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RESEARCH ARTICLE

Non-linear scaling of oxygen consumption and heart rate in a very large cockroach species (*Gromphadorhina portentosa*): correlated changes with body size and temperature

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SUMMARY

Although well documented in vertebrates, correlated changes between metabolic rate and cardiovascular function of insects have rarely been described. Using the very large cockroach species *Gromphadorhina portentosa*, we examined oxygen consumption and heart rate across a range of body sizes and temperatures. Metabolic rate scaled positively and heart rate negatively with body size, but neither scaled linearly. The response of these two variables to temperature was similar. This correlated response to endogenous (body mass) and exogenous (temperature) variables is likely explained by a mutual dependence on similar metabolic substrate use and/or coupled regulatory pathways. The intraspecific scaling for oxygen consumption rate showed an apparent plateauing at body masses greater than about 3g. An examination of cuticle mass across all instars revealed isometric scaling with no evidence of an ontogenetic shift towards proportionally larger cuticles. Published oxygen consumption rates of other Blattodea species were also examined and, as in our intraspecific examination of *G. portentosa*, the scaling relationship was found to be non-linear with a decreasing slope at larger body masses. The decreasing slope at very large body masses in both intraspecific and interspecific comparisons may have important implications for future investigations of the relationship between oxygen transport and maximum body size in insects.

Key words: insect, scaling, body size, metabolic rate, heart rate, cuticle mass, temperature.

INTRODUCTION

The rates of physiological processes are strongly impacted by temperature and body mass (Schmidt-Nielsen, 1984). Metabolic, respiratory and cardiovascular system rates respond characteristically to increasing temperature by increasing, and vary allometrically with body mass (Stahl, 1967; Schmidt-Nielsen, 1984). In vertebrates, the oxygen cascade is arranged in series from a respiratory exchanger to cardiovascular flow and finally diffusion into the body tissues. The matching of rates of oxygen transport by components in the cascade has been demonstrated and described (Taylor et al., 1996; Weibel et al., 1996). For some groups such as insects, the linkage between respiratory and circulatory systems is not as direct (Wasserthal, 1996). In contrast to vertebrates, the tracheal respiratory system of insects allows for direct exchange of gases with tissues, whereas the cardiovascular system circulates hemolymph within the body cavity (Chown and Nicolson, 2004). Although the cardiovascular system is unlikely to play a major role in gas exchange, scaling relationships similar to that for metabolic rate have been documented in insects (Edwards and Nutting, 1950; Birchard and Arendse, 2001). This correlation may be due to the supply rate of shared metabolic substrates (e.g. carbohydrates and lipids) and indicates that statistical correlates between respiratory and cardiovascular function are present even when these systems are not directly coupled in series for oxygen transport (Weibel et al., 1996; Birchard and Arendse, 2001).

We examined the heavy-bodied Madagascar hissing cockroach, *Gromphadorhina portentosa* (Schaum) (Blaberidae: Oxyhaloinae), to further characterize the relationship between cardiovascular and respiratory systems in a very large insect species. We investigated the effect of temperature and body mass on $\dot{V}_{O_2}$ and heart rate. These data were used to determine whether concordant relationships between $\dot{V}_{O_2}$ and heart rate exist across body mass and temperature treatments.

MATERIALS AND METHODS

Insects

All cockroaches were maintained and handled according to guidelines provided by the George Mason University Animal Care and Use Committee. The cockroaches used in this study were obtained from an established laboratory colony maintained for over 5 years. The colony was kept at 28±2°C within an incubator under a 12h:12h light/dark cycle and food was supplied once a week. The base diet of the colony was standardized by always having dry cat food available. However, to maintain the health of the colony we often added supplemental food (e.g. apples, lettuce). Nymphs of both sexes and only adult males were studied in order to avoid the influence of gravidity on our analysis. Sex was determined for larger instars by assessing the condition of three morphological characters known to be dimorphic between *G. portentosa* sexes (Bell, 1981).

