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Standard metabolic rate variation among New Zealand Orthoptera

Mariana Bulgarella[a,b,*], John Haywood[c], Eddy J. Dowle[d], Mary Morgan-Richards[a], Steven A. Trewick[a]

[a] Ecology, College of Science, Massey University Manawatū, Private Bag 11-222, Palmerston North 4442, New Zealand
[b] School of Biological Sciences, Victoria University of Wellington, PO Box 600, Wellington 6140, New Zealand
[c] School of Mathematics and Statistics, Victoria University of Wellington, PO Box 600, Wellington 6140, New Zealand
[d] Anatomy Department, Otago University, PO Box 56, Dunedin 9054, New Zealand

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ABSTRACT

Standard metabolic rates (SMR) of ectotherms reflect the energetic cost of self-maintenance and thus provide important information about life-history strategies of organisms. We examined variation in SMR among fifteen species of New Zealand orthopteran. These species represent a heterogeneous group with a wide geographic distribution, differing morphologies and life histories. Gathering original data on morphological and physiological traits of individual species is a first step towards understanding existing variability. Individual metabolic rates of ectotherms are one of the first traits to respond to climate change. Baseline SMR datasets are valuable for modeling current species distributions and their responses to a changing climate. At higher latitudes, the average environmental temperature decreases. The pattern that cold-adapted ectotherms display higher SMR at colder temperatures and greater thermal sensitivity to compensate for lower temperatures and the shorter growing and reproductive seasons is predicted from the metabolic cold adaptation (MCA) hypothesis. We predict higher SMR for the orthopteran species found at higher latitudes. We further compared the index of thermal sensitivity Q_{10} per species. We used closed-system respirometry to measure SMR, at two test temperatures (4 °C and 14 °C), for the fifteen species acclimated to the same conditions. As expected, we found significant differences in SMR among species. The rate of oxygen consumption was positively correlated with body mass. Our findings do not support the MCA hypothesis. In fact, we found evidence of co-gradient variation in SMR, whereby insects from higher elevations and latitudes presented lower SMR. We discuss our findings in relation to life histories and ecology of each species. The novel physiological data presented will aid in understanding potential responses of these unusual species to changing climatic conditions in Aotearoa/New Zealand.

1. Introduction

Metabolism comprises the suite of biochemical processes by which energy and materials are transformed to support life functions and structures (Glazier, 2005). The standard metabolic rate (SMR) of ectotherms represents the energy cost of maintenance metabolism (McNab, 1999; Hulbert and Else, 2004). Variation in SMR in ectotherms is mainly determined by body size and temperature (Angilleta et al., 2004; Brown et al., 2004) with environmental, behavioural, developmental and evolutionary factors also taking part (Waters and Harrison, 2012; Dupoué et al., 2017). Understanding how metabolic rates evolve is of importance for ecological theory (Schaefer and Walters, 2010; Shokri et al., 2022) and determining the drivers of physiological responses of insects is important for predicting species distributions and their responses to climate change (Dupoué et al., 2017).

Ectotherms such as insects depend on environmental temperature to mediate their physiological activity, with temperature influencing individuals differently through their life cycle (Angiletta, 2009; Jankowski et al., 2013). Temperature determines patterns of daily activity, movement (Hertz et al., 1993), adult body size (Sibly and Atkinson, 1994; Angilleta et al., 2004), and reproduction (Savage et al., 2004), among others. The metabolic cold adaptation hypothesis (MCA) predicts that ectotherms from colder climates (high latitudes or elevations) have elevated metabolic rates at the same test temperature compared to those from warmer environments (Wharton, 2011; Williams et al., 2016) and steeper thermal performance curves (Terblanche et al., 2009). It is suggested that elevated metabolic rates allow the cold-adapted species/populations to meet the increased costs of growth and development

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[*] Corresponding author.
E-mail address: Mariana.Bulgarella@vuw.ac.nz (M. Bulgarella).

