

Longevity, calling effort, and metabolic rate in two populations of cricket

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Abstract Intraspecific variation in a resting metabolic rate (RMR) is likely to be an important determinant of energetic-resource use and may influence the resources subsequently available for allocation to traits not directly associated with somatic maintenance. The influence of RMR on resource availability could be especially important for condition-dependent sexual traits, such as cricket calls, that are themselves energetically costly to produce. RMR may also be associated with longevity, either negatively because individuals with a high RMR burn resources faster and die young, or positively as individuals with high RMR are more able to accrue resources to fuel survival. Additionally, the associations between RMR and other characters may vary across populations if differential selection or drift shapes these traits. Here we tested for differences in RMR, body mass, calling effort, and longevity in two populations of cricket *Gryllodes sigillatus* and then evaluated the potential influence of RMR on calling and longevity. We find that RMR, calling effort, and longevity varied across populations, but mass did not. Controlling for population and mass, RMR was not significantly associated with calling effort, but was negatively associated with longevity. These findings suggest that male crickets that live fast die young.

Keywords Attractiveness · Life history · Resource allocation · Reactive oxygen species · Sexual signaling

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Introduction

In energetic terms, fitness is dependent on successful allocation of energy resources to competing demands and these allocation decisions are thought to underlie trade-offs, including that between somatic maintenance and reproductive activity (Roff 2002). Trade-offs are conceptually simple—once a resource has been allocated to one activity, it cannot be allocated to another—but are complicated by the fact that the total resource pool available to certain individuals may be larger allowing them to allocate more to all activities (Getty 1998; Tomkins et al. 2004). While this problem can be partly circumvented by accounting for total resource availability and basal expenditure, it nevertheless follows that individuals from different populations could differ in the energy spent on somatic maintenance and in the trade-off between this and other fitness-enhancing activities.

The resting metabolic rate (RMR) of an individual is one measure of the basal cost of somatic maintenance, representing the unavoidable costs of maintaining bodily functions, and it shows tremendous variability both between and within species (McNab 2005; Rezende et al. 2004; Snodgrass et al. 2005; Arnqvist et al. 2010; Sinclair et al. 2011; also see Hosken and Withers 1997, 1999). RMR seems to play a major role in mediating energetically costly activity (Nilsson 2002; Biro and Stamps 2010; Ketola and Kotiaho 2010) and may therefore influence resource availability for other activities, especially for energetically expensive traits like those used in sexual signaling.

The energy available for allocation to various fitness-enhancing sexual characters underlies the concept of condition and condition dependence (Rowe and Houle 1996; Hunt et al. 2004a; Tomkins et al. 2004). One

interpretation of condition is that it represents the energy that is not needed for the basic somatic maintenance—it instead represents “residual” energy after maintenance costs are accounted for (Rowe and Houle 1996; Tomkins et al. 2004; Ketola and Kotiaho 2009). As a result, RMR should be negatively associated with sexual-trait expression, all else being equal. However, while there is abundant evidence that sexual-trait expression depends on condition (reviewed in Cotton et al. 2004; Tomkins et al. 2004), relatively few studies have investigated associations between expensive secondary sexual traits and metabolic rate (MR), other than to show that some of these characters (like producing an acoustic call) can elevate MR (e.g., Bailey et al. 1993; Kotiaho et al. 1998; Reinhold et al. 1998). Nevertheless, sexual traits are generally found to be energetically demanding (reviewed in Kotiaho 2001). Thus, it is possible that RMR could trade off with the expression of exaggerated sexually selected characters (Getty 1998; also see Ketola and Kotiaho 2010). Alternatively, under the “increased-intake hypothesis” (Bennet and Ruben 1979), it is possible that a high RMR could allow greater quantities of energy to be converted to sexual traits, and thus, high RMR would be positively associated with sexual-character exaggeration (Biro and Stamps 2010; Ketola and Kotiaho 2010). A general consensus on this has yet to be reached, as there have been relatively few studies of sexual characters and physiological parameters like metabolic rate (Laivaux and Irschick 2006).