Respirometry

Oxygen consumption rate (routine metabolic rate) was measured using a closed manometric system previously described (Bichard, 1991). The present study included the following modifications: chamber dimensions were either 7×6 cm (for smaller instars) or 10×5 cm (for larger instars and adults). Pressure changes within the reaction chamber were balanced by the plunger movements of a syringe decreasing the volume within an oxygen-filled 2 ml micrometer syringe or a 1 ml tuberculin syringe depending on ambient temperature and size of the animal. To avoid the metabolic effect of feeding (Muthukrishnan and Pandian, 1987), individuals used in the study were fasted for at least 24 h before measurements were taken. The $\dot{V}_{O2}$ of the two smallest instars (0.07–0.25 g) was determined from measurements on groups of three individuals. Although some insects experience group effects on metabolism, this phenomenon is typically associated with eusocial species (e.g. Hou et al., 2010; Waters et al., 2010) and as such these effects are not likely to be influential in the unitary *G. portentosa*. Individual oxygen consumption determinations were made over a period of approximately 1.5 h to avoid effects associated with discontinuous gas exchange (Dingha et al., 2005; Contreras and Bradley, 2010). The amount of oxygen depleted during these experimental periods (typically <0.8 ml) was negligible relative to the amount of oxygen contained in the 150 ml chambers and oxygen-filled syringe. All measurements were performed in a dark temperature-controlled water bath and cockroaches were allowed approximately 1 h of acclimation prior to determination of $\dot{V}_{O2}$. Oxygen consumption rate was corrected to ml $O_2 h^{-1}$ STPD (standard temperature and pressure, dry). If an exceptionally high $\dot{V}_{O2}$ was noted for a given body size, the trial was rerun or eliminated from the analysis. Additionally, animals were isolated for at least 48 h following the determination of their oxygen consumption rate and eliminated from the analysis if they molted or died. Oxygen consumption rate as a function of body size was determined from measurements on 93 individuals ranging in mass from 0.06 to 10.61 g at 28°C.

Heart rate measurements

Heart rate was determined using impedance measurements as previously described (Birchard and Arendse, 2001). All cockroaches were fasted for 24 h prior to anesthetization with carbon dioxide. Stainless steel wire electrodes were implanted and insects were allowed a post-operation recovery period of 24 h before measurements began. Heart rate was not determined for the smallest instars (<0.19 g). All heart rate experiments were conducted within a laboratory incubator to control ambient temperature. Cockroaches were allowed a 1 h acclimation period in the incubator prior to heart rate measurement. In order to determine a standard heart rate and ascertain the relationship with size, the heart rate of 32 *G. portentosa* ranging in mass from 0.19 to 9.12 g was measured at the acclimated colony temperature of 28°C. Measurements were taken in 30 min sessions two to three times over a 24 h period. This group of measurements was then averaged to calculate heart rate. Following all measurements, electrodes were removed and individuals isolated for approximately 48 h. Those animals that died during this time period were removed from the analysis. Heart rate was recorded as beats min^{-1}.

Temperature treatments

We conducted a series of temperature trials to compare thermal effects on $\dot{V}_{O2}$ and heart rate. For $\dot{V}_{O2}$, respirometry methods followed those described above with the following modification: measurements were made on cockroaches with a mass range of 0.74–10.78 g. The number of animals studied was 19, 22, 20 and 30 cockroaches at 16, 21, 28 and 34°C, respectively. In each temperature trial, cockroaches were acclimated to the experimental temperature for a minimum of 1 h prior to measurements. Individual animals were exposed to temperatures in the following order: 34, 21, 28 and 16°C. Before and after each trial, individuals were housed at 28°C.

In order to determine the temperature sensitivity of heart rate, measurements were taken at 12, 16, 20, 24, 28 and 32°C with 7 animals in each temperature trial. All trials were conducted inside an incubator using the protocols described above. Animals were exposed to temperatures in the following cycle, repeated twice over a 48 h period: 12, 16, 20, 24, 32 and 28°C. To assess the impact of presenting temperature classes in a rank order, we conducted preliminary trials where the exposure order was varied and multiple measurements were taken at 28°C. In these trials we exposed animals to temperatures in two ordering schemes: 28, 24, 20, 16, 12, 28, 32 and 28, 32, 28, 24, 20, 16, 12°C. Using paired *t*-tests we found no significant differences between 28°C runs despite these measurements being taken at different stages in the trials ($P<0.872$ to $P<0.126$). A minimum acclimation period of 1 h was allowed in between each temperature trial. Rates for both temperature trial cycles were averaged and then analyzed.

Inert tissue measurements

It has been suggested that the ratio of metabolically active tissue to inactive tissue may partially explain the variation in $\dot{V}_{O2}$ scaling exponents observed among some insect taxa (Coelho and Moore, 1989; Kirkton et al., 2005). To examine this and its potential effect on our results, we performed a comparative examination of dry and wet masses of eviscerated animals. A group of 72 cockroaches ranging in mass from 0.06 to 10.56 g were killed and then eviscerated so that most of the contents of the hemocoel were removed. Specimens were placed in individual weighing pans that had been in a drying oven for 1 week before use. Dissected specimens were weighed for wet mass to the nearest 0.1 mg. Specimens were dried for 1 week at 50°C. Upon removal from the drying oven, all specimens were immediately placed in a desiccator over Drierite©. Dried specimens were removed individually from the desiccator for dry mass weighing.

