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Abstract

Metabolic rate determines an individual's rate of resource acquisition, assimilation, growth, survival and reproduction. Studies involving a broad range of taxa and body sizes typically result in whole-organism metabolic rate scaling to the ¾ power of body mass. Competing models have been proposed to explain this allometric relationship. The nutrient supply network model of West *et al*. (1997) proposes that the ¾ power relationship results from the fractal nature of space-filling nutrient supply networks. The model of Kozlowski *et al*. (2003) proposes that the scaling of metabolic rate with body mass will vary from 2/3 to 1 among different taxa, depending on the degree to which increasing body size depends on increasing cell size or number. The present study measured resting metabolic rates across a broad range of body sizes in nymphs of *Melanoplus sanguinipes* F. and also analyzed published reports of metabolic rates in adult Orthoptera. The two sets of data were in close agreement: the scaling exponent for the ontogenetic series of *M. sanguinipes* was 0.92, and for the interspecific, phylogenetically corrected regression with adult Orthoptera, was 1.06. Both scaling exponents were significantly greater than the 0.75 predicted by the nutrient supply network model.

Key words

grasshoppers, *Melanoplus*, ontogenetic growth, metabolic theory of ecology, allometric scaling

Introduction

Metabolic rate of an organism, r, can be related to body mass, m, by a power function:

$$r = am^b$$

Examination of scaling exponents (b) over a broad range of taxa and body sizes, typically show an allometric relationship between body size and metabolic rate, with a value of b typically close to 0.75; that is, for a 4-fold increase in body mass, metabolic rate increases only 3-fold (Schmidt-Nielsen 1997, Savage *et al*. 2004a). Metabolic rates determine an individual's rates of resource acquisition, assimilation, growth, survival, and reproduction (Brown *et al*. 1997, Savage *et al*. 2004b). These individual processes then constrain processes at higher levels of organization: at the population, community, and ecosystem levels (Duncan *et al*. 2007). If body size is a real constraint on metabolic rate, then understanding of the metabolic rate and body-size relationship is a necessary component of life history theory, population dynamics, community organization, and ecosystem functions (Savage *et al*. 2004b). For instance, in physiologically based models of population processes, realistic depiction of acquisition and allocation of resources could involve body size effects.

The relationship of metabolic rate with body size has been a subject of speculation and investigation since Max Rubner, in the 1880's, measured metabolic rates in dogs of various sizes (Schmidt-Nielsen 1997). Rubner (as reported in Schmidt-Nielsen 1997), found that mass-specific metabolic rate declined with increasing size. Kleiber (1961) promoted the idea that the allometry arose from the need to dissipate heat. An elephant with the mass-specific metabolic rate of a mouse would not have enough surface area to dissipate the heat generated. But if this were the sole reason behind the allometry, then metabolism should scale with body size as the ratio of surface to volume, or 2/3, rather than ¾ as is more commonly found (Savage *et al*. 2004a).

Recently, debate has been renewed over theories to account for the ¾ power law, and whether it is really universal or not (Glazier 2005, Kozlowski & Konarzewski 2005, Brown *et al*. 2005, Chown *et al*. 2007, White *et al*. 2007). West, Brown and Enquist developed a theory to explain ¾ scaling based on the fractal dimension of nutrient supply networks (West *et al*. 1997), such as blood vessels in vertebrates or tracheae in insects. According to their theory, metabolic rates are limited by the rate at which an individual can transport materials within the body, this scaling with body mass to the ¾ power. They have extended their theory to include unicelluar organisms based on the geometric relationships between, for instance, the length of a mitochondrium and the surface area of its folded, internal membranes (West *et al*. 1999).

