

LETTER

Locomotion Reveals Contrasting Responses in Body Mass-Scaling of Metabolic Rates Between Winged and Wingless Arthropods

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ABSTRACT

Metabolism fuels fundamental biological processes and commonly scales with body mass with an exponent, b , between 2/3 and 1. We, here, explore how differences in physical activity can reveal contrasting interspecific metabolic scaling between major groups of arthropods. The Metabolic-level Boundaries Hypothesis predicts that increased behavioural activity increases b . We test this hypothesis by comparing b during flight, non-flight locomotion, and rest in winged and wingless insects, and spiders. We find that interspecific b values increase with activity only with flight in winged insects which co-occurs with a substantial flight-related rise in metabolic level. Spiders show a shallower interspecific metabolic scaling relative to insects, potentially reflecting slower life-history strategies with increasing body size. Consequently, large resting or walking insects consume 6–15 times more oxygen than do spiders of corresponding size and activity level. These fundamental differences offer new insights into the evolutionary dynamics of arthropod energetics.

1 | Introduction

Metabolism reflects the collective biochemical processes that transform energy and materials into biological structures and functions (Glazier 2005). Understanding metabolic rates is critical because of their profound physiological, ecological and evolutionary implications (Brown et al. 2004; Humphries and McCann 2014). Aerobic respiration is the main contributor of metabolic energy production in heterotrophs and is strongly linked to individual body size (Brown et al. 2004; Glazier 2005; Kleiber 1932; Peters 1983). The relationship between respiration rate (R) and body mass (M) is commonly described as a power function of the form: $R = aM^b$ (Kleiber 1932), where a is the

mass-scaling coefficient, and b is the metabolic mass-scaling exponent. Here, we use the rate of oxygen consumption as an indirect measure of (aerobic) metabolic scaling, in line with most of this field (Glazier 2010; Harrison et al. 2022; White et al. 2022). Observed variation in intra- and inter-specific b values has been associated with various intrinsic differences (Glazier 2022; Glazier and Gjoni 2024), including behaviour (Duell et al. 2022; García-Gómez et al. 2024; Glazier 2010, 2014), developmental stage (Glazier 2024), ontogenetic body surface area change (Hirst et al. 2014) and extrinsic ecological changes such as temperature, habitat and mortality risk (Glazier 2010, 2014; Harrison et al. 2022; Killen et al. 2010; Norin 2022; Tan et al. 2019).

To explain interspecific metabolic scaling differences among animal groups, we need to understand the evolution of energetic differences in relation to adult body size among species, within a clade or functional group. An adaptationist approach is to examine whether there is a change in life history (Kozłowski et al. 2020; White et al. 2022), including the energetic pace of life, as species size increases. Such a change could be towards an energetically faster-paced adult life history (e.g., greater investment in production, including reproduction, traded off against survival) with increasing species size in one clade, which could increase b relative to that of a contrasting clade, in which larger species exhibit a greater slowing of adult life history, and a more pronounced decline in energetic cost with increasing body size. A slowing of the adult life history as species size increased could achieve increased survival, by reducing encounters with natural enemies or reducing metabolic costs that could otherwise increase starvation risk; such slowing of metabolic rates in larger species would reduce b , though would likely be traded off against reduced production rates. An alternative, but complementary, approach to understanding observed differences in b between different groups of phylogenetically or ecologically related organisms (Burgess et al. 2017; DeLong et al. 2010; Glazier 2005, 2010), examines size-related changes in proximate mechanisms (Duell et al. 2022; Glazier 2014; Harrison et al. 2022): these include changes in resource supply or waste removal capacity (feeding, respiratory and excretory surfaces and transport networks); in energy demands, such as for food handling, defence, locomotion or production; and in associated changes in body composition that alter the energy requirements per unit of body mass.

Here, we focus on differences in interspecific scaling of oxygen consumption between groups of arthropods varying in levels and types of physical activity. The Metabolic-level Boundaries Hypothesis (MLBH) (Glazier 2005, 2010), specifically addresses the effects of metabolic activity. The MLBH posits that ecological differences among organisms govern their metabolic level, or the elevation of the metabolic scaling relationship, which in turn influences the scaling exponent b (Glazier 2010). Metabolic level (L) can be approximated as the mass-specific metabolic rate at the geometric midpoint of a respiration rate-body mass relationship (Glazier 2009, 2010). The MLBH predicts that as L increases during physical activity above the resting state (which excludes quiescent states such as torpor or diapause), b should also increase. This increase in the b value towards 1 could happen if metabolic rates, heavily influenced by muscular activity, are likely to scale with muscle mass, which is often proportional to body mass (Glazier 2010). As a result, metabolic rates are expected to scale increasingly with tissue mass, or volume, as activity levels increase, causing b values to approach 1. To achieve an interspecific increase in b value with increased activity, measured in adults among species with different body sizes, a disproportionately greater increase in metabolic rate during activity relative to that at rest, would be required with increasing species body size. An alternative analysis that provides a similar prediction considers that metabolic rate or power is the product of force and velocity, and force is proportional to the cross-sectional area of body and appendage muscles, and hence scales with an exponent near to $2/3$ if body size increase is isomorphic (Hirt et al. 2017). Moreover, exploratory movement velocity in insects scales positively with body mass as $M^{0.19}$ (Hirt et al. 2017)

and walking speed among different-sized individuals across two families of vagrant spiders scales as $M^{0.20}$ for mean speed and $M^{0.35}$ for maximum speed (Boehm et al. 2021). Therefore, by multiplying the scaling of force and velocity we can predict the value of b to increase to between about 0.86 and 1.02 (i.e., $[0.67 + 0.19$ for mean speed] and $[0.67 + 0.35$ for maximum speed]), at least for non-flight locomotion, if force is proportional to muscle cross-sectional area. Therefore, b is expected to increase with increased activity level, although its actual predicted value will depend on whether body size increase across species is isomorphic in form, and whether activity levels vary with species body size.

