nobody has measured signal costs of passive and cooperative signalers because those costs have always been assumed to constitute an insignificant fraction of the energy budget. Even within the high end of the energy continuum, both absolute and relative energetic signal costs vary across three orders of magnitude (Table 1, Fig. 2). In terms of absolute costs, male orthopterans (e.g. the trilling katydid) expend the most energy per unit mass producing their acoustic mate attraction signals, followed by a notably loud and hyperactive woodland passerine, the Carolina wren. By comparing the ratio of energy for signal production to energy spent at rest, we can establish an index to compare the relative effort put into signaling (compare along diagonal isolines in Fig. 2). Here we see that male wolf spiders, orthopterans and hylid treefrogs put the most energy into signals relative to their resting metabolisms. Passerine birds have a relatively constant ratio. Roosters and male electric fish are tied, both in terms of absolute and relative metrics. Female electric fish use the least energy for signaling. As with bat navigational sonar, navigation signals in electric fish are a negligible fraction of the total energy budget (Julian et al., 2003; Speakman et al., 1989; Speakman and Racey, 1991).

The gymnotiform case study – comparing signal costs by sex

Gymnotiform electric fish warrant a closer look because we have data on energetic costs of signal production for both sexes. Gymnotiform electric fish signal around the clock for electrolocation, but also signal for social function during their hours of activity, primarily at night. Three of the five gymnotiform families can modulate the power in their signals by remodeling the excitable membranes in their electrogenic cells in accordance with the prevailing social conditions through the fast actions of melanocortin peptides (Franchina et al., 2001; Markham et al., 2009; Markham and Stoddard, 2005). Stronger signals command more active space in territorial species and may be more potent in social interactions because they provide greater stimulation to receivers at close range; increasing active space and increasing stimulation are not mutually exclusive benefits of stronger signals. An example of the effect of signal amplitude on male territorial behavior is seen in field playback trials on territorial male gymnotiform electric fish (Fig. 3). Male

Table 1. Energetic costs of signal production and resting metabolic rate are shown for 24 species for which we found comparable data