Data analysis

Allometric scaling relationships of $\dot{V}_{O2}$, heart rate and cuticle mass were determined by least squares regression analysis of $\log_{10}$-transformed data. These data were examined for influential outliers and for meeting the assumptions of the allometric model (zero intercept, linearity and homoscedasticity). The effect of temperature on oxygen consumption and heart rate was examined using ANCOVA and repeated measures ANCOVA analysis (with body mass as the covariate). Additionally, we calculated Q_{10} values to further examine temperature effects. Assumptions associated with ANCOVA (i.e. homogeneity of slopes and no interaction between independent variables) were met. We also examined non-transformed $\dot{V}_{O2}$ and heart rate data to better characterize any response patterns observed across varying temperatures and body masses. Standard error was used for confidence intervals on all statistics.

To examine our *G. portentosa* data in relation to other cockroach (Blattodea) species, $\dot{V}_{O2}$ data were taken from previous literature (Table 1). As previously (Coehlo and Moore, 1989), data were corrected to 25°C. Interspecific allometric analysis was performed using the same statistical criteria as for the intraspecific *G. portentosa* analysis. All statistical analyses were carried out using SYSTAT 11 software (Systat Software, Inc., Chicago, IL, USA). To rank

Table 1. Cockroach species included in interspecific metabolic rate and body mass analysis

Taxon	Case ID[a] (Fig. 6)	Body mass (g)	Metabolic rate (µl O_2 h^{-1})*
Blatella germanica	1	0.05	31.12
Diploptera punctata	2	0.16	29[b]
***Perisphaeria* spp.**	3	0.32	46.02
Blatella orientalis	4	0.38	131.14
Nauphoeta cinerea	5	0.52	132.54
Periplaneta americana	6	0.85	266.90
Leucophaea maderae	7	2.80	527.50
Eublaberus posticus	8	2.20	748
Blaberus discoidalis	9	4.04	645.10
Blaberus giganteus	10	5.17	799.63
Bysotria fumagata	11	4.95	990
Gromphadorhina portentosa	12	9.1	753.3
Macropanesthia rhinoceros	13	26.52	1510[b]

Text in bold indicates wingless species (see also Fig. 6).

[a] References: (1) Gunn, 1935; Hostetler et al., 1994; (2) Stephenson et al., 2007; (3) Marais and Chown, 2003; (4) Gunn, 1935; (5) Coehlo and Moore, 1989; (6) Gunn, 1935; Dehnel and Segal, 1956; (7) Coehlo and Moore, 1989; (8) Herreid and Full, 1984; (9) Birchard and Arendse, 2001; (10) Enger and Savalov, 1958; Bartholomew and Lighton, 1985; (11) Herreid and Full, 1984; (12) this study; (13) Woodman et al., 2007.

[b] $\dot{V}_{O_2}$ approximated from measurements of CO_2 output.

*Metabolic rate has been temperature corrected to 25°C.

simple linear and non-linear regression models, we used TableCurve 2D (v5.01), which ranks models based on r^2, adjusted r^2, fit standard error and *F*-statistics.

RESULTS

A summary of regression models and their parameters is presented in Table 2. Oxygen consumption rate increased with body mass across our sample (N=92, P<0.0001). However, locally weighted scatterplot smoothing (LOESS) and residual plots indicate the relationship is better described as curvilinear with the slope decreasing significantly at a mass greater than 3 g (slope above 3 g was 0.32, N=38, P<0.09 and below 3 g was 0.67, N=54, P<0.0001). An exponential function was selected as the best curve-fit simple model (N=92, P<0.0001; Fig. 1A). Heart rate (beats min^{-1}) was found to decrease with increasing body mass in *G. portentosa* (N=32, P<0.0120). As with the relationship for $\dot{V}_{O_2}$, body mass was found to have a curvilinear relationship with heart rate. When individuals with masses greater than 3 g were removed or analyzed separately, the regression models were non-significant (slope above 3 g was –0.19, N=10, P<0.167 and below 3 g was 0, N=22, P<0.99). A power regression model was selected as the best curve-fit simple equation (N=32, P<0.0109; Fig. 1B).