Among species of terrestrial arthropods, the MLBH prediction that the value of b is higher during activity than at rest, is supported by data on energy use in insects during flight (Glazier 2010; Niven and Scharlemann 2005). However, to our knowledge, no attempt has been made to evaluate this prediction also during non-flight locomotion in both winged and wingless insects, or to compare such patterns to other globally widespread terrestrial arthropods, such as spiders. Insects represent over 60% of all extant arthropod species (Chown et al. 2007), a phylum dominating global animal abundance and biomass (McGavin 2001); therefore, quantifying their metabolic scaling relationship has important implications for understanding energetics and nutrient flow through natural ecosystems. The inclusion of spiders in testing the MLBH is important as they commonly co-occur with insects, but are often considered to have lower metabolic rates than insects (Anderson 1970), although this suggestion is contentious (Lighton and Fielden 1995). Whereas lower metabolic rates and a lower scaling exponent have been reported for spiders in comparison to insects (McCue et al. 2016), others have reported that a single relationship sufficiently describes metabolic scaling of both these arthropod groups (Lighton and Fielden 1995). Hence, the question of whether spiders and insects have different metabolic rates and scaling exponents remains unresolved. How metabolic rate scales with body size across winged and wingless insect species also remains a topic of debate (Chown et al. 2007; Riveros and Enquist 2011), particularly whether the relationship follows the 0.75 exponent predicted by resource supply models (Banavar et al. 2010), including the Metabolic Theory of Ecology (MTE; Brown et al. 2004). Our study therefore examines how locomotion type and evolutionary history, shape metabolic scaling, providing insights into the variability between winged and wingless arthropods.

Previous attempts to compare between spiders and insects have tended to ignore phylogenetic relationships and have focused predominantly on resting metabolic rates (Lighton and Fielden 1995; McCue et al. 2016). However, flight and non-flight locomotor activities provide a potentially strong contrast with resting metabolism in nature. Moreover, the presence of wings, or the capacity for flight, may influence metabolic rates even at rest. While a previous study compared resting metabolic rates between winged and wingless insects and spiders (Glazier 2010), revealing differences among these groups, it did not examine variation in their active metabolic rates. Metabolic rates associated with non-flight locomotion are important to consider in winged and wingless insects to test how the presence of wings influences metabolic requirements during similar non-flight locomotor activity (directed walking and running) within insects, and between insects and spiders.

To rigorously compare insects and spiders and to test the MLBH, we assembled the largest comparative dataset on active metabolic rates for both groups from the literature. Additionally, we integrated published datasets on resting metabolic rates for insects (Chown et al. 2007) and spiders (McCue et al. 2016). We tested the hypotheses that: (1) metabolic rate scales differently with body size across arthropod groups. While Glazier (2010) reported steeper metabolic scaling in spiders than in winged insects, other studies, such as McCue et al. (2016), suggest the opposite pattern, with steeper scaling in insects. (2) Active metabolic rate scales more steeply than resting metabolic rates in all three arthropod groups as predicted by the MLBH. (3) Both winged and wingless insects have higher (non-flight) active and resting metabolic levels (denoted as L_{nf} and L_r , respectively) than spiders. This pattern is predicted from previous findings that insects, particularly winged species, tend to have higher metabolic rates due to their more active lifestyles and greater reliance on energetically demanding locomotion strategies (Chown et al. 2007; Reinhold 1999). Finally, (4) winged insects have higher L_{nf} and L_r than wingless insects. This can be caused by the overhead costs of maintaining flight capability, including the associated musculature. Previous research suggests that insects capable of flight generally have higher baseline metabolic rates than their flightless relatives, even when controlling for body mass (Reinhold 1999). While wingless insects may invest more in leg musculature for terrestrial non-flight locomotion, this does not necessarily translate into equivalent metabolic costs, as leg muscles typically rely on lower-energy, slow-twitch fibres (Marden and Allen 2002).

Our study highlights the differences in interspecific metabolic scaling within arthropods, between winged insects and wingless insects and spiders (Glazier 2010). We show that an increase in isometric metabolic scaling is only found for flight across winged insect species. In contrast, wingless insects and spiders maintain consistent metabolic scaling across activity levels, with lower exponents in spiders. These findings support the predictions of the MLBH for winged insects, but not for wingless insects and spiders. Here, metabolic scaling appears more influenced by activity in highly muscular, more athletic flying insects, compared to their less muscular and less active counterparts (Glazier 2008, 2010). Our study highlights the role of locomotor strategy and probably of speed—both locomotor and life history in shaping metabolic scaling patterns across arthropods, the world's largest group of animals.