In contrast to models that predict a single scaling exponent, other theories allow for heterogeneous scaling exponents across taxa. For instance, the cell-size theory developed by Kozlowski *et al*. (2003), is based on the idea that metabolic scaling depends on the number and size of cells comprising an organism (Davison 1955). If larger body size within an evolutionary lineage results solely from an increase in cell size, metabolism should scale 2/3 with body size, whereas, if larger body size results solely from an increase in numbers of cells, then the metabolism-body size relationship should be isometric (scaling factor of 1.0). A combination of increased cell size and number would result in scaling exponents between 2/3 and 1, which allows for different exponents across different lineages. In the view of Kozlowski *et al*. (2003), the ¾-power scaling that is commonly observed, results from a combination of heterogeneous exponents derived from many different taxa.

In this paper, we analyze published data to determine metabolic scaling across species of Orthoptera, and additionally describe metabolic scaling in an ontogenetic series within a single species. Glazier (2005) pointed out a distinction between intraspecific studies of growing organisms and interspecific metabolic scaling patterns. Intraspecific scaling relationships reflect ontogenetic changes as an organism grows during its lifetime, whereas interspecific relationships reflect evolutionary changes as species transform in evolutionary

Table 1. Live weights and metabolic rates (MR) from published reports for 32 species of Orthoptera.

Source	Family	Species	Live Weight (g)	MR (J hr^{-1})
Qiu *et al.* 1994	Acrididae	*Chorthippus dubius*	0.083	1.44
Mispagel 1981	Acrididae	*Bootettix punctatus*	0.109	0.87
Fielding & DeFoliart, this study	Acrididae	*Melanoplus sanguinipes*	0.424	6.23
Mispagel 1981	Acrididae	*Melanoplus complanipes*	0.145	1.10
Harrison *et al.* 1991	Acrididae	*Melanoplus bivittatus*	1.500	14.11
Duke &Crossley 1975	Acrididae	*Trimertropis saxatilis*	0.155	1.16
Massion 1983	Acrididae	*Trimertropis suffusa*	0.175	0.82
Forlow & MacMahon 1988	Acrididae	*Trimertropis pallidipennis*	0.281	3.13
Mispagel 1981	Acrididae	*Trimertropis sp.*	0.223	2.01
Forlow & MacMahon 1988	Acrididae	*Arphia psuedonietana*	0.328	3.52
Forlow & MacMahon 1988	Acrididae	*Arphia conspersa*	0.381	3.88
Ashby 1997	Acrididae	*Xanthippus corallipes*	0.731	13.72
Bailey & Riegert 1973	Acrididae	*Encoptolophus sordidus*	0.233	1.65
Armstrong & Mordue 1985	Acrididae	*Schistocerca gregaria*	1.690	14.30
Kirkton *et al.* 2005	Acrididae	*Schistocerca americana*	1.782	22.87
Quinlan & Hadley 1993	Romaleidae	*Taeniopoda eques*	2.043	8.75
Quinlan & Hadley 1993	Romaleidae	*Romalea guttata*	2.874	9.58
Mispagel 1981	Tanaoceridae	*Tanaocerus koebeli*	0.380	2.23
Nespolo *et al.* 2003	Mogoplistidae	*Hophlosphyrum griseus*	0.036	0.29
Prestwich & Walker 1981	Gryllidae	*Oecanthus celerinictus*	0.049	0.58
Prestwich & Walker 1981	Gryllidae	*Oecanthus quadripunctatus*	0.053	0.59
Van Hook 1971	Gryllidae	*Pternonemobius fasciatus*	0.106	1.67
Full *et al.* 1990	Gryllidae	*Teleogryllus commodus*	0.950	20.47
Prestwich & Walker 1981	Gryllidae	*Anurogryllus arboreus*	0.377	2.91
Hack 1997	Gryllidae	*Acheta domesticus*	0.369	4.13
Prestwich & O'Sullivan 2005	Gryllotalpidae	*Scapteriscus borellii*	0.863	4.35
Prestwich & O'Sullivan 2005	Gryllotalpidae	*Scapteriscus vicinus*	0.978	5.89
Mispagel 1981	Tettigoniidae	*Insara covilleae*	0.283	3.17
Stevens & Josephson 1977	Tettigoniidae	*Euconocephalus nasutus*	0.650	8.10
Stevens & Josephson 1977	Tettigoniidae	*Neoconocephalus robustus*	0.870	13.99
Van Hook 1971	Tettigoniidae	*Conocephalus fasciatus*	0.184	2.58
Bailey *et al.* 1993	Tettigoniidae	*Requena verticalis*	0.370	2.46