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necessary for completing life cycles in relatively cooler and shorter growing seasons (Chown and Gaston, 1999; Terblanche et al., 2009). Response to a change in temperature (thermal sensitivity) results from the capacity of a single genotype to vary in metabolic rate across a thermal gradient. To facilitate comparison among organisms/studies thermal sensitivity (Q_{10}) is estimated from the rate of change in metabolic rate across 10 °C temperature intervals (Schmidt-Nielsen, 1997; Lake et al., 2013). Cold-adapted invertebrates are thought to have greater thermal sensitivity with steeper performance curves resulting in higher Q_{10} estimates (Shik et al., 2019). While the MCA hypothesis is controversial (reviewed in Addo-Bediako et al., 2002), physiologists still agree that the pattern occurs often enough to warrant investigation (Williams et al., 2016) and has the potential to improve species distribution models (Willot et al., 2023).

There is an increased interest globally in the likely and predicted responses of insects to climatic changes in temperature, water availability, elevated CO_2 levels and their interaction, as well as the effects on the plants upon which many of them feed (Hoffmann and Parsons, 1997; Hill et al., 1999, 2002; Thomas et al., 2001; Bale et al., 2002). Universal responses to warming include dispersal in space (range shifts), time (phenological shifts) and reductions in body size (Gardner et al., 2011; Verberk et al., 2021). A study on the vulnerability of arthropod species inhabiting the phyllosphere to thermal extremes concluded that warming tolerance was similar for herbivores with different feeding mode and microclimate preferences, with little margin to resist the more frequent and intense heat waves (Pincebourde and Casas, 2019). Individual metabolic rates in ectotherms increase with increasing temperatures, but only up to a certain upper thermal limit (Sinclair et al., 2016). Thus, individual metabolic rates are one of the first traits to respond to global warming (Bruno et al., 2015; Verberk et al., 2016).

Fig. 1. Photographs illustrating ten of the orthopteran species included in this study. **A.** *Hemiandrus pallitarsis* Anostostomatidae, **B.** *Teleogryllus commodus* Gryllidae, **C.** *Sigaus australis* Acrididae, **D.** *Hemideina crassidens* Anostostomatidae, **E.** *Caedicia simplex* Tettigoniidae, **F.** *Deinacrida connectens* Anostostomatidae, **G.** *D. rugosa* Anostostomatidae, **H.** *Motuweta riparia* Anostostomatidae, **I.** *Pachyrhamma edwardsii* Rhaphidophoridae, and **J.** *Neonetus* new species Rhaphidophoridae. Photograph credits: Steve Trewick except for **F)** Christopher Stephen, **G)** Carey Knox, and **H)** Samuel Purdie.

Within this study we focus on a single insect order whose distribution covers a large latitudinal/elevational gradient in New Zealand. The Orthoptera are an abundant, widespread and diverse group of insects with more than 25,700 species (Song et al., 2015). Niche, life history and body mass vary considerably among species (Whitman, 2008) providing huge scope for the study of physiological responses to changing temperatures. This monophyletic order has been present on Earth for ~300 million years; it is divided into two suborders: Ensifera (crickets, katydids, wētā and relatives) and Caelifera (grasshoppers, locusts and their allies) (Zhang et al., 2013).

The New Zealand Orthoptera are dominated by two families of Ensifera, Anostostomatidae and Rhaphidophoridae, which contribute an estimated 50 and 75 species, respectively (Pratt et al., 2008; Dowle et al., 2024). Despite their relative abundance, little is known about the physiology and morphology of the majority of New Zealand species. A few endemic species in the genus *Hemideina* have received some attention by physiologists (Sinclair et al., 1999; Wharton, 2011; Minards et al., 2014; Bulgarella et al., 2015; King and Sinclair, 2015), and a study found that metabolic loci in 18 species of *Deinacrida* and *Hemideina* show evidence of genes being under positive selection across the wētā phylogeny (Twort et al., 2019). We surveyed variation in SMR in 15 New Zealand orthopteran species representing the families Anostostomatidae (9), Rhaphidophoridae (3), Grillidae (1), Tetigoniidae (1) and Acrididae (1) (Fig. 1, Table 1). Climatic conditions vary over latitudinal and elevational ranges from warm northern species (low latitude) to high elevation species in the south (high latitude). Based on the MCA hypothesis, we expect that the cold-adapted species collected from high latitude and high elevation would have elevated metabolic rates and greater thermal sensitivity compared to species collected from low latitude and low elevation.