Temperature had a significant effect on $\dot{V}_{O_2}$ across all samples ($F_{3,77}$=50.56, P<0.0001). The shape of the relationship between $\dot{V}_{O_2}$ and mass did not show significant variation with temperature. Because of the curvilinear relationships described above, the effect of temperature was evaluated in two ways: (1) using data from multiple instars and (2) using data from adult animals greater than 7 g (mean 9.1 g) where size appears to have a minimal effect on $\dot{V}_{O_2}$. Mean $\dot{V}_{O_2}$ values for adult animals (multiple instars in parentheses) were 1.51 (1.30), 0.84 (0.81), 0.51 (0.59) and 0.31 (0.27) ml O_2 h^{-1} for 34, 28, 21 and 16°C, respectively (Fig. 2A,B). Q_{10} values for $\dot{V}_{O_2}$ in this analysis ranged from 2.08 to 2.45 (2.23–4.46). Temperature had a significant effect on heart rate ($F_{5,15}$=69.883, P<0.0001). The mean heart rate in adults (multiple instars in parentheses) was 76.15 (83.43), 63 (69.79), 47 (54.00), 35.75 (37.86), 26 (27.14) and 15 (16.57) beats min^{-1} for 32, 28, 24, 20, 16 and 12°C, respectively (Fig. 2C). Heart rate Q_{10} values ranged from 1.39 to 2.5 (1.56–3.43) in this analysis. The relationships between mean $\dot{V}_{O_2}$ and temperature (N=4, P<0.0150) and mean heart

Table 2. Statistical models, r^2 values and *P*-values used in examining the relationships among oxygen consumption ($\dot{V}_{O_2}$), heart rate and body mass in *Grompahdorhina portentosa* and other cockroaches

Models	Eqn	*N*	*a*	*b*	*c*	r^2	*P*
Gromphadorhina portentosa							
Body mass × $\dot{V}_{O_2}$ (all)	$y=aX^b$	92	–0.046±0.016	0.52±0.026		0.81	0.0001
Body mass × $\dot{V}_{O_2}$ (>3 g)	$y=aX^b$	38	–0.36±0.140	0.32±0.186		0.08	0.0900
Body mass × $\dot{V}_{O_2}$ (<3 g)	$y=aX^b$	54	–0.041±0.017	0.67±0.035		0.87	0.0001
Body mass × $\dot{V}_{O_2}$ (all)	$y=a+be^{-x}$	92	0.087±0.027	–0.46±0.023		0.81	0.0001
Body mass × heart rate (all)	$y=aX^b$	32	1.91±0.014	–0.078±0.029		0.19	0.0120
Body mass × heart rate (>3 g)	$y=aX^b$	10	1.98±0.096	–0.19		0.22	0.1670
Body mass × heart rate (<3 g)	$y=aX^b$	22	1.92±0.018	0		0	0.9980
Body mass × heart rate (all)	Power(*a*,*b*,*c*)	32	1.92±0.018	–0.14±0.049	2.13±1.540	0.19	0.0109
$\dot{V}_{O_2}$ × temperature	$y=aX^b$	4	–0.622±0.175	0.055±0.007		0.96	0.0150
Heart rate × temperature	$y=aX^b$	6	–27.044±3.258	3.417±0.141		0.99	0.0001
Body mass × cuticle mass	$y=aX^b$	72	–0.563±0.007	1.05±0.011		0.99	0.0001
Blattodea							
Body mass × metabolic rate	$y=aX^b$	13	2.33±0.054	0.74±0.071		0.91	0.0001
Body mass × metabolic rate	$y^{-1}=a+{}^{b}e^{-x}$	13	0.28±0.012	0.13±0.016		0.91	0.0001

Standard error (±s.e.m.) is indicated where relevant.