In addition to potential associations between sexual characters and RMR, measures of MR are frequently negatively associated with longevity (reviewed in Speakman 2005). This trade-off is assumed to underlie the classical “live-fast-die-young” life-history strategy, and following this logic, a high RMR could be considered a fitness cost because fitness will be constrained by the amount of energy that can be allocated to non-maintenance functions (de Jong and van Noordwijk 1992; Hunt et al. 2004a; Tomkins et al. 2004). However, while a number of studies suggest that a high RMR has a negative effect on male longevity or reproductive effort, no experimental study has investigated the effect of RMR on both male fitness components together.

Here we assess the effects of RMR on a sexually selected trait (calling effort) and longevity in the decorated cricket, *Gryllodes sigillatus*. In crickets, male calling effort is a good measure of male mating success, because in both field (Bentsen et al. 2006) and laboratory studies (Hunt et al. 2005), females strongly prefer males that call more per night. Previous work on these crickets collected from the University of Western Australia has reported positive associations between RMR and some aspects of calling (Ketola and Kotiaho 2010). This is not consistent with the trade-off predicted under allocation models of sexual

selection, but is consistent with increased acquisition and higher quality individuals being able to invest more in sexual signals. Here we assess these relationships in two different populations of the cricket: one collected from Huntingdale, Western Australia (WA) and one from the southern United States of America, as it is possible that different populations have different selection histories, which have generated differences in the association between these traits. We initially test for differences in these traits between populations, and then assess potential associations between RMR and calling effort and longevity.

Materials and methods

Animal culturing

The animals used in this study are descended from two collections of approximately 500 crickets made in Las Cruces, New Mexico in 2001 (USA) and in Huntingdale, Western Australia in 2007. This corresponds to 70 and 16 generations of breeding in the lab, respectively. Since being brought into the laboratory, these stocks (henceforth referred to as USA and WA populations, respectively) have been maintained at $28\pm 1^\circ\text{C}$ under a 10D:14L light cycle. Each population is maintained in four large ($30\times 30\times 15$ cm) plastic boxes, each containing multiple layers of cardboard egg-trays for shelter. These boxes were provided with ad libitum food (Friskies GoCat Senior cat food) and water. Approximately 500 animals were housed in each box. Once the animals in each population box began to eclose to adulthood, damp cotton-wool egg pads were provided and left for females to oviposit upon for 1 week. The hatchlings emerging from these egg pads were collected daily and split between four fresh boxes to replace the stocks at the same level. Outbreeding within these populations was ensured by splitting hatchling animals between boxes at each generation. To obtain adult males for this study, final instar nymphs were randomly taken from the stock cultures, and separated and housed with an excess of food and water in individual containers ($5\times 5\times 5$ cm). Each cricket was also provided with a piece of egg carton for shelter.

Measurement of calling effort

Ten-day-old post-eclosion virgin male crickets were haphazardly collected from each population to measure their calling effort. Calling effort was assessed using a custom-built apparatus consisting of individual recording chambers ($5\times 5\times 5$ cm), each equipped with a lid-mounted condenser microphone (C1163, Dick Smith®), all of which were connected to a PC fitted with a data acquisition unit

[DaqBook 120, IOTect, Cleveland, OH; see Bertram and Johnson (1998) for a detailed description of such a device]. Our data acquisition unit was programmed to select and activate one microphone at a time, with the sampling speed set such that each recording chamber was sampled 10 times per second. At each sampling interval, the PC recorded an entry to a data file: recording a value of 1 if the received signal is 10 dB or more above the background noise and a value of 0 if not. The resulting data file therefore is a binary (calling/not calling) record of call activity over the test period. For each night of testing, the recording apparatus was activated at 6 p.m. and deactivated at 9 a.m. the next day, giving us a 15-h activity record. Calling activity was \log_{10} transformed prior to statistical analysis to ensure normality.