2 | Methods

2.1 | Data Collection

We obtained species-specific rates of oxygen consumption during locomotor activity by searching the literature that provided these rates during flight and non-flight locomotion, such as walking or running, depending on the species. We carried out literature searches on Web of Science and Google Scholar up to the end of 2019 using the search terms arthropod/insect/spider + active/flight/non-flight locomotion/resting + respiration/respiration rate*, and [*<insect or spider order/infracorder>*] + [activity type] + metabolic rate*/metabolism. We further identified related literature from reference lists of relevant papers.

We identified data for oxygen consumption from published compilations of Chown et al. (2007) and McCue et al. (2016). Original data on resting rates were obtained from the primary publications whenever possible, to ensure that the data satisfied our own screening criteria (see below). We also included more data from additional literature searches. Only rates of oxygen consumption measured in adults were used to avoid variation arising from differences in developmental stage. Finally, although we use the term 'oxygen consumption rate' to describe our measurements, we do use 'metabolic rate', 'metabolic level' or 'metabolic scaling' where we want to emphasise the link with the metabolic scaling literature.

For flight and non-flight locomotion, if the rate of oxygen consumption at different running and flying speeds were available, we selected the running and flying speeds measured at the air temperatures that were closest to the corresponding field temperatures reported in the study, if available, or otherwise nearest to a standard temperature of 22°C. In addition, we included rates of oxygen consumption at rest where a resting state could be reasonably assumed from cyclic gas exchange, as this is commonly indicative of a resting state (Chown and Nicolson 2004). However, as gas exchange information was not always available, animals observed to be motionless, or displaying minimal movements, were also included. When multiple measurements for the same species were available, we reduced multiple measurements to a single data point by first selecting for flow-through respirometry methods, and then any indication of real-time monitoring of activity. This ensured that each species was represented by only one metabolic rate estimate in our final dataset.

If data were available for both males and females of a species, we obtained a mean value from both sexes. While our primary focus was on oxygen consumption rates, we also included studies that reported metabolic rates in other units (e.g., Watts or CO₂ production). We standardised all measures of oxygen consumption rate to $\mu\text{L O}_2 \text{ ind}^{-1} \text{ h}^{-1}$ by converting energetic measures using an oxyjoule equivalent of 20 J mL O₂⁻¹ (Makarieva et al. 2008) and by converting CO₂ production data using a respiratory quotient (RQ) of 0.84 (Lighton et al. 1987) when specific RQ values were not provided. We standardised body mass to wet mass (mg WM) assuming that dry mass is 30% that of wet mass (Edney 1977), unless the original study suggested a different conversion factor, which we followed. We also noted the presence or absence of wings for each insect species (referred to as wing status). However, it was not always possible to ascertain the functionality of wings, as winged insects may differ greatly in their capacity for flight. Although the categorical classification of wing status as presence or absence is simplistic, such a classification may help to identify general metabolic differences associated with varying potential for flight.

2.2 | Data Analyses

2.2.1 | Temperature Correction for Metabolic Rate Estimates

To account for the effect of temperature on metabolic rate measurements, we standardized all oxygen consumption estimates using a Q_{10} correction factor of 2.5. This value is based

on commonly observed thermal sensitivities of arthropod metabolic rates reported in previous studies (e.g., Irlich et al. 2009; Seebacher et al. 2015).

The oxygen consumption rate at the reference temperature ($R_{\text{corrected}}$) was calculated for each observation using the following equation:

$$R_{\text{corrected}} = R_{\text{obs}} \times Q_{10}^{\frac{(T_{\text{ref}} - T_{\text{obs}})}{10}}$$

where R_{obs} is the observed rate of oxygen consumption at temperature T_{obs} (°C), T_{ref} is the reference temperature (20°C) and Q_{10} is assumed to be 2.5.

We implemented this correction in R using a custom function and applied it to all oxygen consumption rate data in our dataset. The corrected values were then used for subsequent analyses of metabolic scaling relationships across taxa.

However, given the uncertainty surrounding Q_{10} values, particularly for flight metabolism in large insects, where temperature sensitivity may be low or variable (Johnson et al. 2023), we performed additional analyses for flying insects using Q_{10} values of 2 for small and 1 for large insects (> 55 mg WM, identified by Duell et al. 2022).

2.2.2 | Model Fitting and Prior Choice

We used a Bayesian likelihood approach for our analysis because it is flexible, accommodates negative log-transformed values and allows for accurate modelling through adaptable functions and prior distributions. We first translated our hypotheses into the following linear model:

$$\log M \sim \text{Normal}(\mu, \sigma)$$

$$\mu = \alpha + \beta X + \delta$$

where log aerobic metabolic rate (M) is assumed to be normally distributed with an unknown mean (μ) and standard deviation (σ). The mean (μ) is defined by a linear model that includes an intercept (α), a random effect (δ), and fixed predictors. For winged insects, we included three fixed predictors—body size, metabolic activity type (resting, flight-active and non-flight-active)—whereas for wingless insects and spiders, we included two predictors (resting and non-flight-active), all represented by βX . These parameters contain all main effects (body size and metabolic activity type) for which we had a priori expectations. The predictor and response data consist of individual measurements of rate of oxygen consumption and body size. All variables were $\log_{10}$ -transformed before model fitting. After transformation, predictor variables were centered and scaled to improve model fitting and interpretation.

