

Relationship of metabolic rate to body size in Orthoptera

Authors: Fielding, Dennis J., and DeFoliart, Linda S.

Source: Journal of Orthoptera Research, 17(2): 301-306

Published By: Orthopterists' Society

URL: https://doi.org/10.1665/1082-6467-17.2.301

The BioOne Digital Library (https://bioone.org/) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (https://bioone.org/subscribe), the BioOne Complete Archive (https://bioone.org/archive), and the BioOne eBooks program offerings ESA eBook Collection (https://bioone.org/esa-ebooks) and CSIRO Publishing BioSelect Collection (https://bioone.org/esa-ebooks) and CSIRO Publishing BioSelect Collection (https://bioone.org/csiro-ebooks).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commmercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Relationship of metabolic rate to body size in Orthoptera

Accepted August 10, 2008

DENNIS J. FIELDING AND LINDA S. DEFOLIART

(DJF, LSDF) United States Department of Agriculture, Agricultural Research Service, Subarctic Agricultural Research Unit, P. O. Box 757200, Fairbanks, AK 99775, USA. Email: dennis.fielding@ars.usda.gov; linda.defoliart@ars.usda.gov

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 3/4 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 ³/₄ 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.

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 3/4 as is more commonly found (Savage et al. 2004a).

Recently, debate has been renewed over theories to account for the 3/4 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 3/4 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 34 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 3/4-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 The relationship of metabolic rate with body size has been a 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 ($N=12~{\rm spp.}$). 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

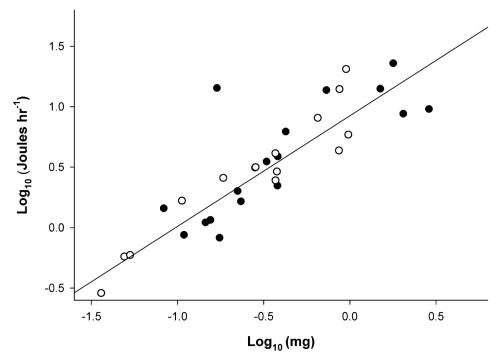


Fig. 1. Metabolic rates vs wet mass of adult Orthoptera from published reports, standardized to $25\,^{\circ}$ C. Open circles: Ensifera, closed circles: Caelifera. Regression line, not corrected for phylogenetic correlation: Y = 0.911 X + 0.925.

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 \pm 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 CO₂ 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 CO₂ 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 CO₂ 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, O2 consumption was estimated from the amount of CO2 produced per individual. Although an oxygen analyzer was available, its precision was not high enough for open-flow measurements. Therefore, rates of CO₂ production were converted to O2 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 CO₂ 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 CO₂ analyzer and an O₂ analyzer (model FC-1B, Sable Systems, Las Vegas, Nevada, USA). The total amount of CO₂ and O₂ passing through the gas analyzers was determined as described above. The ratio of CO, produced to O, consumed (RQ) was thus determined for 10 nymphs at 3 temperatures: 24, 30, 36°C.

Data analysis.— Rates of O₂ consumption (ml O₂ individual⁻¹ h⁻¹)

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

Phylogenetic correction ¹	Slope (s _b)	95% C. L.	Intercept	\mathbf{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 $\log_{10}(\text{respiration})$ on $\log_{10}(\text{mass})$ for first- through fifth-instar nymphs of *M. sanguinipes* at different temperatures (°C). N = 25 at each temperature (five individuals each of five instars).

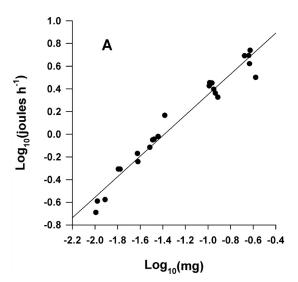
Temperature	Slope (s _b)	95% C. L.	Intercept	\mathbf{r}^2
15	0.99 (0.080)	0.82-1.15	0.81	0.89
18	0.79 (0.097)	0.59-0.99	0.78	0.76
21	0.84 (0.056)	0.73-0.96	1.06	0.92
24	0.90 (0.040)	0.82-0.99	1.25	0.96
27	0.94 (0.052)	0.84-1.05	1.35	0.94
30	0.92 (0.044)	0.83-1.01	1.41	0.96
33	0.92 (0.056)	0.80-1.03	1.50	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

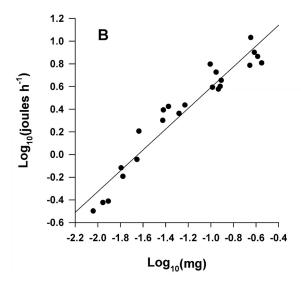
were converted to units of energy (J individual 1 h 1) by a factor of 20.1 (Elliot and Davison 1975, Schmidt-Nielsen 1997). For the intraspecific ontogenetic series, the scaling exponent was determined as the slope of the least-squares regression of \log_{10} (metabolic rate) on \log_{10} (body mass) (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 leastsquares 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 -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.