Sp. no.	Species	Common name	Signal type	$\dot{V}_{O_2\,signal}$ (ml O_2 g^{-1} h^{-1})	$\dot{V}_{O_2\,resting}$ (ml O_2 g^{-1} h^{-1})	Signal factorial scope ($\dot{V}_{O_2\,signal}/\dot{V}_{O_2\,resting}$)	Reference
Arachnida – Araneae							
1	*Hygrolycosa rubrofasciata*	Wolf spider	Drumming	4.580	0.220	20.82	Kotaho et al., 1998
Insecta – Orthoptera							
2	*Anurogryllus arboreus*	Trilling short-tailed cricket	Acoustic call	3.576	0.315	11.35	Prestwich and Walker, 1981
3	*Anurogryllus muticus*	Trilling cricket	Acoustic call	9.060	1.700	5.33	Lee and Loher, 1993
4	*Gryllotalpa australis*	Trilling cricket	Acoustic call	4.883	0.420	11.63	Kavanagh, 1987
5	*Oecanthus celerinictus*	Trilling tree cricket	Acoustic call	2.931	0.437	6.71	Prestwich and Walker, 1981
6	*Oecanthus quadripunctatus*	Trilling tree cricket	Acoustic call	3.342	0.476	7.02	Prestwich and Walker, 1981
7	*Teleogryllus commodus*	Chirping cricket	Acoustic call	1.170	0.850	1.38	Lee and Loher, 1993
8	*Teleogryllus oceanicus*	Chirping cricket	Acoustic call	0.270	1.250	0.22	Lee and Loher, 1993
9	*Gryllus lineaticeps*	Chirping variable field cricket	Acoustic call	0.774	0.464	1.67	Hoback and Wagner, 1997
10	*Euconocephalus nasutus*	Trilling katydid	Acoustic call	15.790	2.610	6.05	Stevens and Josephson, 1977
11	*Neoconocephalus robustus*	Trilling katydid	Acoustic call	13.880	1.920	7.23	Stevens and Josephson, 1977
Insecta – Lepidoptera							
12	*Achroia grisella*	Lesser wax moth	Ultrasonic call	2.320	1.340	1.73	Reinhold et al., 1998
Osteichthyes – Gymnotiformes							
13.1	*Brachyhypopomus gauderio*	Feathertail electric fish, male	Electric signal	0.127	0.995	0.13	Salazar and Stoddard, 2008
13.2	*Brachyhypopomus gauderio*	Feathertail electric fish, female	Electric signal	0.016	0.432	0.04	Salazar and Stoddard, 2008
Amphibia – Anura							
14	*Hyla cinerea*	Green treefrog	Acoustic call	0.770	0.135	5.70	Prestwich et al., 1989
15	*Hyla gratiosa*	Barking treefrog	Acoustic call	1.120	0.105	10.67	Prestwich et al., 1989
16	*Hyla squirella*	Squirrel treefrog	Acoustic call	2.110	0.140	15.07	Prestwich et al., 1989
17	*Hyla versicolor*	Grey treefrog	Acoustic call	0.960	0.080	12.00	Taigen and Wells, 1985
18	*Hyperolius viridiflavus*	Painted reed frog	Acoustic call	1.110	0.290	3.83	Grafe et al., 1992
19	*Physalaemus pustulosus*	Túngara frog	Acoustic call	0.350	0.310	1.13	Bucher et al., 1982
Aves							
20	*Gallus gallus domesticus*	Domestic rooster	Crowing	0.150	1.020	0.15	Horn et al., 1995
21	*Ficedula hypoleuca*	Pied flycatcher	Song	0.620	0.550	1.13	Ward et al., 2004
22	*Thryothorus ludovicianus*	Carolina wren	Song	9.300	3.560	2.61	Eberhardt, 1994
23	*Serinus canaria*	Roller canary	Song	0.640	0.610	1.05	Ward et al., 2003
24	*Taeniopygia guttata*	Zebra finch	Song	0.222	0.162	1.37	Franz and Goller, 2003

Some variation can be expected in how restful animals actually are in a respirometry chamber – for instance, some birds sit quietly whereas Carolina wrens are notably jumpy.

Brachyhypopomus diazi cruise their territories at night and will approach and nudge electrodes playing digitized signals played at realistic voltages. The probability that a territorial male approaches a playback electrode is linearly proportional to the intensity of the electric playback signal. A stronger stimulus might indicate a greater threat and thus elicit a greater chance of response; conversely, the male might simply be more likely to detect a stronger signal. We also see that females prefer to mate with larger males, which produce larger electric signals (Curtis and Stoddard, 2003). For any of these reasons, territorial or sexually selected species may be under selective pressure to boost signal power.

Brachyhypopomus gauderio (Giora and Malabarba, 2009) is a sexually selected species of electric fish that inhabits basins south of the Amazon, recently split from *B. pinnicaudatus* (Giora and Malabarba, 2009). Males produce signals of greater amplitude and duration than females (Fig. 4A). We combined pharmacology and oxygen respirometry to analyze the cost of electrogenesis ($\dot{V}_{O_2\,EOD}$) in both sexes of this species (Salazar and Stoddard, 2008). First, we took baseline measurements of oxygen consumption and signal