2.2.3 | Bayesian Analysis

Models were assessed using Bayesian inference, to estimate the probability of a hypothesis or set of parameters, θ , given the data, y , or $p(\theta|y)$ (Hooten and Hobbs 2015) (e.g., the probability that the metabolic scaling slope is different than the value of 0.75 expected

from the Metabolic Theory of Ecology, MTE; Brown et al. 2004), rather than in the probability of our data per se (Korner-Nievergelt et al. 2015). Specifically, we generated joint posterior distributions for each model via the Hamiltonian Monte Carlo method using *rstan* (Stan Development Team 2022) via the *brms* (Bürkner 2017) package in R (version 4.3.2; R Core Team 2022).

We ran four independent chains for 4000 iterations of each model, with the first 1000 iterations discarded as warm-up. We set the prior for the main slope of body size at Normal (0.75, 2), corresponding to the 0.75 slope predicted by the MTE (Brown et al. 2004). All other priors were centered at zero with Normal (0, 1), except for sigma, which was assigned Exponential (1). We assessed chain convergence using the Gelman-Rubin statistic, ensuring that all *Rhat* values were < 1.1 (Gelman and Rubin 1992). Finally, we evaluated model fit using posterior predictive plots (Conn et al. 2018). Here, we used the joint posteriors to summarise the median and 95% credible intervals of parameters of interest, including derived quantities, such as marginal slopes (Hooten and Hobbs 2015).

We then estimated the mean and 95% credible intervals (CrI) for each model parameter and for each derived quantity, from the joint posterior distribution of each model. We also estimated the probability that a parameter was greater or less than zero by dividing the number of estimates that were greater than or less than zero by the total number of posterior estimates ($n = 4000$) (Korner-Nievergelt et al. 2015). Finally, we applied posterior predictive checks, in which we generated 4000 posterior predictions across each value of a predictor variable, to assess model performance. To ensure that model predictions were reasonable, we plotted the median and 95% CrI of the predicted values against the observed values. In all cases, the observed values were similar to the predicted values, indicating that model predictions were reasonable. Last, to assess how well the model fit the data, we measured the correlation between observed and predicted values.

To compare differences in the rate of oxygen consumption between insects and spiders, and to test the MLBH predictions, we used metabolic level per gram of body mass (L) (Glazier 2009) as a geometric mid-point (of a logged range) for our arthropod sample to minimize bias when comparing across different body sizes (Glazier 2008, 2022).

3 | Results

3.1 | Scaling of Active and Resting Metabolic Rates With Body Size

Rates of oxygen consumption depend differently on body mass in winged insects according to their different metabolic states: flight ($bf = 1.04$; 95% CrI: 0.97–1.10), non-flight activity ($b_{nf} = 0.97$; 95% CrI: 0.76–1.18) and resting ($br = 0.76$; 95% CrI: 0.74–0.78). The scaling of oxygen consumption with body size across species of winged insects therefore increases more steeply during flight compared with at rest (Figure 1a). Although the mean scaling value for non-flight activity is similar to that for flight, this estimate of b_{nf} is less reliable because of its large CrI range that overlaps with those for flight and for resting. Wingless insects do not differ in the metabolic mass-scaling exponent between