The objectives of our study were (1) to measure and compare standard metabolic rates and the index of thermal sensitivity, Q_{10}, for 15 orthopteran species so that these data form a base for future work (made publicly available via repositories such as 'Zenodo' and 'ShareTrait') and (2) to test for elevated standard metabolic rates and thermal sensitivity in orthopterans inhabiting higher latitudes and elevations of Aotearoa/New Zealand as predicted by the metabolic cold adaptation hypothesis.

2. Materials and methods

2.1. Study species and sampling localities

Our sampling included representatives from 15 species in the suborders Caelifera ($n = 1$) and Ensifera ($n = 14$, Fig. 1, Table 1). Specifically, we included 9 species of wētā that belong to the Anostostomatidae family. New Zealand wētā are a diverse group comprised of approximately 50 endemic species (Trewick et al., 2022). All are flightless and nocturnal. We included representatives of tree hole-dwelling herbivorous species (*Hemideina broughi, H. crassidens, H. maori, H. thoracica,* and *H. trewicki*) and their close relatives, the giant wētā (*Deinacrida connectens* and *D. rugosa*). Within the tusked wētā, *Motuweta riparia* is one of three species in which adult males bear mandibular tusks when mature. This carnivorous species inhabits stream banks in North Island rainforests, where it conceals itself during the day in ground cavities. All *Hemiandrus* ground wētā hide during the day in purpose-made burrows and emerge to hunt for invertebrate prey at night (Taylor-Smith et al., 2016).

Three species of rhaphidophorids endemic to New Zealand were included. These are flightless and nocturnal but range in habitat and size. Our sample includes a small undescribed forest floor-dwelling species from the genus *Neonetus* (Fitness, 2016), a tree hole-inhabiting species (*Talitropsis sedilloti*), and a large species that aggregates in cave entrances (*Pachyrhamma edwardsii*).

Three diurnal species were studied; the gryllid *Teleogryllus commodus* is common in open grassland habitats and coastal areas, particularly in the North Island, the large tetigoniid *Caedicia simplex*, a species found in both New Zealand and Australia that feeds on shrubs during the day, and the flightless grasshopper *Sigaus australis*, endemic to the alpine and subalpine zone of the South Island (Dowle et al., 2014).

We collected insects in several locations across the North and South islands of New Zealand between March 2011 and January 2013 (Department of Conservation collection permits WE-31,465-FAU, NM-32,444-FAU, TW-32,116-FAU, WA-22,197-RES, WE-32,885-RES). This sampling provided a total of 73 individuals representing 15 species in 10 orthopteran genera and five families (Table 1). Specimen collection information is detailed in Supplementary Table S1 in Supplementary File S1.

Animals were transported to the laboratory where they were kept in individual plastic containers (17 × 17 × 9 cm) with wire mesh in the lids

Table 1
Taxonomic, ecological traits and geographic information for the 15 orthopteran species included in this study.

Suborder	Family	Species	Habitat	Diurnal or nocturnal	Diet	Locomotion	Latitude (°S)	Longitude (°E)	Elevation (m)
Caelifera	Acrididae	*Sigaus australis*	grasslands, alpine	diurnal	herbivorous	jump	43.46670	171.53330	1813
Ensifera	Anostostomatidae	*Deinacrida connectens*	scree, alpine	nocturnal	herbivorous	walk	41.74563	173.80714	1350
Ensifera	Anostostomatidae	*Deinacrida rugosa*	grasslands, lowlands	nocturnal	herbivorous	walk	41.08333	174.78333	102
Ensifera	Anostostomatidae	*Hemiandrus pallitarsis*	ground, lowlands	nocturnal	carnivorous	walk	41.23295	174.82708	173
Ensifera	Anostostomatidae	*Hemideina broughi*	tree holes forest, highlands	nocturnal	herbivorous	walk	41.73791	171.78861	566
Ensifera	Anostostomatidae	*Hemideina crassidens*	tree holes forests, high/ lowlands	nocturnal	herbivorous	walk	39.89741	176.01261	1011
Ensifera	Anostostomatidae	*Hemideina maori*	under rocks, alpine	nocturnal	herbivorous	walk	43.46670	171.53330	1808
Ensifera	Anostostomatidae	*Hemideina thoracica*	tree holes forest, lowlands	nocturnal	herbivorous	walk	40.47148	175.60943	179
Ensifera	Anostostomatidae	*Hemideina trewicki*	tree holes forest, lowlands	nocturnal	herbivorous	walk	39.85000	176.88333	401
Ensifera	Anostostomatidae	*Motuweta riparia*	forest floor	nocturnal	carnivorous	walk	37.63890	178.37620	1
Ensifera	Gryllidae	*Teleogryllus commodus*	grasslands, lowlands	diurnal	herbivorous	walk	40.86271	173.03211	2
Ensifera	Rhaphidophoridae	*Neonetus* sp.	forest floor, lowlands	nocturnal	omnivorous	jump	40.38068	175.61621	186
Ensifera	Rhaphidophoridae	*Pachyrhamma edwardsii*	usually caves, lowlands	nocturnal	omnivorous	jump	40.86271	173.03211	2
Ensifera	Rhaphidophoridae	*Talitropsis sedilotti*	tree holes, forest	nocturnal	omnivorous	jump	40.38068	175.61621	186
Ensifera	Tettigoniidae	*Caedicia simplex*	shrub forest, lowlands	diurnal plus	herbivorous	fly	40.38068	175.61621	186