time. Brown *et al.* (1997) questioned the relevance of intraspecific studies to theories of metabolic scaling, primarily because of the typically narrow range of body sizes involved, but there is no reason why their model should not apply to growing organisms, and they later adapted their model to explain rates of ontogenetic growth (West *et al.* 2001, Gillooly *et al.* 2002). Glazier (2005) argues that intraspecific studies are important to an understanding of metabolic scaling, because similar structural or physiological constraints may set boundaries on what can evolve within, as well as among, species.

Regardless of their relevance to the theory of metabolic scaling, studies of ontogenetic series in Orthoptera are valuable for understanding the metabolic demands of growth and development, and thus we report measurements of metabolic rates of an acridid, *Melanoplus sanguinipes*, over five nymphal stadia.

Methods

Inter-specific metabolic scaling with adult body size.—Published reports of metabolic rate of adults of various species of Orthoptera were used to establish the relationship between size and metabolic rate (Table 1). Additionally, we measured metabolic rates and live weights in 25 adult *M. sanguinipes* from Alaska using methods described below. Most papers reported resting metabolic rate, as opposed to standard metabolic rate, which is measured using fasting animals. All rates were standardized to 25°C by using the Q_{10} value, if the source reported rates at more than one temperature. If Q_{10} was not reported, a value of 2.0 was used, a value derived from enzyme kinetics (Schmidt-Nielsen 1997). Most sources reported body mass as live weight, but those that reported only dry weights were converted to live weight by a factor of 4, an average value from data reported in the literature and measurements made in our laboratory. Some sources reported significantly different body mass or metabolic rate among populations. When significant differences existed, a population near the midpoint of body mass was selected to represent that species.

If metabolic rates for males and females were reported separately, reported values for males only were included in the analysis, because many of the papers, mainly those dealing with the Ensifera, measured the energetic costs of calling and thus reported data for males only (N = 12 spp.). For eight of the species, data were available for males and females. A Wilcoxon paired-sample test of differences in mass-specific metabolic rates between the sexes was nonsignificant (T_+ = 13; $P > 0.50$; N = 8). For the remaining 12 spp., only composite values including both sexes were reported.

Effect of ontogenetic growth on metabolic rates within a species.—Nymphs of *M. sanguinipes* (F2 descendants of grasshoppers collected near Delta Junction, Alaska) were reared in cages indoors, with Romaine lettuce and wheat bran provided *ad libitum*. These grasshoppers were allowed to self-regulate their internal temperature with 75-W incandescent lamps suspended directly above the cages, with a

