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Scaling of gas exchange cycle frequency in insects

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Previously, it has been suggested that insect gas exchange cycle frequency (f_C) is mass independent, making insects different from most other animals where periods typically scale as $\text{mass}^{-0.25}$. However, the claim for insects is based on studies of only a few closely related taxa encompassing a relatively small size range. Moreover, it is not known whether the type of gas exchange pattern (discontinuous versus cyclic) influences the f_C –mass scaling relationship. Here, we analyse a large database to examine interspecific f_C –mass scaling. In addition, we investigate the effect of mode of gas exchange on the f_C –scaling relationship using both conventional and phylogenetically independent approaches. Cycle frequency is scaled as $\text{mass}^{-0.280}$ (when accounting for phylogenetic non-independence and gas exchange pattern), which did not differ significantly from $\text{mass}^{-0.25}$. The slope of the f_C –mass relationship was shallower with a significantly lower intercept for the species showing discontinuous gas exchange than for those showing the cyclic pattern, probably due to lower metabolic rates in the former. Insects therefore appear no different from other animals insofar as the scaling of gas exchange f_C is concerned, although gas exchange f_C may scale in distinct ways for different patterns.

Keywords: allometry; scaling; phylogenetic-independent contrasts; ventilation; size effects

1. INTRODUCTION

The ways in which physiological and life-history characteristics scale with body size have profound implications for organism functioning and ecology. Knowledge of the scaling of metabolic rate and its temperature dependence can be used to explain much of the variation found in mortality rates, population growth rates, species richness, energy flux and trophic dynamics (Brown *et al.* 2004). Differences in the scaling of various physiological rates may also help explain variation in performance limits (Weibel *et al.* 2004) and the survival of stress or disturbance (McNab 2006). In consequence, the scaling of organismal characteristics has been widely investigated.

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Although much is known about scaling in insects, several significant aspects of insect physiology remain underexplored. In particular, how ventilation frequency and cycle frequency (f_C) in the discontinuous gas exchange (DGE) and cyclic gas exchange (CGE) patterns shown by many insects at rest (Marais *et al.* 2005) scale with mass have been poorly investigated. The few studies undertaken to date suggest that ventilation frequency increases with mass (Greenlee *et al.* 2007), while f_C is size invariant (Lighton 1991; Klok & Chown 2005). These findings are unusual. In endothermic vertebrates, ventilation frequency typically scales as $\text{mass}^{-0.25}$ (e.g. Stahl 1967; but also see Mortola & Limoges 2006). More generally, periods in a wide variety of organisms tend to scale negatively (Peters 1983), and apparently, sufficiently and frequently as $\text{mass}^{-0.25}$ for quarter-power scaling to be considered pervasive (Brown *et al.* 2004).

In consequence, it appears that gas exchange in insects differs fundamentally from ventilation in endotherms, and that insects also form an unexplained exception to the way rates typically scale with mass. However, all of the studies of the scaling of f_C in insects are characterized by one or more problems that make it difficult to draw general conclusions from them. First, a few species are typically examined, thus reducing the power of the analysis and probably biasing the estimate of the regression slope (see Quinn & Keough 2002). Second, the studies tend to cover a small size range which may further influence the likelihood of detecting significant relationships. Finally, most studies concern species from a single taxon and/or use corrections for phylogenetic non-independence, which do not allow the form of the relationship to be estimated. Therefore, it is difficult to discern whether the difference between insects and other animals is real or is instead a consequence of the approach adopted. Here, we resolve this question by investigating the scaling of gas exchange f_C across a wide mass (four orders of magnitude) and taxonomic (80 species from 14 orders) range of insects that show either CGE or DGE at rest, using a phylogenetic generalized least-squares (PGLS) approach to correct for phylogenetic non-independence. In addition, we also determine whether the relationship between mass and f_C differs among species showing CGE or DGE patterns.

2. MATERIAL AND METHODS

A database of f_C and body mass (M_b) was compiled from the primary literature on insect gas exchange patterns measured using gas analysis (see Marais *et al.* (2005) and White *et al.* (2007) for additional details; electronic supplementary material, S1). Species for which f_C was identified by means of abdominal pumps were excluded. Although a relationship exists between gas exchange f_C and abdominal or thoracic pumping (see Chown & Nicolson 2004), ventilation of the latter kind may take place several times within a single ‘burst’ or open phase during DGE. Thus, ventilation frequency as a consequence of muscular contraction and gas exchange f_C are not functionally equivalent.