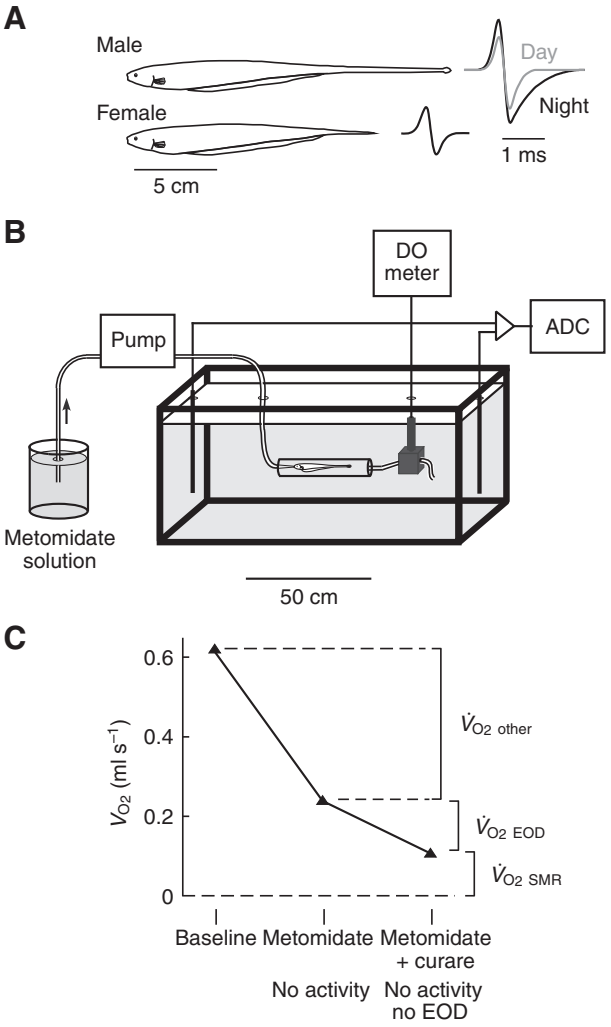

Fig. 4. (A) The gymnotiform electric fish *Brachyhypopomus gauderio* shows extreme sexual dimorphism in the size of the tail and the amplitude and duration of the electric organ discharge (EOD). (B) The energetic cost of electric signals in stationary fish was determined through oxygen respirometry and pharmacology (Salazar and Stoddard, 2008). The fish was held in an electrically transparent ceramic tube, respired with the regular water or with the tranquilizer (+) metomidate. While the fish was tranquilized, its gills were irrigated with oxygenated water. Dissolved oxygen (DO) was measured while the EOD was digitized with an analog-to-digital converter (ADC). (C) Energetic compartments were separated with pharmacology and arithmetic. When the fish was on GABA binding enhancer (+) metomidate HCl, the EOD continued but the fish was still and lacked muscle tone. The curare analog flaxedil blocked the EOD, leaving just the standard metabolic rate minus muscle tone.

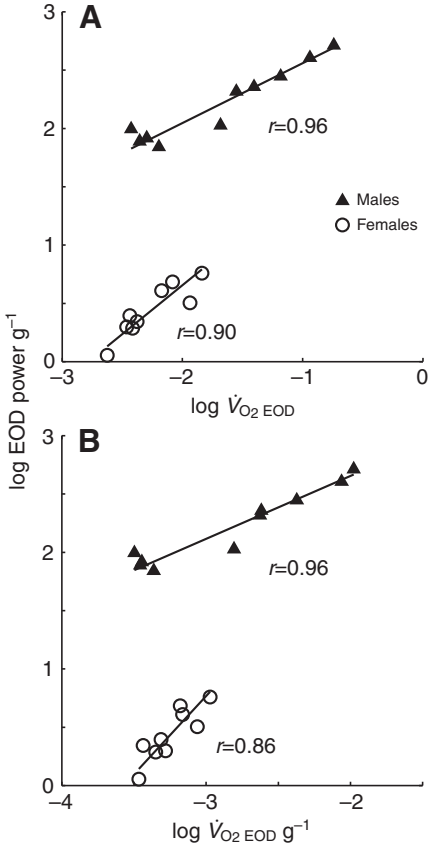

Fig. 5. The proof of the method to assess energetic cost of electric signaling lies in the tight correlations between energy consumed in electrogenesis ($\dot{V}_{O_2\ EOD}$) and EOD power (estimated by the time integral of voltage-squared). The correlations are equally strong for (A) whole-animal metabolic rates and (B) mass-corrected metabolic rates (Salazar and Stoddard, 2008).