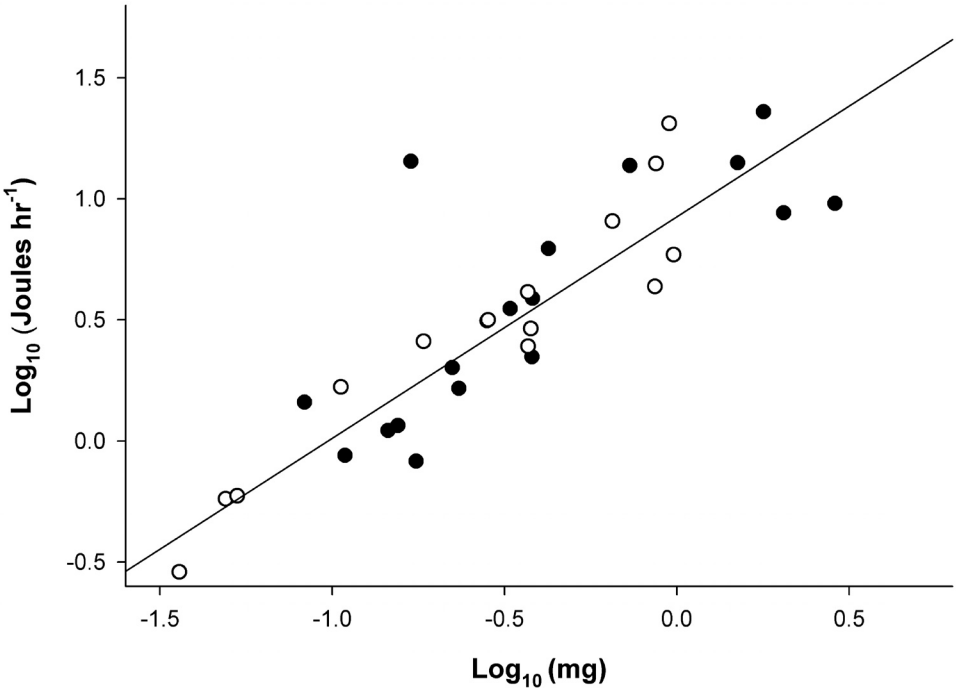

Fig. 1. Metabolic rates *vs* wet mass of adult Orthoptera from published reports, standardized to 25 °C. Open circles: Ensifera, closed circles: Caelifera. Regression line, not corrected for phylogenetic correlation: Y = 0.911 X + 0.925.

16-h photophase.

Open flow-through techniques were used to measure resting respiratory rates in nymphs of *M. sanguinipes* at a range of temperatures from 15 to 39 °C, to determine the effects of temperature on metabolic scaling (Glazier 2005). Adults were not included because the metabolically inert exoskeleton forms a relatively greater proportion of body mass in adults than in nymphs and could consequently distort the analysis. Weight of grasshoppers was determined to the nearest mg immediately before measurements were taken. Nymphs were confined to cylindrical glass chambers (2 cm diameter and 7.5 cm long). The respiration chambers were held within insulated chests equipped with a thermoelectric module, heat sinks, and fans. The thermoelectric device was controlled by a proportional-integral controller (model TC-24-12, TE Technology, Inc., Traverse City, Michigan, USA) which maintained temperature within the chamber to ± 0.5 °C. Room air, from which carbon dioxide and water had been removed by passing through a column of Dryerite and Ascarite, was pulled through the chambers. The air stream then flowed through a column of magnesium perchlorate to remove any water vapor released by the insects before flowing through an infrared CO_2 analyzer (model 6252, Li-Cor, Lincoln, Nebraska, USA). Air flow was regulated by a mass-flow controller (Smart-Trak model 100, Sierra Instruments, Inc., Monterey, California, USA), at a rate of 100 ml min^{-1}, corrected to standard temperature and pressure. Analog signals from the gas analyzers were converted to digital output and recorded with a computer running data acquisition software (DATACAN, Sable Systems, LLC, Las Vegas, Nevada.). Continuous time plots of CO_2 concentration in the air stream were converted to ml h^{-1} based on the flow rate of 100 ml min^{-1}. By integrating the curve against time, the total ml CO_2 in the air stream was determined.

Activity of the grasshoppers within the chambers was monitored with an infrared activity detector (AD-2, Sable Systems, Las Vegas, Nevada, USA) which produces voltage proportional to the amount of movement within the chamber. Only data recorded when the grasshopper was inactive for 5 min or more were included in the analyses.