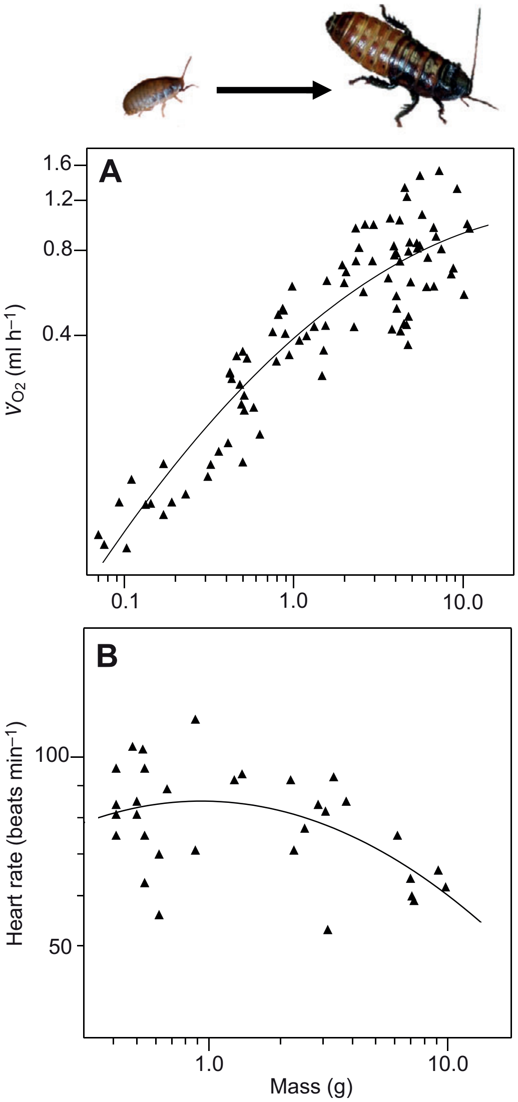

Fig. 1. Curvilinear relationship of (A) oxygen consumption rate (N=92, a=0.09±0.027, b=–0.46±0.023, r^2=0.81, P<0.0001) and (B) heart rate (N=32) to body mass (N=32, a=1.92±0.018, b=–0.14±0.049, c=2.13±1.54, r^2=0.19, P<0.0109) in *Gromphadorhina portentosa* ranging in mass from 0.06 to 10.61 and 0.19 to 9.12 g, respectively.

rate and temperature (N=6, P<0.0001), while significant, were not comparable.

The relationship between body mass and cuticle mass (using dry mass of eviscerated cockroaches as a surrogate measure) was found to be isometric (Fig. 3; N=72, P<0.0001). Examinations of non-transformed $\dot{V}_{O_2}$ and heart rate data were consistent with the patterns observed in the log$_{10}$-transformed data including an inverse functional response to body mass (Fig. 4) and a matched response to temperature (Fig. 5).

The interspecific analysis of mean $\dot{V}_{O_2}$ and mean body mass across Blattodea species produced a 3/4 scaling exponent (N=13, P<0.0001; Fig. 6). However, residual analysis showed the relationship is non-linear, appearing to begin to plateau at body masses between 2 and 4 g. Therefore, as in the intraspecific analysis of *G. portentosa*, an exponential function was selected as the best model to describe this relationship (Fig. 6).

DISCUSSION

Our findings suggest that in *G. portentosa* $\dot{V}_{O_2}$ and cardiovascular function respond in a co-ordinated fashion over a wide range of body masses and temperatures. For body mass, this finding is consistent with a previous study in cockroaches (Birchard and Arendse, 2001). Additionally, we found that (1) the scaling relationships were not linear and had a decreasing slope at the greatest body masses and (2) there is an isometric scaling relationship between metabolically active tissue and inert cuticle mass across instars. Below we discuss some implications of these findings.

A recent review of metabolic scaling exponents in terrestrial arthropods (Glazier, 2005) revealed more variation than previous estimates. Intraspecific scaling is affected by many factors including photoperiod, age, temperature, sex and season (Newell et al., 1974; Rogowitz and Chappell, 2000; Nespolo et al., 2003; Strauss and Reinhold, 2010). Intraspecific exponents in cockroaches have been shown to range from 0.75 to 1.29 (Gunn, 1935; Woodland et al., 1968; Chown et al., 2007) and can vary within populations, e.g. pesticide-resistant *vs* pesticide-susceptible individuals (see Dingha et al., 2009). The wingless and relatively lethargic *G. portentosa* is one of the largest extant insect species (7–12 g). In the present study we found a scaling exponent of 0.52, one of the lowest yet reported. We believe this low scaling exponent may be a statistical issue resulting from fitting a linear model to a non-linear data set (see Packard and Birchard, 2008). The non-linear scaling for *G. portentosa* could be related to an ontogenetic increase in the proportion of total mass represented by the inactive cuticle, i.e. adult ornamentation (Coehlo and Moore, 1989; Kirkton et al., 2005). We documented a pattern of isometric scaling in cuticle mass (Fig. 3), similar to other insect studies (Lease and Wolf, 2010). Thus, our results do not support proportionally greater adult cuticle mass as an explanation for the non-linear metabolic scaling in *G. portentosa*.