production in a resting fish. Second, we respired the fish with a tranquilizing solution containing the GABA binding enhancer (+) metomidate, which eliminated activity and muscle tone while allowing the electric organ discharge (EOD) to persist (Fig. 4B). Third, we injected the fish with a curare analog, which silenced the electric organ. By subtraction, we partitioned the energy budget into three components: standard metabolic rate (SMR), electricity production and 'other', which consists of activity and muscle tone (Fig. 4). The extremely high correlation between the cost of electrogenesis and the power in the signal vouch for the reliability of this method (Fig. 5). We found that females allocate a small fraction (~3%) of their daily energy budget to electrogenesis, but males averaged 15%, with considerable inter-individual variation, as expected in a sexually selected species.

Subsequent analysis of this data set has revealed a trade-off between energy allocated to signaling and energy allocated to self-maintenance (Fig. 6). In sexually mature male *B. gauderio*, energy spent on general cellular metabolism ($\dot{V}_{O_2\ SMR}$) is inversely correlated with energy spent on electrogenesis ($\dot{V}_{O_2\ EOD}$), whereas in females, energy spent on general metabolism and electric signaling are positively correlated. The relationship holds whether one considers whole-animal or mass-corrected metabolic rates. Thus, it appears that the male pattern of high allocation to signal energy comes at the cost of general cellular maintenance. Exactly which compartment pays the cost is not clear. Is it the overall rate of cellular metabolism or just some part, such as immune function? Do individuals adjust this trade-off across their lives, or do different individuals establish different balances of signal *versus* self-maintenance?

Speakman posited alternate energy allocation models that could account for positive and inverse relations between signal metabolism and resting metabolism as described above for female and male *B. gauderio* (Speakman, 1997). These have been termed the 'performance model' and the 'allocation model', respectively (Careau et al., 2008). Under the performance model, resting metabolic rate determines the energy available to tissues, which, in turn, determines activity level. Thus, resting metabolic rate and

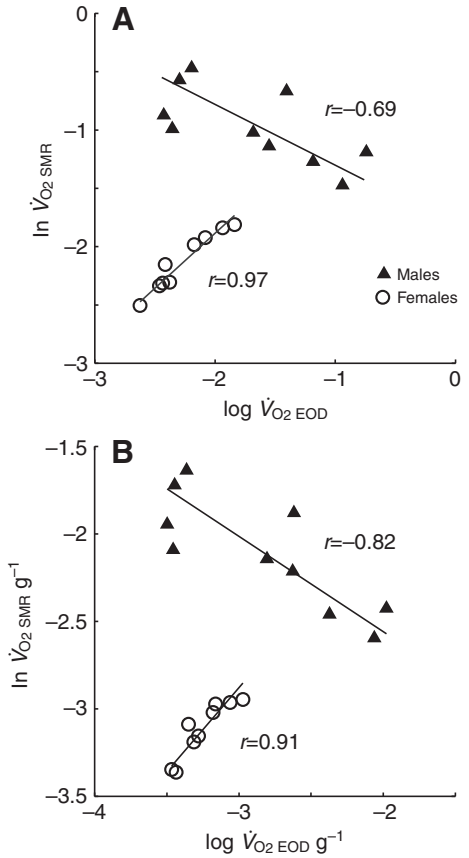

Fig. 6. In female *Brachyhypopomus gauderio*, energy allocated to electrogenesis ($\dot{V}_{O_2\,EOD}$) correlates positively with the standard metabolic rate ($\dot{V}_{O_2\,SMR}$). In males, however, the correlation is negative, suggesting a trade-off in which males obtain the energy to boost signal power by reducing energy allocated to cellular metabolism. The correlations apply to (A) whole-animal and (B) and mass-corrected measurements.