Open-flow (or flow-through) measurements were used because of this method's greater sensitivity and ability to capture metabolic rates during intervals of inactivity. For purposes of comparison with published metabolic rates, O_2 consumption was estimated from the amount of CO_2 produced per individual. Although an oxygen analyzer was available, its precision was not high enough for open-flow measurements. Therefore, rates of CO_2 production were converted to O_2 consumption using a respiratory quotient (RQ) value of 0.90, determined from measurements using closed-system techniques. Grasshopper nymphs maintained on a diet of lettuce and bran were confined to the same glass chambers described above. Air was drawn from outdoors. Water and CO_2 were removed from the airstream as described above. The chambers were flushed with the outside air for 5 min and then sealed. The amount of time the grasshoppers remained sealed within the chambers was based on size: about 1 h for 1st and 2nd instars to 20 min for larger nymphs. After an appropriate amount of time, the airflow was directed through the chamber again and the bolus of air from the chamber passed through the CO_2 analyzer and an O_2 analyzer (model FC-1B, Sable Systems, Las Vegas, Nevada, USA). The total amount of CO_2 and O_2 passing through the gas analyzers was determined as described above. The ratio of CO_2 produced to O_2 consumed (RQ) was thus determined for 10 nymphs at 3 temperatures: 24, 30, 36 °C.

Data analysis.— Rates of O_2 consumption (ml O_2 $individual^{-1}$ h^{-1})

Table 2. Parameters of phylogenetic generalized least squares models of $\log_{10}$(respiration) on $\log_{10}$(mass) for Orthoptera.

Phylogenetic correction[1]	Slope (s_b)	95% C. L.	Intercept	r^2
null	0.91 (0.071)	0.76-1.06	0.925	0.933
Grafen	1.06 (0.109)	0.99-1.29	0.942	0.751
log Grafen	1.07 (0.112)	0.84-1.30	0.945	0.740
taxonomic	1.02 (0.090)	0.84-1.21	0.926	0.817

[1] See text p.316 for a description of different methods of estimating phylogenetic relatedness.

Table 3. Parameters of linear regression of $\log_{10}$(respiration) on $\log_{10}$(mass) for first- through fifth-instar nymphs of *M. sanguinipes* at different temperatures (°C). N = 25 at each temperature (five individuals each of five instars).

Temperature	Slope (s_b)	95% C. L.	Intercept	r^2
15	0.99 (0.080)	0.82-1.15	0.81	0.89
18	0.79 (0.097)	0.59-0.99	0.78	0.76
21	0.84 (0.056)	0.73-0.96	1.06	0.92
24	0.90 (0.040)	0.82-0.99	1.25	0.96
27	0.94 (0.052)	0.84-1.05	1.35	0.94
30	0.92 (0.044)	0.83-1.01	1.41	0.96
33	0.92 (0.056)	0.80-1.03	1.50	0.93
36	0.93 (0.050)	0.82-1.03	1.62	0.94
39	0.93 (0.044)	0.84-1.02	1.61	0.93

were converted to units of energy (J individual^{-1} h^{-1}) by a factor of 20.1 (Elliot and Davison 1975, Schmidt-Nielsen 1997). For the intraspecific ontogenetic series, the scaling exponent was determined as the slope of the least-squares regression of $\log_{10}$(metabolic rate) on $\log_{10}$(body mass) (Proc GLM, SAS Institute 2002). The method of least-squares was used for this analysis because we assumed that measurement of the independent variable, body weights, involved relatively small errors.

For the interspecific analysis, phylogenetic generalized least-squares regression (phylogr package, version 1.0.6, R Development Core Team 2008) was used to correct for phylogenetic nonindependence of observations. In this method, calculations of regression parameters are modified by incorporation of a matrix of phylogenetic covariances (Grafen 1989, Garland & Ives 2000, Ives & Zhu 2006). The covariances are generally taken to be proportional to the length of branches shared by pairs of species on a phylogenetic tree. For many clades, including Orthoptera, phylogenetic trees are not available in which branch lengths are quantitative estimates of time since divergence. In this case, a taxonomic tree (Eades & Otte 2008) was used to generate the covariance matrix. Because of the arbitrary nature of estimating the degree of relatedness from taxonomic trees (Grafen 1989), four different methods were tested and compared (Table 2). The first method, suggested by Grafen (1989) and referred to in Table 2 as 'Grafen', set the height of each node in the tree equal to the number of daughter taxa minus one. The second method, referred to as 'log Grafen' in Table 2, used the $\log_e$-transformed branch lengths from the first method. The third method was simply the number of shared nodes at the suborder, superfamily, family, subfamily, and genus levels, and is referred to as 'taxonomic' in Table 2. The fourth method, which we refer to as the 'null' method in Table 2, was to set all covariances to zero (*i.e.*, no phylogenetic correlation).