in a climate-controlled room at 14 ± 1 °C with a 14:10 h light:dark cycle. We provided *Hemideina* and *Deinacrida* wētā (Anostostomatidae) with a roost hole made from hollowed harakeke stalk (*Phormium tenax*), and moisture via a damp paper towel. Leaves of mahoe (*Melicytus ramiflorus*), taupata (*Coprosma repens*) and miro (*Prumnopitys ferruginea*) were provided *ad libitum*. We supplemented the diet weekly with soy pellets for protein (Horleys, Naturalac Nutrition Ltd., Auckland, New Zealand). We kept katydids, crickets and grasshoppers in cages under the same conditions described, with grass and water provided *ad libitum*. We allowed for a 15–day acclimation period to captive conditions at 14 °C prior to metabolic measurements. The Cook Strait giant wētā (*Deinacrida rugosa*) is a threatened species, and we were permitted four wild individuals for four days before they were returned to their natural habitat following metabolic rate measurements.

2.2. Respirometry

We estimated SMR of adult individuals from their rate of oxygen (O_2) consumption in a closed system (Lighton, 2008; Bulgarella et al., 2015). Wētā were fasted for three days prior to measurements to avoid specific dynamic action and to standardize fuel sources (Sinclair et al., 2011). This fasting time was chosen because these large insects feed intermittently in the wild (Wehi et al., 2013). Diurnal insects (cricket, katydid and grasshopper) were fasted overnight when possible. We used adult animals to avoid moulting periods, which alter metabolic rates (Camp et al., 2014) and metabolic measurements were conducted outside of the reproductive period, ensuring animals were non-reproductive. All metabolic trials were performed in the dark during the day, which corresponds to resting conditions for the nocturnal species (wētā) and induces resting in diurnal species. A study that included an activity detector found that tree wētā remain mostly inactive during respirometry (King and Sinclair, 2015). Our observations are consistent with King and Sinclair (2015)'s findings, wētā species remained calm and inactive inside the respirometry chamber. However, we did not measure activity levels of the study subjects. Before each respirometry run, each individual was weighed (± 0.1 g; Avery Berkel FB711 balance, UK; except for *Neonetus* sp. for which a ± 0.0001 g AG204 analytical balance (Mettler Toledo Ltd, Hamilton, New Zealand) was used) and placed in an open-ended, glass cylinder selected to minimize excess volume for each species. This was sealed with an airtight rubber bung through which an O_2 optode (Ocean Optics Inc., Florida, USA) passed. The O_2 optode was connected to a fiber optic O_2-sensing system located outside the respirometry chamber (Tau Theta Instruments LLC, Colorado, USA), which recorded O_2 partial pressure at 2 s intervals over each 2 h run. The O_2 levels in the testing cylinder did not drop below 19 kPa. The O_2-sensing system was calibrated for multiple temperatures and O_2 percentages by the manufacturer and recalibrated after each reading using a double point calibration (0 and 21 vol% O_2). The environmental temperature was monitored continuously to ± 0.5 °C accuracy with a DS1921K Thermochron iButton (Maxim, California, USA). We did not observe condensation in the chamber after any run, suggesting that there was relatively little respiratory water loss under these conditions. All experiments were carried out in Palmerston North, New Zealand at 179 m a.s.l.