Our results for the relationship between heart rate and body mass in *G. portentosa* (b=–0.078) are very similar to those reported previously (Birchard and Arendse, 2001) for *Blaberus discoidalis* (b=–0.099). While neither of these data sets fits a linear model, the correlated change of heart rate with body mass is still apparent. Interestingly, as observed in our comparison of $\dot{V}_{O_2}$ and body mass, there is a notable change in the heart rate of individuals above 3 g in body mass. Specifically, when animals are 3 g or heavier, $\dot{V}_{O_2}$ appears to plateau (Fig. 1A) and heart rate appears to drop (Fig. 1B). Because of this similarity we think it is reasonable to suggest that changes in cardiac function and $\dot{V}_{O_2}$ are correlated with body mass in *G. portentosa*.

The temperature coefficient data in this study are consistent with previously reported Q_{10} values in insects (Nespolo et al., 2003; Stabentheiner et al., 2003). The sensitivity values we report for heart rate are consistent with values reported for other poikilotherms (Edwards and Nutting, 1950; Romero and Hoffman, 1996; Korsmeyer et al., 1997; Coehlo and Amaya, 2000). In our examination of multiple instars we recovered high temperature coefficients between the lowest temperature classes (around 16°C; Fig. 2A,C), which could be interpreted as a functional break associated with cold torpor. However, in our adult-only analyses this break disappeared entirely for $\dot{V}_{O_2}$ and the coefficient was reduced in heart rate trials (Fig. 2B,D). Thus, we are skeptical of any physiological significance associated with Q_{10} values from the multiple instars analysis.

The similar effect of endogenous (body mass) and exogenous (temperature) variables (Figs 1–5) is consistent with a mutual dependence on similar metabolic substrates and/or some sort of coupling of these systems in *G. portentosa* as suggested previously

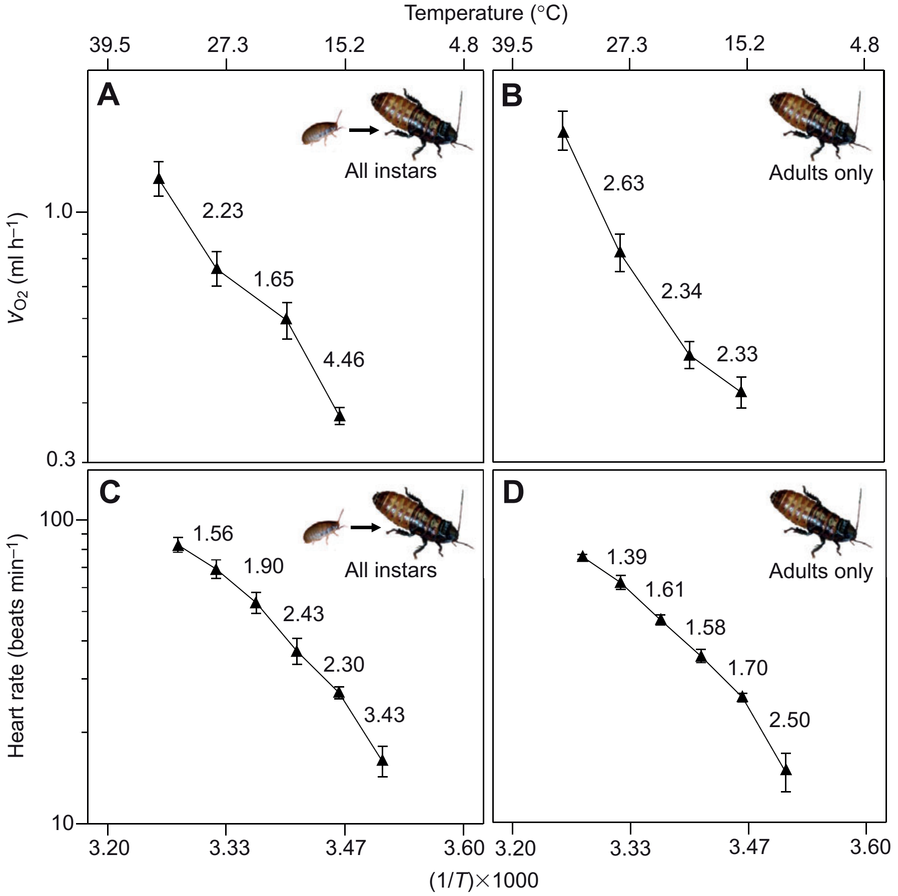

Fig. 2. Arrhenius plots of means (with standard error) for (A,B) oxygen consumption rate and (C,D) heart rate in *G. portentosa*. Temperature coefficients (Q_{10}) appear above lines. The top *X*-axis denotes temperature (in °C), and the bottom *X*-axis is equivalent to (1/*T*)×1000 where *T* is temperature in K. A and C are derived from temperature trials on multiple instars whereas B and D are derived from a subset of the trials that only included animals weighing 7 g or more (adults). Note that in the plots including all instars, an inflection point (bold Q_{10}) occurs around 16°C; however, this break is not observed in the adult-only sample.