Cycle duration was transformed to gas exchange f_C (in mHz). The gas exchange pattern (continuous, cyclic or discontinuous) was assigned based on the method provided by Marais *et al.* (2005). For species that show more than one of the three primary gas exchange patterns, a simple majority rule was used to identify the predominant pattern and only data from that pattern were included. Peaks in CO_2 production are relatively reliable indicators of burst timing and only burst frequency was extracted (for rationale, see White *et al.* 2007). In some cases, it was necessary to sum the durations of the C-, F- and O-periods to obtain an

Table 1. Results of phylogenetically adjusted (phylogenetic) or conventional PGLS analyses. (Frequency is always treated as the dependent variable. Type, classification for gas exchange pattern (CGE or DGE). λ , a measure of phylogenetic correlation. Type and mass \times type columns present coefficients from the regression analyses (where significant). The coefficient for type quantifies the extent to which the intercept for DGE species differs from that for CGE species. AIC, Akaike information criterion; w_i , Akaike weight. Cycle frequency in mHz; mass (M_b) in g. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; n.s., not significant.)

model variables	group	model	λ	AIC	w_i	slope \pm s.e.	type	mass \times type
f_C versus M_b	all	conventional	0	97.32	0.002	$-0.366 \pm 0.050^{***}$		
	all	phylogenetic	0.82	90.80	0.047	$-0.342 \pm 0.062^{***}$		
f_C versus M_b + type	all	conventional	0	96.17	0.003	$-0.338 \pm 0.052^{***}$	n.s.	
	all	phylogenetic	0.84	85.47	0.679	$-0.280 \pm 0.064^{***}$	$-0.335 \pm 0.123^{**}$	
f_C versus M_b + type + $M_b \times$ type	all	conventional	0	97.11	0.002	$-0.280 \pm 0.077^{***}$	n.s.	n.s.
	all	phylogenetic	0.84	87.34	0.267	$-0.261 \pm 0.083^{***}$	$-0.364 \pm 0.147^*$	n.s.
f_C versus M_b	CGE	phylogenetic	0.79	48.58		$-0.297 \pm 0.092^{**}$		
	DGE	phylogenetic	1	41.15		$-0.195 \pm 0.085^*$		

estimate for DGE frequency. Similarly, cycle duration in cyclic species was in some cases calculated as the sum of inter-burst and burst phase durations and then transformed to f_C . All data were log transformed prior to analyses. Species that showed only continuous patterns were excluded from the database since extraction of pattern frequencies from these VCO₂ traces is often impracticable and/or requires access to the raw data files (Nespolo *et al.* 2007). Of the 80 species examined, 49 were classified as 'discontinuous' and 31 as 'cyclic' gas exchangers.

An insect phylogeny was built based on Marais *et al.* (2005), Chown *et al.* (2007) and Greenlee *et al.* (2007; electronic supplementary material, S2). PGLS were performed following Halsey *et al.* (2006). In the PGLS analysis, an estimate of the phylogenetic covariance is given by λ . Each model was implemented either with or without phylogenetic adjustment. Because the branch lengths in the phylogeny are unknown, the PGLS analysis was conducted with the assumption that all branches in the phylogeny were of equal length. This is equivalent to a punctuational model of evolution in which all changes occur at speciation events.

Three models for the influence of M_b on f_C were examined using the two approaches outlined previously. The models either included M_b , M_b and gas exchange type, or both variables and their interaction term. The analyses were repeated separately for each group to derive slope values. The Akaike information criterion (AIC) and Akaike weights (w_i) were used to select the most appropriate model.

3. RESULTS

No significant difference was found among the ordinary least squares slopes of the f_C - M_b scaling relationship for the DGE and CGE groups (table 1). However, the inclusion of phylogenetic information substantially improved model fit, with the best model including gas exchange type ($w_i = 0.679$). With a term for gas exchange type in the model, the overall slope of the M_b - f_C relationship (-0.280) did not differ significantly from -0.25 ($t_{79} = 0.468$; $p > 0.5$). The second most likely model for the scaling of f_C was the phylogenetic model that also included an interaction term between M_b and gas exchange type ($w_i = 0.267$), albeit that the interaction term was not significant (table 1). The M_b - f_C slope was shallower in species showing DGE than those with CGE (figure 1). The latter had an M_b - f_C slope marginally greater than -0.25 ($t_{30} = 1.929$; $p = 0.0316$), while the former did not differ significantly from -0.25 ($t_{48} = 0.647$; $p = 0.26$), while their intercepts differed considerably.