We calculated O_2 consumption rates for each individual from fractional oxygen concentrations from each completed run. We discarded the first 15 min of each run as equilibration time (McGaughran et al., 2009). Rates of O_2 consumption (ml O_2/h) were calculated using a modification of Vleck's (1987) equation: $V(F_i\text{-}F_f)/(1\text{-}F_f)t$ where V is the volume of air in the chamber, F_i and F_f are the initial and final O_2 lifetime (in µ*sec*), respectively, and t is the duration of the measurement period, expressed in hours (Nespolo et al., 2003). We measured O_2 consumption for each individual at two test temperatures: 4 °C and 14 °C, either on the same day or on consecutive days. The order of the temperatures was randomised. We selected these temperatures based on data of the temperature ranges in the point localities where the different species were collected (climate data from WorldClim database, Hijmans et al., 2005; Supplementary Table S2 in Supplementary File S1).

2.3. Statistical analyses

We used R v.4.4.0 (R Core Team, 2024) for all statistical analyses. Graphs were generated using ggplot2 in R (Wickham, 2016). Values of SMR and body mass were $\log_{10}$-transformed prior to analyses, to linearize the power law relationship and as a variance-stabilizing transformation. The log-transformed SMR was fitted as a response variable in a linear mixed effects model with initial fixed-effect covariates of log-transformed mass, temperature (either 4 °C or 14 °C), latitude, elevation and sex. Due to the wide range in recorded elevations, this explanatory variable was standardized to be a z-score with zero mean and unit variance, prior to inclusion within fitted models. Interaction terms were included in the full model initially, between temperature and each of latitude, elevation and sex. A random intercept was included for each insect, to allow for the dependence between paired observations at the two test temperatures. Backwards stepwise regression was used to select the variables in the final model using the 'step' function (R Core Team, 2024). This process starts with the full complement of terms in a linear model and works backwards, removing terms to produce the greatest decrease in Akaike's Information Criterion (AIC). When the removal of any further variables would produce an increase in AIC the process stops, and we are left with the final variables selected. The effect size and associated standard error, F-statistic (F), degrees of freedom (*df*), R^2 value and associated p-value (p) are reported, with the pseudo-R^2 value from the 'r.squaredGLMM' function given for the final mixed-effect model. Statistical significance was assumed at $p < 0.05$.

We calculated the index of thermal sensitivity, Q_{10}, the magnitude of change in SMR over a 10 °C change in temperature, using the equation: $Q_{10} = (R_2/R_1)^{10/(T2\text{-}T1)}$ (Schmidt-Nielsen, 1997), where R_1 is the rate at the lower temperature (T_1), and R_2 the rate at the higher temperature (T_2), for each individual (Supplementary File S2) and the mean Q_{10} per species.

3. Results

3.1. Body mass variation

The 15 species studied varied greatly in body mass, ranging from 0.08 g in the smallest cave wētā (*Neonetus* sp.) to 25.5 g in a female Cook

Table 2

Body mass values measured for each sex and species of New Zealand orthopteran included in this study. Values correspond to mean ± standard error (SE). If no value is presented, we did not measure any individuals of that sex. When no SE is presented, only one individual of that sex was measured. Species have been ranked based on increasing mean Q_{10} values.

Species	Mean mass males (g) (*n*)	Mean mass females (g) (*n*)	Mean Q_{10}
Hemideina crassidens	4.10 ± 0.20 (2)	6.72 ± 0.28 (4)	1.19
Sigaus australis	–	0.79 ± 0.30 (3)	1.22
Hemideina broughi	–	11.82 ± 1.11 (4)	1.24
Pachyrhamma edwardsii	1.90 ± 0.10 (2)	2.80 (1)	1.35
Hemideina maori	1.85 ± 0.27 (4)	2.90 (1)	1.37
Neonetus sp.	0.09 ± 0.00 (4)	0.13 ± 0.02 (2)	1.39
Deinacrida connectens	2.32 ± 0.06 (5)	–	1.56
Talitropsis sedilotti	–	0.50 ± 0.10 (2)	1.59
Caedicia simplex	0.40 ± 0.10 (2)	0.62 ± 0.11 (4)	1.60
Hemideina thoracica	4.10 (1)	3.44 ± 0.28 (5)	1.60
Teleogryllus commodus	0.45 ± 0.06 (4)	0.40 ± 0.06 (3)	1.63
Motuweta riparia	2.76 ± 0.52 (3)	2.20 (1)	1.64
Deinacrida rugosa	8.80 ± 1.39 (3)	25.50 (1)	1.65
Hemideina trewicki	2.93 ± 0.26 (3)	4.36 ± 0.71 (3)	1.73
Hemiandrus pallitarsis	0.57 ± 0.05 (4)	0.70 ± 0.00 (2)	2.36