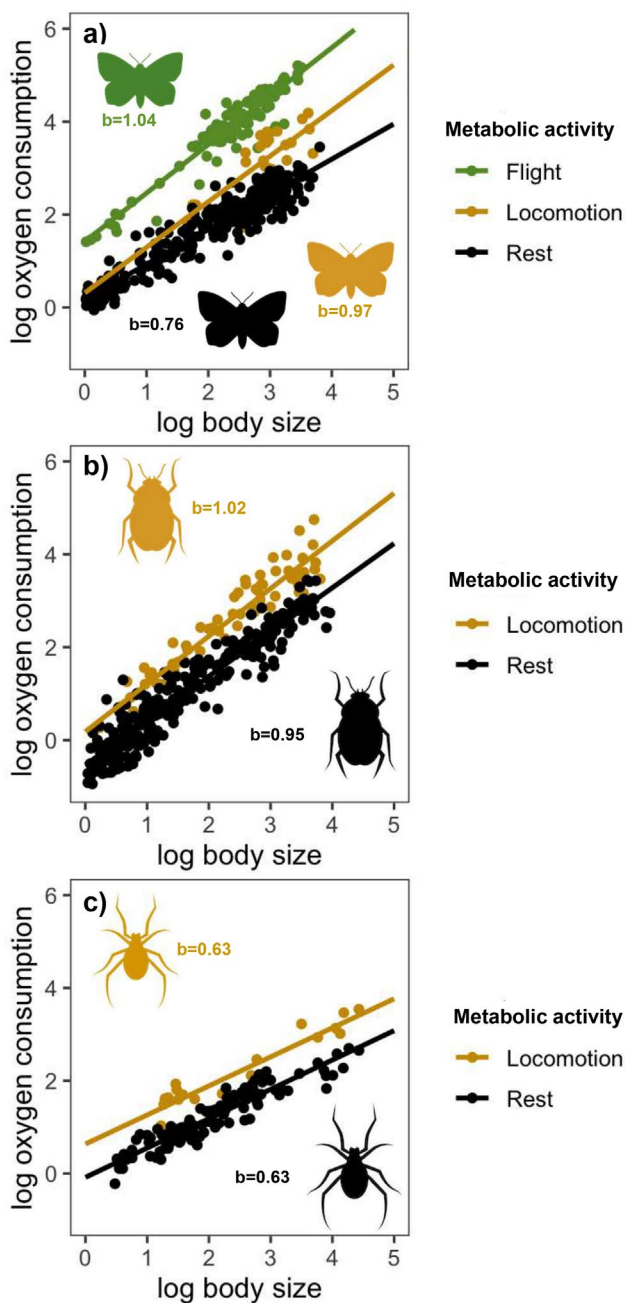


FIGURE 1 | The interspecific relationship between $\log_{10}$ -transformed oxygen consumption rate ($\mu\text{LO}_2\text{ind}^{-1}\text{h}^{-1}$) and $\log_{10}$ -transformed body mass (mg wet mass), for different arthropod groups: (a) Winged insects during flight ($b_f=1.04$), non-flight locomotion ($b_{nf}=0.97$), and rest ($b_r=0.76$) (b) Wingless insects during non-flight locomotion ($b_{nf}=1.02$) and rest ($b_r=0.95$). (c) Spiders during (non-flight) locomotion ($b_{nf}=0.63$) and rest ($b_r=0.63$). The green and yellow lines indicate the scaling relationship for active metabolic rate (i.e., flight and non-flight locomotion, respectively) and the black line indicates the scaling relationship for resting metabolic rate.

non-flight locomotion ($b_{nf}=1.02$; 95% CrI: 0.93–1.10) and resting ($b_r=0.95$; 95% CrI: 0.91–0.99; Figure 1b). Similar to wingless insects, spiders do not differ in metabolic scaling during non-flight locomotion ($b_{nf}=0.63$; 95% CrI: 0.54–0.72) and resting ($b_r=0.63$; 95% CrI: 0.59–0.68; Figure 1c). However, spiders exhibit a lower metabolic scaling exponent compared to winged and wingless

insects, suggesting variation in metabolic scaling among taxonomic groups as well as among activity levels (Figure 1c).

We also found (see Supporting Information) no qualitative change in our findings when we assumed no thermal sensitivity of oxygen consumption for large flying insects ($Q_{10}=1$ for species with adult masses >55 mg, see Duell et al. 2022). Moreover, we did not find that two distinct allometric relationships—one for smaller-bodied and one for larger-bodied species, found by Duell et al. (2022)—better described the data compared to the single scaling relationship shown in Figure 1 (Supporting Information).

3.2 | Active and Resting Metabolic Levels

Winged insects exhibit notable differences in metabolic levels (L , derived as $\log_{10}$ of the $\mu\text{LO}_2\text{g}^{-1}\text{h}^{-1}$ value) across distinct activity modes: flight, non-flight locomotion, and resting states. During flight, winged insects have a high oxygen consumption rate at the geometric mid-point mass (81.28 mg wet mass) ($L_f=4.49$), necessitated by the energy-intensive demands of sustained aerial movement. There is an 83% probability that the rate of oxygen consumption during flight is higher than during non-flight locomotion ($L_{nf}=3.27$), indeed the former is on average 16.6 times greater. Additionally, there is an 81% probability that oxygen consumption during non-flight locomotion is higher than at rest ($L_r=2.74$), with an average difference corresponding to a 3.4-fold increase. This pattern reflects reduced energy expenditure during terrestrial movement (e.g., non-flight locomotion) and inactive (e.g., rest) states (Figure 2a). Moreover, at this geometric mid-point mass, wingless insects, without flight capabilities had a 68% probability of exhibiting higher oxygen consumption during non-flight locomotion ($L_{nf}=3.22$) compared to rest ($L_r=2.84$; Figure 2b), with the average difference corresponding to a 2.4-fold increase. Spiders have a 78% probability of exhibiting higher oxygen consumption during non-flight locomotion ($L_{nf}=2.90$) than at rest ($L_r=2.21$; Figure 2c), with an average difference corresponding to a 4.9-fold increase. Our results reveal an interesting nuance not captured in the original formulation of hypotheses 3 and 4: although spiders have lower L_r than wingless insects, they both show a higher L_{nf} relative to L_r , suggesting that both spiders and wingless insects exhibit a greater metabolism for activity relative to rest.

Oxygen consumption rates at the geometric mid-point mass were similar between winged and non-winged insects both during non-flight locomotion (winged $L_{nf}=3.27$; wingless $L_{nf}=3.22$) and at rest (winged $L_r=2.74$; wingless $L_r=2.84$) and were approximately 2–4 fold higher than in spiders in the same respective activity states ($L_{nf}=2.90$; $L_r=2.21$).