Measurement of resting metabolic rate

At 11 days post-eclosion, crickets that had not been fed for 12 h were weighed to the nearest milligram using a microbalance (Mettler Toledo UMX2). Flow-through respirometry was used to assess RMR, measured as CO_2 production (Terblanche and Chown 2007; Arnqvist et al. 2010; Sinclair et al. 2011), and all measures were made during the day under weak fluorescent light. Compressed zero air (a 21% O_2 and 79% N_2 mix) was scrubbed of any residual CO_2 and water (with ascarite and drierite, respectively) and fed through a Sable Systems (Las Vegas, NV, USA) RM8 eight-channel multiplexer (housed inside a Sanyo MIR 553 incubator temperature controlled at 28°C) and into 125-ml cuvettes housing the crickets at 100 ml/min (controlled at $\pm 1\%$ with a mass-flow control meter; Sierra Instruments, Monterey, CA, USA) (Arnqvist et al. 2010; Sinclair et al. 2011). The multiplexer regulates the flow to individual crickets, with one channel used as a blank for initial and final baseline readings to control for drift. The mass-flow meter regulated airflow, which was switched sequentially through each chamber for 20 min at a time, with sampling every second. Crickets from each population were randomly assigned to cuvettes so that any effects of the timing of sampling were randomized across treatments (Sinclair et al. 2011). A thermistor probe was placed next to the cuvettes in the incubator to monitor the thermal environment. Air exiting the cuvettes fed into a LiCor LI-7000 infrared gas analyzer (Lincoln, NE, USA) and CO_2 production and temperature data were acquired at 1 Hz via a Sable Systems UI2 analog–digital interface connected to a PC running Sable Systems Expedata software. This software was used to calculate metabolic rate using only data from the last 10 min of each recording to allow for CO_2 washout. We chose the most stable part of the recording (min. 300 readings, Chown and Nicolson 2004) to calculate mean CO_2 production per cricket.

We also checked to see if there was differential movement of crickets (by population) in the cuvettes, as this could influence subsequent RMR comparison. We did this by setting up a separate sample of males (i.e., not those on which we sampled RMR so as to avoid disturbance impacting RMR measurement) in the cuvettes, and we assessed movement by scanning males every 5 min for 30 min and scoring movement on a binary scale (moving/not moving). A rank–sum score was calculated for each population and compared using a normal approximation because the sample size was large (28, 14 males/population). There was no significant difference in ranks ($P > 0.4$), so any subsequent population differences in RMR are not likely to be due to differences in movement by crickets, and we note here that movement shows up clearly in CO_2 traces and for this reason, we only used stable parts of the recording.

Measurement of longevity

Immediately after measuring RMR, each cricket was returned to its individual container and longevity assessed daily until death. Containers were cleaned and fresh food and water provided weekly.

Statistical analysis

To test if populations varied in the traits we were investigating, we used a multivariate analysis of variance (MANOVA) including body mass, mean RMR, longevity, and calling effort as the response variables and population as the main effect. To investigate potential associations between body mass, RMR, longevity, and calling effort, another MANOVA was run with population as the main effect, body mass and RMR as covariates, and calling effort and longevity as response variables. Body mass and population were included in this model as both influence RMR and (potentially) the response variables, hence our need to control for both terms. For each model, we used a process of model simplification that sequentially removed nonsignificant interaction terms from the full model (Grafen and Hails 2002). In each instance, the reduced model is presented. All analyses were performed using JMP (version 6, SAS Institute 2005). In total, we measured 73 crickets, 37 from the USA and 36 from WA.

Results

MANOVA revealed that the multivariate combination of RMR, longevity, calling effort, and body mass differed significantly across populations (Table 1). Univariate post-hoc ANOVAs revealed this difference was driven by differences in RMR, longevity, and calling effort, while

body mass did not differ between populations (Table 1). The WA population called more and had a higher RMR, but the USA population lived longer. We note that the population difference in RMR remains if we use ANCOVA to control for body mass effects on RMR (body mass: $F_{1,70}=10.3$, $P=0.002$; population: $F_{1,70}=38.5$, $P<0.001$).

MANOVA revealed that RMR, mass, and population all significantly influenced the multivariate combination of longevity and calling effort (Wilks' lambda >0.53 , $F_{2,68}>3.2$, $P<0.045$). Univariate post-hoc ANCOVAs revealed that both population and body mass significantly influenced calling effort (population: $F_{1,69}=8.1$, $P=0.014$; body mass: $F_{1,69}=17.3$, $P<0.001$), but RMR did not ($F_{1,69}=0.37$, $P=0.54$). Heavier crickets called more [β (regression coefficient) \pm SE = 14.9 ± 3.5], as did crickets from Western Australia [WA mean (minutes \pm SE) = 53.9 ± 15.5 ; USA = 7.3 ± 2.4].