Strait giant wētā (*D. rugosa*; Table 2), a 319-fold range of body mass. The four wild *D. rugosa* individuals loaned for this study included three males and one female, which differed considerably in size. The mean body mass of the smaller males was 8.8 ± 1.39 g (Table 2).

3.2. Comparison of metabolic rates among species

A linear mixed effects model was used to investigate predictors of SMR (log-transformed O_2 consumption) with explanatory variables selected via backward stepwise regression. The variables included in the final model were log-transformed mass, temperature, and standardized elevation (R^2 for fixed effects = 0.827, pseudo-R^2 including random effect for paired temperatures = 0.964). The model summary of the final model is presented in Appendix S1 in Supplementary File S1. There were no significant interactions between any of the explanatory terms. Positive associations were found for SMR with both mass and temperature, in each case when other explanatory variables were held constant ($\beta_{\text{logMass}} = 0.648 \pm 0.034$, $F = 363.992$, $df = 1{,}70$, $p < 0.001$; $\beta_{\text{temp}} = 0.179 \pm 0.013$, $F = 181.480$, $df = 1{,}72$, $p < 0.001$) (Fig. 2). A negative association was found between SMR and standardized elevation, when holding other explanatory variables constant ($\beta_{\text{elev}} = -0.045 \pm 0.020$, $F = 5.096$, $df = 1{,}70$, $p = 0.027$). Fig. 3 shows a partial residual plot for standardized elevation, produced with the visreg package (Breheny and Burchett, 2017). Given the quite strong positive correlation (of 0.676) between latitude and elevation, having both those covariates in the model was not supported, and elevation was preferred using AIC. Sex was not significant in the model ($\beta_{\text{SexMale}} = -0.00212 \pm 0.039$, $F = 0.003$, $df = 1{,}69$, $p = 0.957$), consistent with previous studies that have found no statistically significant differences in SMR between sexes (e.g., Bulgarella et al., 2015; King and Sinclair, 2015). When comparing SMR, we found that the smallest-sized species, the cave wētā *Neonetus* sp. presented the lowest values of SMR while the West Coast bush wētā *H. broughi* presented the highest values of SMR, with the other species somewhere in between (Fig. 2). *Teleogryllus commodus* specimens showed the highest intra-specific variability in SMR values, when measured at either of the two test temperatures (Fig. 2).

Individual values of Q_{10} ranged from 1.01 in one tree wētā *Hemideina crassidens* to 3.07 in one ground wētā *Hemiandrus pallitarsis* (Supplementary File S2). Mean Q_{10} per species ranged from 1.19 to 2.36 (Table 2). Thus, a rise of 10 °C in temperature caused the rate of O_2 consumption of the orthopteran species to stay almost the same or to increase twofold. The exception were three individuals, a ground wētā, *H. pallitarsis* and a tree wētā, *H. trewicki* which increased O_2 consumption threefold with a 10 °C rise in temperature, and a tusked wētā, *M. riparia* that showed a 2.72-fold increase in O_2 consumption with a 10 °C temperature change. We also assessed mean Q_{10} per species versus latitude but found no pattern of association (Fig. 4).

4. Discussion

We present novel standard metabolic rate data for 15 orthopteran species occurring in New Zealand, with animals held in the same laboratory under the same conditions (e.g., Messamah et al., 2017). Overall, for all species, there is a positive relationship between the rate of O_2 consumption, measured at either 4 °C or 14 °C, and body mass. The largest-bodied species (giant wētā *Deinacrida rugosa*, West Coast bush wētā *Hemideina broughi* and Wellington tree wētā *H. crassidens*) presented the highest SMR compared to the smallest wētā, katydids and crickets.