(Birchard and Arendse, 2001). However, future studies that simultaneously measure $\dot{V}_{O_2}$ and heart rate within single individuals will be necessary to explicitly evaluate the relatedness of these physiological processes in insects.

In their interspecific analyses of $\dot{V}_{O_2}$ within Blattodea, Coelho and Moore (Coelho and Moore, 1989) reported a scaling exponent of 0.78 and Chown et al. (Chown et al., 2007) reported a scaling exponent of 0.83. Our updated data set for Blattodea was notably different from those used in prior analyses, not only in the number of species but also because we included two of the largest insect species ever included in such analyses. While we found a similar scaling exponent to those in prior analyses, log transformation failed to linearize our data. Such statistical issues with allometric analyses have been found previously in other interspecific studies, notably in the scaling of metabolic rate in mammals (Packard and Birchard, 2008). This analysis indicates a decrease in slope with

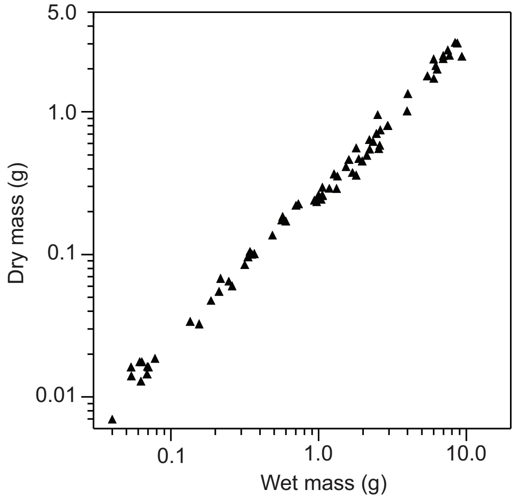

Fig. 3. Isometric scaling relationship between wet (pre-desiccation) and dry (post-desiccation) tissue masses across *G. portentosa* instars (*N*=72, *a*=–0.563±0.007, *b*=1.05±0.011, r^2=0.99; *P*<0.0001). Animals were eviscerated prior to wet measurement.

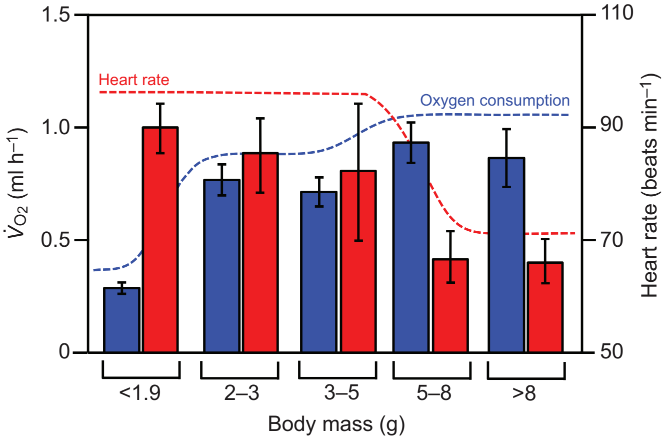

Fig. 4. Bar plots (with standard error) depicting the relationship between non-transformed oxygen consumption rate (blue bars) and heart rate (red bars) for several body mass categories of *G. portentosa*. The general relationships of heart rate (red) and oxygen consumption (blue) with body mass are indicated by dashed lines.