Results

The literature search produced data for adults of 32 different species (Table 1). The range of body mass for adult Orthoptera covered almost two orders of magnitude, from 0.036 to 2.87 g live weight. The interspecific scaling exponent for adult Orthoptera without phylogenetic correction was 0.911 (Table 2, Fig. 1), was remarkably close to the intraspecific scaling exponent for *M. sanguinipes* nymphs. The different methods of estimating relatedness for the phylogenetic corrections produced scaling exponents that were similar to one another and tended to be greater than the uncorrected regression, although confidence intervals overlapped. All methods produced scaling exponents significantly greater than 0.75.

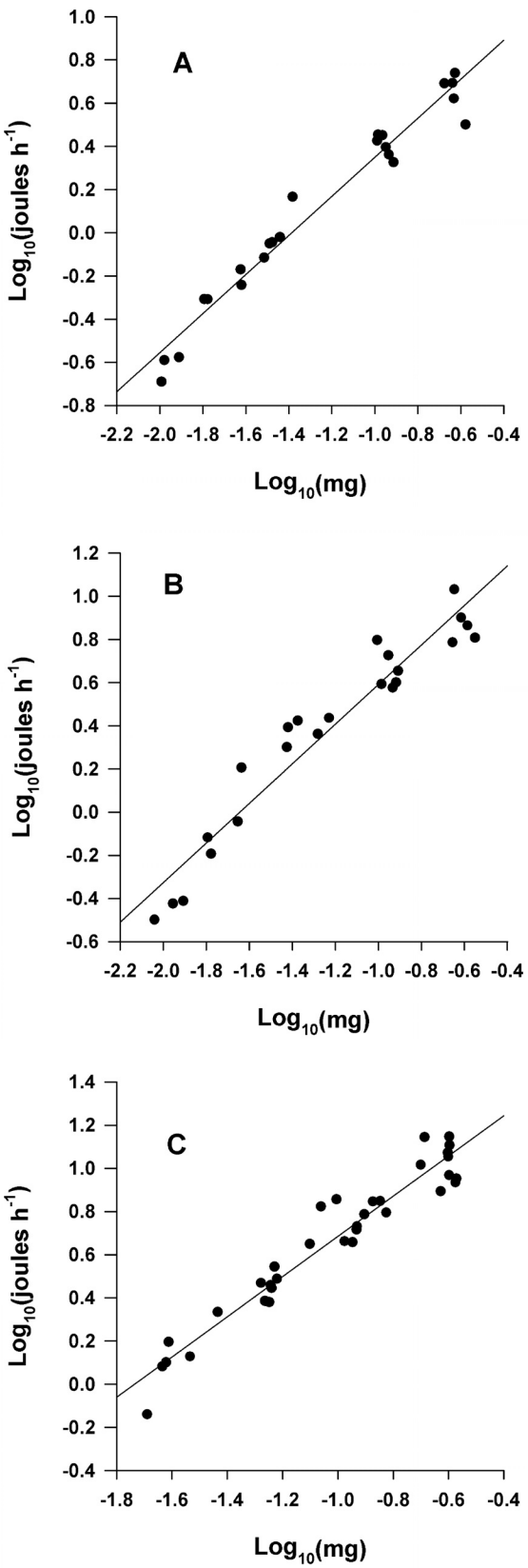

Fig. 2. Metabolic rates of nymphs of *M. sanguinipes* at A) 24°C, B) 30°C, C) 36°C.