4 | Discussion

Leveraging our extensive database of resting metabolic rates, which includes 608 arthropod species (over 50% more species than in Chown et al. 2007), our analysis revealed that interspecific metabolic scaling deviated from the 0.75 value predicted by the MTE (Brown et al. 2004). Metabolic exponents varied across activity types and taxa, revealing distinct patterns between winged and wingless arthropods. In support of the MLBH

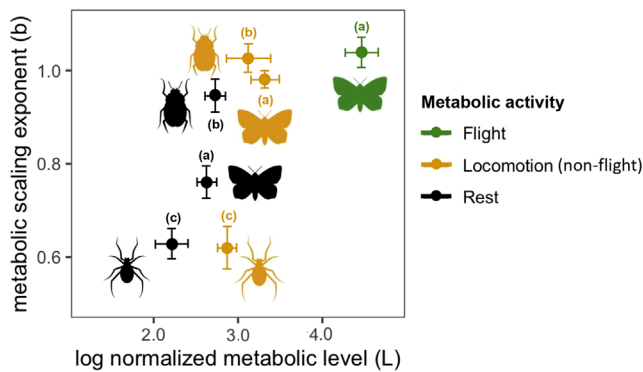


FIGURE 2 | The relationship between interspecific metabolic scaling exponents (b_f , b_{nf} , and b_r , respectively) and log10-transformed mass-specific metabolic level (L_f , L_{nf} and L_r , $\mu\text{LO}_2 \text{ gWM}^{-1} \text{ h}^{-1}$) estimated as the geometric mid-point of the body size range of the total arthropod sample. (a) Winged insects differ in metabolic level during flight, non-flight locomotion, and resting phase ($L_f = 4.49 \log_{10} \mu\text{LO}_2 \text{ gWM}^{-1} \text{ h}^{-1}$, $L_{nf} = 3.27 \log_{10} \mu\text{LO}_2 \text{ gWM}^{-1} \text{ h}^{-1}$, and $L_r = 2.74 \log_{10} \mu\text{LO}_2 \text{ gWM}^{-1} \text{ h}^{-1}$, respectively). (b) Wingless insects differ in metabolic level during non-flight locomotion and resting phase ($L_{nf} = 3.22 \log_{10} \mu\text{LO}_2 \text{ gWM}^{-1} \text{ h}^{-1}$, and $L_r = 2.84 \log_{10} \mu\text{LO}_2 \text{ gWM}^{-1} \text{ h}^{-1}$, respectively). (c) Spiders differ in metabolic level during non-flight locomotion and resting phase ($L_{nf} = 2.90 \log_{10} \mu\text{LO}_2 \text{ gWM}^{-1} \text{ h}^{-1}$, and $L_r = 2.21 \log_{10} \mu\text{LO}_2 \text{ gWM}^{-1} \text{ h}^{-1}$, respectively). Both winged and wingless insects have a significantly higher L_{nf} than spiders. The green and yellow colour indicate the scaling relationship for active metabolic rate (i.e., flight and non-flight locomotion, respectively) and the black colour indicates the scaling relationship for resting metabolic rate. Error bars represent the 95% confidence intervals of log10-transformed metabolic level L .

(Glazier 2005, 2010), we found near-isometric scaling in winged insects during flight ($b_f = 1.04$), but not during rest. However, wingless insects have near-isometric metabolic scaling across species during both locomotion and rest ($b_{nf} = 1.02$, $b_r = 0.95$, respectively), indicating little variation in scaling across rest and activity. Spiders showed a similar lack of scaling change across activity levels, but with consistently lower exponents ($b_{nf} = 0.63$, $b_r = 0.63$, respectively), indicating a deviation from MLBH predictions, and also suggesting a fundamentally different metabolic scaling pattern from insects. These different metabolic scaling relationships emphasize the need for different allometric equations to accurately describe metabolic rates across arthropod groups (McCue et al. 2016). We next discuss potential influences on differences in both the interspecific metabolic scaling exponent and metabolic level.

4.1 | Differences in Scaling Exponent b

Our observed increase from a lower interspecific b value at rest to isometric metabolic scaling of flight locomotion among species of winged insects, is consistent with MLBH predictions and agrees with previous findings for insects during flight ($b = 1.07$) (Niven and Scharlemann 2005) and sexual signalling ($b = 1.18$) (Doubell et al. 2017).

During maximal activity, the intraspecific metabolic scaling exponent b is predicted to approach 1 (Glazier 2010, 2014) because metabolic rate is primarily driven by the resource demand

of metabolising tissues (Weibel and Hoppeler 2005) if the mass of these tissues, or at least the power they generate, scales proportionally to body mass. Activity is also expected to increase the value of b across species with different-sized adults (i.e., interspecifically), if activity increases metabolic rate more in larger than in smaller species, which would occur if thorax temperatures increased more in larger species. During flight, large insects ($> 50 \text{ mg}$ mass) can have thorax temperatures 5°C – 20°C above air temperature, while smaller insects ($< 50 \text{ mg}$ mass) have body temperatures close to air temperature due to their higher surface-to-volume ratios (Unwin and Corbet 1984). Thus, in flight, higher body temperatures that increase with increasing body size may have contributed to the steep interspecific scaling of flight metabolic rate. However, Duell et al. (2022) compared thorax temperatures and metabolic rates across 13 species of stingless bees and did not provide evidence for steep interspecific metabolic scaling being due to larger species having warmer bodies during flight, although this finding applies to species that were only in the smaller part of the size range examined here. While flight is also associated with higher body temperatures, Glazier (2009) argues that these increases are more likely a side effect of elevated metabolism than a direct driver of changes in b . However, increased heat as a side effect may still feedback to increase flight activity and costs. Other potential influences on flight metabolic scaling include changes in wing morphology and aerodynamic efficiency as species size increases (Duell et al. 2022).