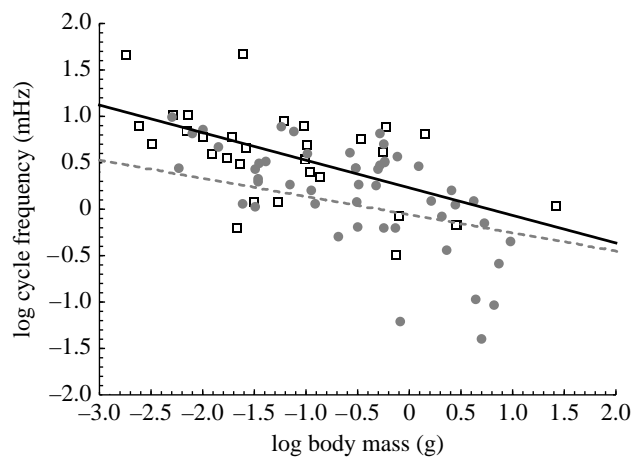


Figure 1. Interspecific mass scaling relationship (phylogenetically independent slopes) of gas exchange cycle frequency (f_C) according to the gas exchange pattern in 80 insect species from 14 orders. Squares, CGE; circles, DGE.

4. DISCUSSION

These results show that, in insects, gas exchange f_C scales negatively, approximately as $\text{mass}^{-0.25}$. Thus, at least for this characteristic of breathing, insects are no different from other animals, in which rates scale interspecifically at broad taxonomic levels with an exponent of -0.25 (see Peters 1983), and no different from those vertebrate taxa where ventilation rate scales similarly. However, the explanatory power of f_C -scaling in insects is weaker than scaling of ventilation frequency in mammals ($r^2 = 0.41$ here and 0.83 in mammals; Stahl 1967). Evolutionary responses to environmental factors probably contribute to the variation in insects (White *et al.* 2007).

For insects, investigations of the scaling of f_C in narrower taxonomic groups have revealed mass independence (e.g. Lighton 1991). This difference may be artefactual (e.g. small size range/limited taxa investigated) or it may reflect variation in the exponents between narrow taxonomic investigations and those covering a broader range of species, as has been found for investigations of the scaling of metabolic rate (Chown *et al.* 2007). In the absence of additional

information, and given the invariance in outcomes among the earlier studies, it seems probable that previous studies have inadvertently been confounded by limited size/taxonomic range. What is apparent is that regardless of whether ventilation frequency scales positively or is size invariant (Greenlee *et al.* 2007), this is very different from the broader pattern revealed in the present study. In consequence, it is difficult to determine why the present results differ from those of Greenlee *et al.* (2007). Nonetheless, it is important to note that abdominal pumping (as measured by Greenlee *et al.* 2007) and gas exchange f_C (this study) are not equivalent because several abdominal pumping cycles may take place during a single open phase of at least the DGE (Chown & Nicolson 2004). Future work will be required to establish why these two characteristics of gas exchange appear to differ in their scaling relationships, and which may be considered the closest analogy to ventilation frequency in other animals. To date, the distinction has not been made clear.

Despite suggestions that CGE and DGE might be different manifestations of the same pattern (Gray & Bradley 2006), the M_b - f_C relationship differs between them. The significant difference in intercepts is probably due to the lower metabolic rate in DGE versus CGE. A much weaker difference in slope, which was not included in the best-fit model, might represent the outcome of selection for DGE, the derived condition in insects (Marais *et al.* 2005). Lower f_C at smaller sizes might affect respiratory water savings in the same way as longer DGE cycles do in animals from xeric environments (Chown & Davis 2003; White *et al.* 2007). However, evidence for such an effect is presently weak. A firm test of these proposals will require comprehensive analysis of the relative roles of size, cuticular and respiratory water loss, and environmental water availability in determining gas exchange pattern. With appropriately focused investigations of species across the size and environment spectra, such analyses could be readily performed.

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