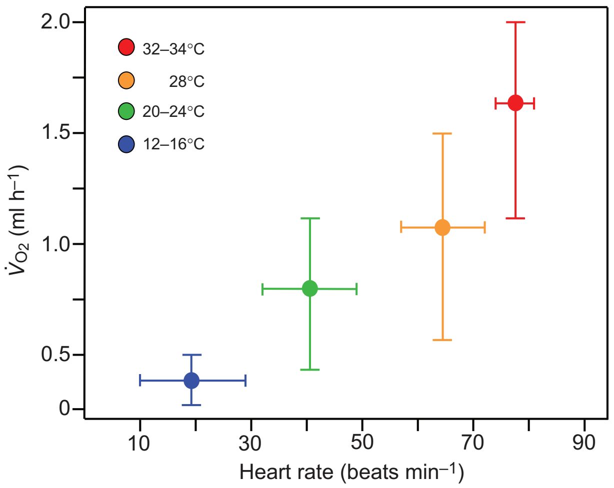

Fig. 5. Plots of non-transformed oxygen consumption rate and heart rate for several temperature categories used in this study. These data reflect values recorded for *G. portentosa* instars larger than 5 g. Bars are the range of these data.

increasing body mass in cockroaches. The wingless (flightless) species included in our interspecific analysis (*Diploptera punctata*, *Perisphaeria* spp., *G. portentosa* and *Macropanesthia rhinoceros*) all occur under the regression line (Fig. 6). This is consistent with the observation that many flightless insects have proportionally lower metabolic rates than their closest winged relatives (Reinhold, 1999). As non-linear scaling may be related to the inactive, flightless ecology of the largest cockroach species in the data set, we further explored our Blattodea dataset by performing an ANCOVA where we used wing status (either winged or flightless) as a factor variable and body mass as the covariate. This analysis suggests a non-significant relationship between wing status and metabolic rate ($F_{1,10}$=3.302, P<0.099). However, studentized residual analysis indicates that the largest species in the dataset (*M. rhinoceros*) is a statistical outlier. When we excluded *M. rhinoceros* from the dataset, a subsequent ANCOVA recovered a significant relationship between wing status and metabolic rate ($F_{1,9}$=6.294, P<0.033). Given these findings, the curvilinearity we observed in Blattodea (Fig. 6) may be a complex result stemming from the metabolic consequences of multiple life history traits (e.g. flightless ecology, large body size, etc.).

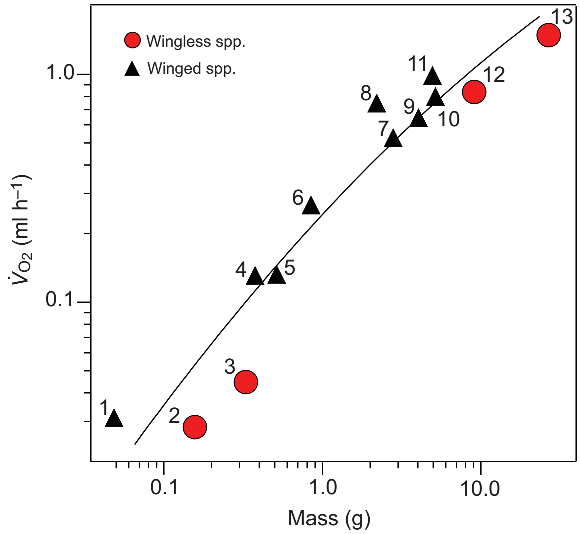

Fig. 6. Curvilinear relationship between mean metabolic rate and mean body mass for selected species of cockroach (N=13, a=0.28±0.012, b=0.13±0.016, r^2=0.91; P<0.0001). Numbers indicate case IDs corresponding to those in Table 1: [1](Gunn, 1935; Hostetler et al., 1994); [2](Stephenson et al., 2007); [3](Marais and Chown, 2003); [4](Gunn, 1935); [5](Coehlo and Moore, 1989); [6](Gunn, 1935; Dehnel and Segal, 1956); [7](Coehlo and Moore, 1989); [8](Herreid and Full, 1984); [9](Birchard and Arendse, 2001); [10](Enger and Savalov, 1958; Bartholomew and Lighton, 1985); [11](Herreid and Full, 1984); [12]this study; [13](Woodman et al., 2007).

Given the inclusion for the first time of species that may be regarded as extant ‘giants’ in our analysis, the patterns we observed may be relevant to the ongoing discussion and investigations into the relationship between maximum body size and the diffusion of gases within the tracheal respiratory exchange system of insects (Chown and Gaston, 2010; Harrison et al., 2010). In a broader sense, the patterns we observed in cockroaches have the potential to contribute to the revitalized discussion of curvilinear metabolic scaling relationships between log–log-transformed data in vertebrates (e.g. Moran and Wells, 2007; Kolkotrones et al., 2010). If similar patterns of metabolic deviation at larger body masses are observed when data for other giant insects are available, our findings for cockroaches may be indicative of a more general phenomenon related to the evolution of body size in insects.

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