An increase in b , as predicted by the MLBH, may only be detected when the increase in oxygen consumption is sufficiently substantial, which is most likely to occur during high-cost activities like flight. Because flying requires significantly more energy than moving on the ground—especially in larger species where the effort to stay aloft grows with size (Glazier 2010)—this may help explain why non-flying forms of movement, despite raising metabolic rate to some degree, do not consistently produce a similar effect on b .

Overall, compared with studies of intraspecific scaling on the same species measured often in the same experiments, interspecific comparisons have more confounding variation in taxonomic affinity, ecological lifestyle and methodology, that may have obscured the effect of increased activity effects on b . Such confounding effects may help explain why we did not detect an increase in b value with activity interspecifically in either wingless insects or spiders, though an increase has been detected intraspecifically within a wolf spider (Kotiaho et al. 1998).

To examine the possibility of a bi-phasic interspecific scaling relationship—described for flight metabolism of large versus small size classes of insects by Duell et al. (2022), we examined our flight metabolic rate data using our sample of 529 taxonomically diverse insect species. In contrast with the findings of Duell et al. (2022) who used a sample of ~ 100 species that were also taxonomically diverse, we found that a single allometric relationship provides the best description of the metabolic scaling, as shown in our Figure 1. Duell et al. (2022) suggested that size-related biomechanical differences may be responsible for some of the change in scaling from hypermetric scaling across species less than $\sim 58 \text{ mg}$ mass, to hypometric scaling across larger species. Duell et al. (2022) also noted that wing-beat frequency is

constant with size across the lower body size ranges but declines with increasing size in larger insect species. It is not clear what aspect of our different datasets produced the difference in the number of interspecific scaling exponents (one vs. two) for flight metabolism. However, we note that although the size-scaling of flight mechanics, or body temperature, may play a role, we do not know the extent to which resting metabolic rate follows a biphasic relationship in the species for which the two studies have flight metabolism data. Therefore, we cannot rule out other influences such as different maintenance costs on adult metabolism, that may also contribute to interspecific scaling of flight metabolic rates.

The low value of the interspecific scaling exponent for metabolic rates of spiders, that we obtained both during locomotion and at rest, is similar to that previously reported for spiders (McCue et al. 2016). The shallower scaling in spiders than in both winged and wingless insects, both at rest and during non-flight locomotion, has substantial effects on metabolic rates at larger sizes. Using the parameter values in Table 1, we calculated that the average oxygen consumption of large (6 g wet mass) winged and unwinged insects is about an order of magnitude greater than for a spider of the same size and activity level. This difference in scaling is consistent with a greater shift along the fast-slow continuum (Stearns 1983), to slower life-history strategies and higher prevalence of sit-and-wait foraging mode among larger spider species (Marczak and Richardson 2008). Over 90% of foraging time can be spent waiting (Samu et al. 2003), which suggests a low-energy foraging strategy. As spiders rarely require prolonged activity for capturing prey (Schmitz 2016), low resting metabolic rates for larger spiders could therefore arise due to their reduced requirement for sustained activity (Reinhold 1999). According to the equal fitness paradigm (Brown et al. 2018), among groups of organisms, the rate of reproduction is countered by the rate of mortality. Thus, slower growth and reproduction (associated with lower metabolic rates) would be associated with lower mortality. Anderson and Prestwich (1985) note that spiders have low-cost methods for both obtaining food

and enhancing survival, including ambush feeding, the production of silk traps and poison, and the ability to disperse passively by ballooning. They also have a well-developed capacity for anaerobic activity (Anderson and Prestwich 1985). A low resting metabolic rate for the larger spiders may also be adaptive for prolonging survival, as it could partly underlie their tolerance to starvation (Overgaard and Wang 2012). Such a trend supports the idea that larger spiders generally exhibit slower life histories. Thus, spiders, which exhibit the lowest metabolic scaling exponents during both non-flight locomotion and at rest, may be considered evolving towards slow life histories with increased species size, likely due to their reliance on ambush predation and reduced locomotor activity. Tests of our hypothesis that lower metabolic scaling across spider species reflects a greater shift towards slower life history should examine more directly whether reproductive rates and mortality scale less steeply with body size across spiders than across insect species. Exploring how metabolic scaling corresponds with variations in life-history strategies (reviewed by Glazier and Gjoni 2024) and how differences in metabolic scaling stem from diverse adaptive life-history strategies can thus reveal evolutionary dynamics shaping arthropod physiology (White et al. 2022).

The deviation in br from a value of 0.75 predicted by the Metabolic Theory of Ecology (Brown et al. 2004), is not attributable to phylogenetic non-independence, as confirmed by our phylogenetically informed analysis (see Supporting Information). Riveros and Enquist (2011) have indicated that including the family Termitidae in interspecific metabolic scaling analyses of insects could significantly alter b_r estimates in smaller datasets. However, excluding Termitidae from our dataset only slightly lowered b_r to 0.76 (95% CrI: 0.752, 0.825). Previous concerns regarding termite data accuracy stem from indirect O_2 consumption estimates from CH_4 production (Riveros and Enquist 2011). Here we overcame this limitation by collating termite data from multiple sources, including studies with direct O_2 use and CO_2 measurements (Wheeler et al. 1996). In addition, given the low or variable temperature sensitivity of flight metabolism in large