Our results do not support the metabolic cold adaptation hypothesis. Our findings support a case of co-gradient variation in which the orthopteran species from higher elevation and latitudes (colder habitats) exhibit lower standard metabolic rates than low elevation and low latitude species (warmer habitats). Several studies failed to find support for the MCA hypothesis at the intra- or interspecific level (Lardies et al., 2004; Steffensen, 2002; Steffensen et al., 1994). Sagebrush lizards from high elevations also exhibited lower metabolic rates when compared to lizards from lower elevations (Sears, 2005). Either lizards from higher elevations reduce metabolic rates to minimize overwinter energetic expenditure or lower elevation lizards emerge earlier in the spring than lizards from high elevations and elevate their metabolic rates to support activity in the cool spring temperatures (Sears, 2005). We do not know the reason for the lower SMR found in the high elevation species. Follow-up studies with orthopterans acclimated to common garden conditions that measure growth and metabolic rates simultaneously in these species may shed some light into the mechanisms involved.

Latitude (Lardies et al., 2004) and elevation (Ashby, 1997) are known to influence the metabolic rate of ectotherms (Chappell, 1983; Willot et al., 2023). We measured metabolic rate in three species collected from elevations above 1300 m a.s.l.; *Hemideina maori, Sigaus australis* and *Deinacrida connectens*. We found a significant negative relationship between SMR and elevation when running a model that also accounts for individual, body mass and temperature.

All three of the alpine-inhabiting orthoptera we studied are freeze-tolerant (Morgan-Richards et al., 2023). Populations of the alpine, diurnal grasshopper *S. australis* are restricted to fragmented high-elevation habitats in the South Island and present high genetic variability (Carmelet-Rescan et al., 2021) with a mean SMR of 0.11 ± 0.04 ml O_2/h at 4 °C. The alpine tree wētā *H. maori*, which can withstand freezing via a hemolymph ice nucleating agent (Sinclair et al., 1999), presented a mean SMR of 0.20 ± 0.04 ml O_2/h at 4 °C, with little variability among the five individuals included in the study. The alpine scree wētā *D. connectens* is another high-elevation species with high extant genetic variation, whose populations have experienced differing degrees of isolation throughout their range (Trewick et al., 2000). Mean SMR for alpine scree wētā at 4 °C was 0.31 ± 0.02 ml O_2/h. Thermal sensitivity of metabolic rate as estimated from Q_{10} is expected to be low for cold-adapted species (Willot et al., 2023) and this was our general observation for the three alpine specialists, but lowland species (such as *Pachyrhamma edwardsii*) had similar low thermal sensitivity (Table 2, Fig. 4). It has been suggested that for alpine species with low thermal sensitivity, tracking climate change by moving higher up their mountain homes might not be possible if oxygen demand-supply balance limits their distribution (Jacobsen, 2020). Loss of habitat for alpine species has been predicted (Koot et al., 2022) so understanding the physiological limits of these species will be valuable for conservation planning.

Most wētā species in this study are large, flightless, nocturnal, herbivores, with long lifespans. For related species with similar diets but inhabiting different habitats, Mueller and Diamond (2001) proposed that net primary productivity may be a good measure of the differences they encounter in food availability. Later, Clark et al. (2016) demonstrated that insect SMR variation seems decoupled from differences in food nutrient content. These findings are in agreement with our study where the SMR of the carnivorous, omnivorous and herbivorous species did not group according to dietary habits.

The high variance in SMR values obtained for the cricket *Telleogryllus commodus* at both test temperatures might be due to activity/movement within the respirometry chamber. Activity is known to have large effects on O_2 consumption or carbon dioxide production (DeVries et al., 2013). Movement of individuals in closed-systems cannot be detected as readily as in flow-through-systems (Lighton and Fielden, 1995; Terblanche et al., 2004) and the movement rate increases with increasing temperature (Gilchrist, 1996; Deere and Chown, 2006). Therefore, the values of SMR presented for the diurnal crickets may be an overestimation as the SMR of behaviourally active insects range from 3 to 30 times their resting rates (Waters and Harrison, 2012). Insects that fly are expected to have a higher SMR than insects that do not fly (Reinhold, 1999; Full, 1997). In our dataset, the only flying species is the katydid *Caedicia simplex*, whose mean SMR values fell in the middle of the 15 species. Thus, we did not observe higher SMR in this tettigoniid common to New Zealand and Australia (Hudson, 1972).