For longevity, univariate post-hoc ANCOVAs revealed a significant negative association between RMR and longevity ($\beta \pm$ SE = -2.09 ± 0.28 , $F_{1,69}=55.4$, $P<0.001$; Fig. 1), but population and body mass had no significant effect on longevity (population: $F_{1,69}=0.006$, $P=0.92$; body mass: $F_{1,69}=0.22$, $P=0.64$). When we assessed the negative association between RMR and longevity by population, the regression intercept and slopes were essentially identical in each population (WA: slope = -2.03 , intercept = 32.9 ; USA: slope = -2.04 , intercept = 32.7). Furthermore, if we included calling effort in the model, because time spent calling could negatively impact longevity, it did not significantly influence longevity ($P>0.09$), but the association with RMR remained.

Discussion

Our major finding was a strong negative association between resting metabolic rate and in longevity in male *G. sigillatus*. This suggests that males that live faster die younger, as has been reported previously for another cricket species, *Teleogryllus commodus* (Hunt et al. 2004b). However, previous work on this species suggested that

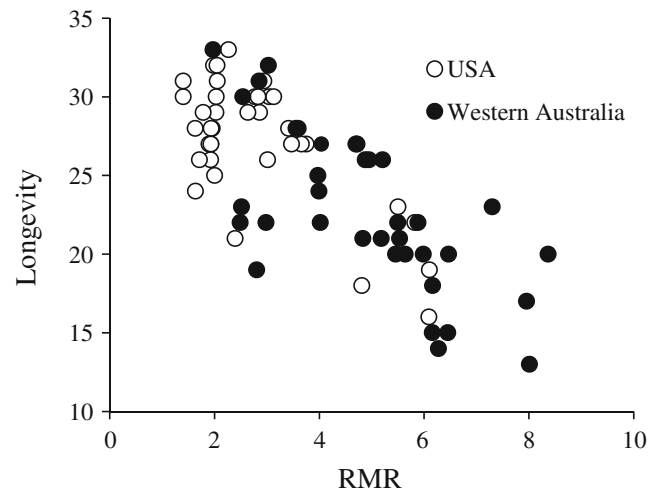


Fig. 1 The relationship between mean RMR (milliliter CO₂/minute \times 1,000) and longevity (day) of populations collected in USA (open circle) and Western Australia (filled circle)

sexual signaling was the primary cause of this association because artificial selection on male longevity altered male age-specific calling effort (Hunt et al. 2006). Similar trade-offs between reproduction and longevity in males have also been reported in other taxa (e.g., Brown et al. 2009). In our study we found no evidence that calling effort influenced longevity, although it must be noted that we only assessed calling on a single evening, early in adulthood. However, RMR was also only assessed once over a similar timeframe and it was found to be negatively associated with longevity. This may simply be because physiological traits are more repeatable than behavioral ones (Hoffmann 1999; Nespolo et al. 2003). An alternate explanation for the RMR–longevity association is that some individuals are stressed (either through illness or some other factor such as inbreeding), and this elevates RMR and reduces lifespan. It is also possible that higher oxygen consumption results in a higher rate of harmful reactive oxygen species (ROS) production (Van Voorhies 2001; Speakman 2005). ROS are known to cause phenotypic and cellular damage, including

Table 1 MANOVA examining differences in traits (body mass, longevity, RMR (CO₂ production), and calling effort) across populations (USA, WA). Univariate ANOVAs are also presented for each trait to show how they contribute to the overall multivariate effect

	MANOVA			Univariate ANOVAs	
	Wilks' λ	$F_{4,68}$	P	$F_{1,71}$	P
Population	0.589	11.873	0.0001		
	USA	WA			
Body mass (g)	0.229 \pm 0.007	0.231 \pm 0.006	0.037	0.849	
Longevity (days)	27.189 \pm 0.652	22.778 \pm 0.831	17.558	0.0001	
RMR (ml/min \times 1,000) ^a	2.805 \pm 0.216	4.888 \pm 0.280	34.849	0.0001	
Calling effort (s) ^b	439.00 \pm 146.27	3,233 \pm 930.75	6.326	0.014	

^a This translates to 0.168 and 0.293 ml CO₂ h⁻¹, respectively.

^b The actual value for calling effort was log₁₀ transformed for comparing means.

accelerating rates of ageing, through oxidative stress (reviewed in Dowling and Simmons 2009), which could explain our findings. A recently conducted series of experiments provides some evidence for this explanation of our RMR–longevity findings, as it links longevity and levels of cellular damage in these crickets (Archer et al. unpublished).