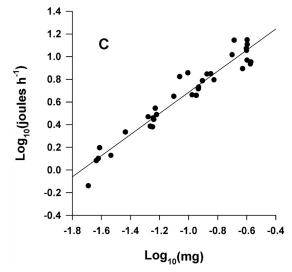


Fig. 2. Metabolic rates of nymphs of M. sanguinipes at A) 24 °C, B) 30 °C, C) 36 °C.

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 O₂ consumption in nymphs and adults of *Encop*tolophus 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 r² 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.

Acknowledgements

We thank A. Pantoja, S. Emmert, and anonymous reviewers for suggestions for improving the manuscript.

References

Addo-Bediako A., Chown S.L., Gaston K.J. 2002. Metabolic cold adaptation in insects: a large-scale perspective. Functional Ecology 16: 332-338.

Armstrong G., Mordue W. 1985. Oxygen consumption of flying locusts. Physiological Entomology 10: 353-358.

Ashby P.D. 1997. Conservation of mass-specific metabolic rate among highand low-elevation populations of the acridid grasshopper *Xanthippus corrallipes*. Physiological Zoology 70: 701-711.

Bailey C.G., Riegert P.W. 1973. Energy dynamics of *Encoptolophus sordidus costalis* (Scudder) (Orthoptera: Acrididae) in a grassland ecosystem. Canadian Journal of Zoology 51: 91-100.

Bailey W.J., Withers P.C., Endersby M., Gaull K. 1993. The energetic costs of calling in the bushcricket *Requena verticalis* (Orthoptera: Tettigoniidae: Listroscelidinae). Journal of Experimental Biology 178: 21-37.

Brown J.H., Enquist B.J., West G.B. 1997. Allometric scaling laws in biology. Science 278: 373.

Brown J.H., West G.B., Enquist B.J. 2005. Yes, West, Brown and Enquist's model of allometric scaling is both mathematically correct and biologically relevant. Functional Ecology 19: 735-738.

Chown S.L., Marais E., Terblanche J.S., Klok C.J., Lighton J.R.B., Blackburn T.M. 2007. Scaling of insect metabolic rate is inconsistent with the nutrient supply network model. Functional Ecology 21: 282-290.

Davison J. 1955. Body weight, cell surface and metabolic rate in anuran Amphibia. Biological Bulletin 109: 407-419.

Duke K.M., Crossley Jr. D.A. 1975. Population energetics and ecology of the rock grasshopper, *Trimerotropis saxatilis*. Ecology 56: 1106-1117.

Duncan R.P., Forsyth D.M., Hone J. 2007. Testing the metabolic theory of ecology: allometric scaling exponents in mammals. Ecology 88: 324.333

Eades D.C., Otte D. Orthoptera Species File Online. Version 2.0/3.3. May, 2008. (http://Orthoptera.speciesfile.org).

Elliot J.M., Davison W. 1975. Energy equivalents of oxygen consumption in animal energetics. Oecologia 19: 195-201.

Fielding D.J. 2004. Developmental time of *Melanoplus sanguinipes* (Orthoptera: Acrididae) at high latitudes. Environmental Entomology 1513-1522.

Forlow L.J., Macmahon J.A. 1988. A seasonal comparison of metabolic and water-loss rates of 3 species of grasshoppers. Comparative Biochemistry and Physiology A-Physiology 89: 51-60.

Full R.J., Zuccarello D.A., Tullis A. 1990. Effect of variation in form on the cost of terrestrial locomotion. Journal of Experimental Biology 150: 233-246.

Garland T., Ives A. R. 2000. Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods. American Naturalist 155: 346-364.