Nymphal weights ranged from 0.007 to 0.347 g. At temperatures of 24 °C and greater, the slopes of $\log_{10}$(metabolic rate) on $\log_{10}$(body mass) were all significantly greater than the 0.75 predicted by the West, Brown, and Enquist (1997, 1999) model (Table 3). At these warmer temperatures, the scaling exponent averaged 0.92 (Table 3, Fig. 2). Below 24 °C, the scaling exponent was inconsistent, varying from 0.81 to 1.06, but because of wide confidence intervals the scaling exponents did not differ significantly from those obtained at warmer temperatures (Table 3). Development is very slow at these cool temperatures (Fielding 2004), and these scaling exponents are probably not reliable or relevant to the discussion.

Discussion

This study of 32 spp. of Orthoptera with a range of body mass spanning almost two orders of magnitude, contradicts the existence of a common metabolic scaling exponent of 0.75 among all taxa. Other recent investigations and reviews of metabolic scaling relationships have reported a variety of scaling exponents from different taxa. In a meta-analysis of 127 data sets, White *et al*. (2007) concluded that there was no single exponent relating metabolic rate to body mass for all taxa, and that scaling exponents for ectotherms were particularly heterogeneous. Glazier (2005) reviewed data for intraspecific scaling exponents for 218 species of animals, and found that about half were significantly different from 0.75. Glazier (2005) concluded that " it becomes apparent that the ¾ power law should at most be regarded as a statistical rule or trend rather than as an inviolable law".

Studies of metabolic scaling in arthropods have been inconsistent, ranging from 0.66 to 0.95 (Reichle 1968, Mispagel 1981, Addo-Bediako *et al*. 2002, Niven & Scharlemann 2005, Chown *et al*. 2007). In studies involving Orthoptera, Hack (1997) measured standard metabolic rate (using fasting animals) in adult male field crickets, *Acheta domesticus*. The scaling exponent, derived from a relatively small range of body sizes, was 0.87 (95% CL = 0.566 to 1.180). In the same paper, Hack compared species of Orthoptera and found a scaling exponent of 0.96. His analysis included only 10 species. Ashby (1997) measured metabolic rates of adult male and female *Xanthippus corallipes* from several populations, the adults of which differed in body size from 0.4 to 3.6 g (sexual differences included). The scaling factor (at 35 °C) was about 0.64, much lower than the interspecific analysis reported here. Bailey and Riegert (1973) measured O_2 consumption in nymphs and adults of *Encoptolophus sordidus*. They reported a scaling exponent of 0.85. Their analysis included more late instars and adults than early instars, weighting the analysis more to the heavier end. When recalculated using group means, thus giving each instar equal weight, the scaling exponent was 0.90. If adults were excluded, the scaling exponent was 0.95. Greenlee & Harrison (2004) reported a scaling exponent of 0.77 during ontogenetic growth (including adults) of *Schistocerca americana*.

Some of the variability in scaling exponents reported in the literature may derive from the variety of temperatures at which metabolic rates were measured. At lower temperatures (< 24°C), the scaling exponent for *M. sanguinipes* in the current study was inconsistent and the r^2 were lower. This species cannot complete development when reared at constant temperatures below 21°C. Nespolo *et al*. (2003) also found differences in slope of the metabolic rate/body mass relationship at different temperatures (over a smaller range of body sizes). In the present study, however, at temperatures greater than 21 °C, the scaling exponent was very consistent, varying less than 5% (Table 3).

Metabolic rate and body mass scaling is of interest because this relationship potentially influences many other processes within the organism, e.g., intake, assimilation, and allocation of resources, and also potentially influences higher level population processes, such as carrying capacity and rates of population growth (Savage *et al*. 2004b). Metabolism/body size relationships apparently differ among taxa. Across taxa, the ¾ power may be a good approximation for explorations of community level or ecosystem processes, but for populations, metabolic/mass relationships specific to that particular taxon should be considered. An understanding of the influence of body size on these population processes may provide insights into the population dynamics and life histories of various Orthoptera.

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