Condition can be thought of as the amount of energy that can be allocated to fitness-enhancing traits (Rowe and Houle 1996; Hunt et al. 2004a) and is frequently positively associated with the degree of sexual signaling (Cotton et al. 2004; Tomkins et al. 2004). As discussed above, higher maintenance metabolism is an unavoidable cost-constraining condition (also see Hawkins and Day 1999; Johnston et al. 2007). Additionally, a previous study on *G. sigillatus* suggested that lower resting metabolic rate is likely to be indicative of higher condition (Ketola and Kotiaho 2010). Nevertheless, in our investigation, the variation in total calling effort observed was not associated with RMR, despite the importance of calling effort in determining male mating success in crickets (e.g., Hunt et al. 2004b, 2005). Again this may simply be because we only assessed calling effort once at a relatively young age, but Ketola and Kotiaho (2010) also found no relationship between total calling effort and RMR in the same cricket species collected in Western Australia, although they did find a positive association between RMR and one characteristic of calling (mean call bout duration). We did not assess this call parameter, but the apparent difference between studies could also be due to differences in the populations tested.

In their study on *G. sigillatus*, Ketola and Kotiaho (2010) suggested that a high RMR could be beneficial by allowing greater quantities of energy to be converted from food to behavior. This is consistent with the “increased-intake hypothesis” (Bennet and Ruben 1979). That is, individuals will be able to ingest and process more food due to an increase in the activity of the alimentary tract such as gut, intestines, and liver (Hume and Biebach 1996; Hammond et al. 2000). The high metabolic activity of organs in the alimentary tract contributes strongly to an individual’s RMR (Alexander 1999), resulting in an increase in RMR with increases in the alimentary tract size (Daan et al. 1990; Lindstrom et al. 1999). The net energy balance will of course depend on the allometry of energetic cost of higher MR versus the energetic gain via increased intake and assimilation. Reinhold et al. (1998) have also investigated the relationship between MR and attractiveness in the wax moth *Achroia grisella*, finding that net MR is positively associated with some characteristics of sexual signaling, most notably pulse rate, in this species. Although we need additional detailed studies on the impact of RMR on specific calling parameters in more acoustic species, it

currently seems that a high RMR is indicative of high rather than low-quality sexual signaling (see Biro and Stamps 2010). However, this relationship does not appear to be universal as RMR was not associated with sexual signaling in the wolf spider *Hygrolycosa rubrofasciata* (Kotiaho et al. 1998), the bank vole *Clethrionomys glareolus* (Radwan et al. 2006), or by us here.

We also found that our two populations varied in RMR, calling effort, and longevity. This suggests that there are genetic differences between these populations as they have been reared under common garden conditions since their introduction to our lab environment. Differences in these traits could represent fundamental differences between the two populations, or they may simply be because the USA population has had more time to adapt to the lab conditions, spending longer in culture prior to our experiment relative to the WA population (70 versus 16 generations). Lab adaptation is often rapid and even small changes in housing conditions can have a substantial impact on life-history trade-offs (e.g., Sgro and Partridge 2000). Recent work has also documented strong interactions (mitochondrial haplotype by gene by environment) influencing metabolic rates (Arnqvist et al. 2010), and this sort of interaction is another potential explanation for the population differences we see here. The lack of significant difference in body mass between populations is probably not surprising as crickets from both populations had ad libitum access to food prior to RMR assessment. We should also note that the longevity difference between populations was only evident when we did not control for RMR; and when RMR was included, it rather than population explained the difference in longevity. This supports our suggestion that males living faster die younger.

In conclusion, we found a strong trade-off between resting metabolic rate and longevity in male *G. sigillatus*. Variation in RMR can thus have important consequences for the overall life-history strategy of an individual, possibly via the link between oxidative stress and longevity. However, we found that RMR was not associated with calling effort. The precise mechanism underlying the longevity effect needs further investigation, as do the difference in RMR and calling effort we found across populations. We additionally suggest that further investigation of calling and RMR is warranted, as it is possible that an elevated RMR has a positive effect on sexual signaling (see also Reinhold et al. 1998; Ketola and Kotiaho 2010).

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