- of size and temperature on developmental time. Nature 417: 70-73.
- Glazier D. S. 2005. Beyond the "3/4-power law": variation in the intra- and interspecific scaling of metabolic rate in animals. Biological Reviews of the Cambridge Philosophical Society 80: 611-662.
- Grafen A. 1989. The phylogenetic regression. Philosophical Transactions of the Royal Society of London, B 326: 119-157.
- Greenlee K.J., Harrison J.F. 2004. Development of respiratory function in the American locust Schistocerca americana I. Across-instar effects. Journal of Experimental Biology 207: 497-508.
- Hack M.A. 1997. The effects of mass and age on standard metabolic rate in house crickets. Physiological Entomology 22: 325-331.
- Harrison J.F., Phillips J.E., Gleeson T.T. 1991. Activity physiology of the 2-Striped Grasshopper, Melanoplus bivittatus - gas-exchange, hemolymph acid-base status, lactate production, and the effect of temperature. Physiological Zoology 64: 451-472.
- Ives A.R., Zhu J. 2006. Statistics for correlated data: phylogenies, space, and time. Ecological Applications 16: 20-32.
- Kirkton S.D., Niska J.A., Harrison J.E. 2005. Ontogenetic effects on aerobic and anaerobic metabolism during jumping in the American locust, Schistocerca americana. Journal of Experimental Biology 208: 3003-3012.
- Kleiber M. 1961. The Fire of Life. Wiley, New York.
- Kozlowski J., Konarzewski M., Gawelczyk A.T. 2003. Cell size as a link between noncoding DNA and metabolic rate scaling. Proceedings of the National Academy of Sciences of the USA 100: 14080-14085.
- Kozlowski J., Konarzewski M. 2005. Is West, Brown and Enquist's model of allometric scaling mathematically correct and biologically relevant? Functional Ecology 18: 283-289.
- Massion D.D. 1983. An altitudinal comparison of water and metabolic relations in 2 species of acridid grasshoppers (Orthoptera). Comparative Biochemistry and Physiology A Physiology 74: 101-105.
- Mispagel M.E. 1981. Relation of oxygen consumption to size and temperature in desert arthropods. Ecological Entomology 6: 423-431.
- Nespolo R.F., Lardies M.A., Bozinovic F. 2003. Intrapopulational variation in the standard metabolic rate of insects: repeatability, thermal dependence and sensitivity (Q(10)) of oxygen consumption in a cricket. Journal of Experimental Biology 206: 4309-4315.
- Niven J. E., Scharlemann J. P. W. 2005. Do insect metabolic rates at rest and during flight scale with body mass? Biology Letters 1: 346-349.
- Prestwich K. N., O'Sullivan K. 2005. Simultaneous measurement of metabolic and acoustic power and the efficiency of sound production in two mole cricket species (Orthoptera: Gryllotalpidae). Journal of Experimental Biology 208: 1495-1512.
- Prestwich K.N., Walker T.J. 1981. Energetics of singing in crickets: effect of temperature in three trilling species (Orthoptera: Gryllidae). Journal of Comparative Physiology B 143: 199-212.
- Qiu X.-h., Li H.-c., Yang Z.-g. 1994. Respiratory metabolism and population energy expenditure of grasshopper Chorthippus dubius (Zub.). Acta Entomologica Sinica 37: 417-425.
- Quinlan M.C., Hadley N.F. 1993. Gas-exchange, ventilatory patterns, and water-loss in two lubber grasshoppers - quantifying cuticular and respiratory transpiration. Physiological Zoology 66: 628-642.
- R Development Core Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. (http://www.r-project.org).
- Reichle D. E. 1968. Relation of body size to food intake, oxygen consumption, and trace element metabolism in forest floor arthropods. Ecology 49: 538-542.
- SAS institute. 2002. SAS for Windows. Ver. 9.1. Cary, NC, USA.
- Savage V. M., Gillooly J. F., Woodruff W. H., West G. B., Allen A. P., Enquist B. J., Brown J. H. 2004a. The predominance of quarter-power scaling in biology. Functional Ecology 18: 257-282.
- Savage V. M., Gillooly J. F., Brown J. H., West G. B., Charnov E. L. 2004b. Effects of body size and temperature on population growth. The American Naturalist 163: 429-441.
- Schmidt-Nielsen K. 1997. Animal Physiology: adaptation and environment. 5th ed. Cambridge University Press, Cambridge, UK.

- Gillooly J.F., Charnov E.L., West G.B., Savage V.M., Brown J.H. 2002. Effects Stevens E.D., Josephson R.K. 1977. Metabolic rate and body temperature in singing katydids. Physiological Zoology 50: 31-42.
 - Van Hook R.I. 1971. Energy and nutrient dynamics of spider and orthopteran populations in a grassland ecosystem. Ecological Monographs 41: 1-.
 - West G.B., Brown J.H., Enquist B.J. 1997. A general model for the origin of allometric scaling laws in biology. Science 276: 122-126.
 - West G.B., Brown J.H., Enquist B.J. 1999. The fourth dimension of life: fractal geometry and allometric scaling of organisms. Science 284: 1677-1679.
 - West G.B., Brown J.H., Enquist B.J. 2001. A general model for ontogenetic growth. Nature 413: 628-631.
 - White C.R., Cassey P., Blackburn T.M. 2007. Allometric exponents do not support a universal metabolic allometry. Ecology 88: 315-323.