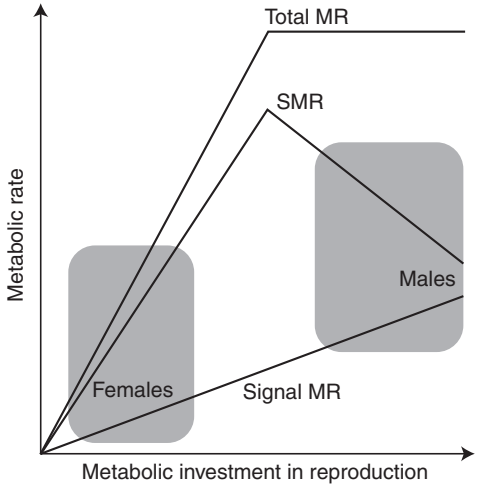

Fig. 7. Model of metabolic allocation and trade-offs, derived from Speakman (Speakman, 1997). As metabolic investment in reproduction rises, both the standard metabolic rate (SMR) and the signal metabolic rate (signal MR) (or other activities) will increase. Eventually, however, the animal reaches a metabolic ceiling and further investment in reproductive behavior necessitates a trade-off in other metabolic compartments, SMR in the case shown here. The investment patterns shown by female and male *Brachyhypopomus gauderio* in Fig. 6 are depicted here within the gray patches.

some other body function (signal energy in this case) are positively related. Under the allocation model, energy availability determines both resting metabolic rate and activity level: if the individual has an absolute ceiling on its energetic output, and its activity is high enough, it will experience a trade-off between resting metabolic rate and activity level. The most common pattern among vertebrates is for resting metabolic rate and activity to be positively correlated, although males tend to show the opposite trend (Careau et al., 2008). It seems unlikely that these two models would operate independently in both sexes of *B. gauderio*, but it might be the case that the allocation model applies to both sexes, whereas only males have a high enough total energy output to experience an energy ceiling and thus a trade-off between SMR and signal energy (Fig. 7).

Androgens mediate sexually dimorphic signal characteristics in electric fish over days or weeks (reviewed in Zakon, 2000; Zakon, 1996). We speculate that, as males come into breeding condition, rising androgen levels regulate the metabolic trade-off between signal energy and SMR. Testosterone treatment of male emberizine sparrows increases activity while lowering resting metabolic rate (Lynn et al., 2000; Wikelski et al., 1999). The opposite has been seen in male house sparrows, *Passer domesticus*, where androgens produce large male plumage signals (black bibs), while simultaneously raising basal metabolic rate (Buchanan et al., 2001). The black bib of the house sparrow consumes no energy once produced and initial melanin synthesis during feather production entails little energetic expense compared with activity. By contrast, the physical activity and acoustic or electric signal production entail significant energetic expense, presumably paid for through other metabolic savings. In addition, SMRs of every male *B. gauderio* we tested exceeded those of every female, despite the presumed trade-off (Fig. 6). Androgens increase signal power in *B. gauderio* (Allee et al., 2009), and also reduce immunocompetence in a variety of vertebrates (Cutolo et al., 2002; Deviche and Cortez, 2005). Thus, males with the strongest signals could be obtaining the energy needed to boost signal power by reallocating energy away from immune function or other ‘discretionary’ functions (Wedekind and Folstad, 1994).

Future areas for research

We wish to highlight two outstanding areas for future inquiry. First, it would be useful to obtain comparable energetic costs for signalers in each of the four categories shown in Fig. 1: low-energy cooperative signalers, low-energy passive signalers, high-energy long-distance signalers and high-energy close-range signalers. Currently, we have the most data for the high-energy long-distance signalers. Phylogenetically controlled contrasts, where possible, would make such comparisons particularly valuable.

Second, outside the context of seasonal survival strategies such as migration and hibernation, little is known about the effects of life history choices on energy allocation (Garland et al., 1992). One would expect short-lived or semelparous species to allocate proportionally more energy to reproductive signals than long-lived or iteroperous species, even at the cost of self-maintenance and long-term survival. In fact, the electric fish *B. gauderio* fits the life-history profile of short-lived species, but we need taxonomically comparable data for longer-lived iteroparous taxa to determine whether whether longevity determines energy allocation to communication signals.

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