TABLE 1 | Summary statistics from the Least Squares Regression (LSR) model implemented in a Bayesian framework, detailing the relationships between $\log_{10}$ -transformed metabolic rate ($\mu L O_2 \text{ ind}^{-1} \text{ h}^{-1}$) and $\log_{10}$ -transformed body mass (mg wet mass). The table includes slopes (b), intercepts, and 95% confidence intervals for three arthropod groups (winged insects, wingless insects, and spiders) across different metabolic activities: Flight, non-flight locomotion, and rest. Estimates of $\log_{10}$ -transformed metabolic level (L , $\mu L O_2 \text{ g}^{-1} \text{ h}^{-1}$) are provided at the geometric midpoint of the body size range. ‘Non-flight’ refers to directed walking or running.

Group	Activity	b	95% CrI	Intercept	95% CrI	$\log_{10}$ metabolic level (L)
Insects with wings	Flight	1.04	0.97–1.10	1.31	1.25–1.37	4.49
Insects with wings	Non-flight locomotion	0.97	0.76–1.18	0.10	–0.13 to 0.34	3.27
Insects with wings	Rest	0.76	0.74–0.78	–0.48	–0.51 to –0.45	2.74
Insects without wings	Non-flight locomotion	1.02	0.93–1.10	0.62	0.52–0.73	3.22
Insects without wings	Rest	0.95	0.91–0.99	–0.17	–0.22 to –0.12	2.84
Spiders	Non-flight locomotion	0.63	0.54–0.72	0.60	0.49–0.71	2.90
Spiders	Rest	0.63	0.59–0.68	–0.10	–0.14 to –0.06	2.21

insects (Heinrich 1980; Johnson et al. 2023), we performed additional analyses using different Q_{10} values for small and large flying insects. While this affected the elevation of metabolic rates, it did not change the overall qualitative differences among activity levels and arthropod groups (Supporting Information).

4.2 | Differences in Metabolic Level

Winged insects have a greater metabolic level during flight (L_f) compared to wingless insects and spiders engaged in non-flight movement. Higher metabolic demands during flight require heightened aerobic capacity, changes in muscle morphology and function, modifications in respiratory and circulatory systems, and adjustments in metabolic pathways to optimise energy utilisation during prolonged flight (Glazier 2010). The overhead costs of maintaining the capacity for active flight likely explain the higher resting metabolic level in flying insects (Reinhold 1999). However, winged and wingless insects exhibit very similar metabolic rates during both rest and non-flight locomotion, while spiders show consistently lower values for both states. Consistent with this pattern the largest wingless insect (6 gWM) had a resting metabolic rate about 6.4-fold higher than that of a similarly sized spider, while at the geometric mid-mass (where L is determined), the winged insect had a rate roughly 3.4-fold higher. These contrasts highlight the impact of flight ability and locomotion strategy on both the slope of metabolic scaling and the absolute levels of metabolism. The role of locomotor strategy in determining resting metabolic rate was also illustrated by McCue et al. (2016) who found that mantis species (Mantidae), which adopt a sit-and-wait foraging strategy, had a lower metabolic level than most other insects and were more similar to that of spiders. By contrast, however, the metabolic scaling of mantis standard metabolic rates was similar to those of other insects, and steeper than in spiders. From this observation, we suggest that the evolution of increased species size in mantises and most insects has not involved as steep a change towards a slower, less energetic life history with increasing species size as we predict has occurred in spiders.

Our findings highlight how locomotor mode and metabolic demand interact to shape metabolic scaling, reinforcing that metabolic scaling is context-dependent rather than universal. Taken together, our results and those of Glazier (2010), underscore that while flight capacity imposes distinct metabolic demands, metabolic energy use during non-flight locomotion and rest does not necessarily differ between winged and wingless insects. Instead, these two insect groups show similar metabolic rates in both states, whereas spiders exhibit consistently lower metabolic levels. By integrating these perspectives, we refine our understanding of how metabolic scaling is shaped by locomotor strategy, activity level and size-dependent evolutionary shifts in energetics across arthropods.

5 | Conclusion

We demonstrate that a single interspecific allometric equation is inadequate for describing metabolic rates in insects and spiders due to their distinct metabolic levels and the differing impacts of activity on their mass-scaling exponents. The variation

in energetic demands between the muscular processes driving flight in winged insects, and the less developed musculature in wingless insects and spiders, likely accounts for the higher metabolic rates during flight activity, particularly in large-bodied species. Moreover, the shallower mass-scaling exponents in spiders at rest and activity, compared to insects, may be explained by slower life history attributes in larger spiders. Our findings emphasise how differences in locomotor strategy, activity level and life history are essential for understanding energy expenditure in natural environments.

Author Contributions

Hanrong Tan, Andrew G. Hirst and David Atkinson conceived the study. Hanrong Tan collected the data and Vojsava Gjoni performed the meta-analysis. Hanrong Tan, Andrew G. Hirst, Pavel Kratina, Vojsava Gjoni and David Atkinson. All contributed to the writing of the paper.

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Data Availability Statement

Data and code are available from the following Dryad repository: <https://doi.org/10.5061/dryad.fn2z34v84>.

Peer Review

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.70277>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** ele70277-sup-0001-Supinfo.pdf.