In insects, typical Q_{10} values range from 2.0 to 2.5, with extreme

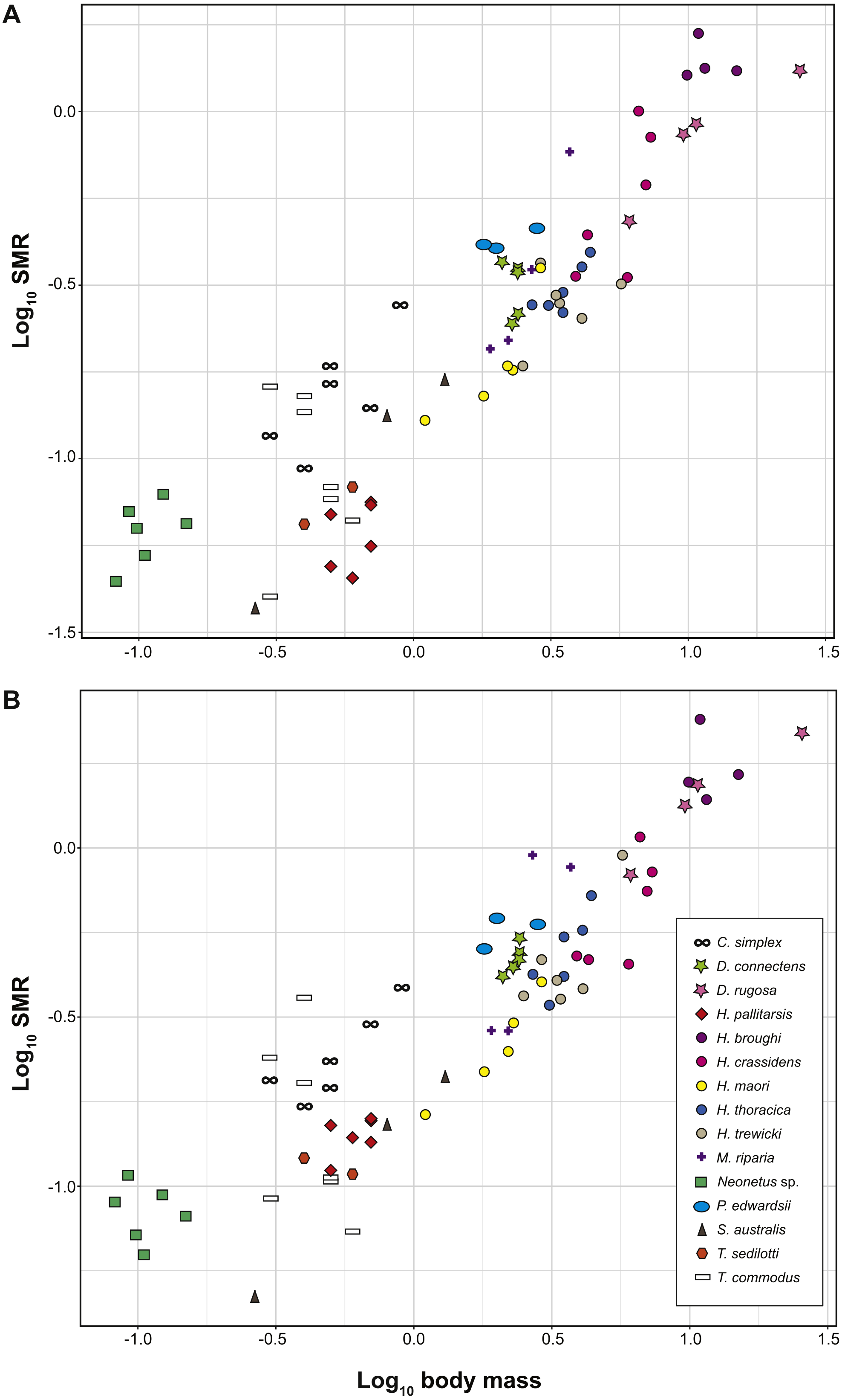

Fig. 2. Bilogarithmic relationships between standard metabolic rate (SMR) and body mass for 15 orthopteran species occurring in New Zealand ($n = 73$). **A.** SMR measured at 4 °C. **B.** SMR measured at 14 °C. Each symbol shape corresponds to a different insect genus with the species shown in different colours. Raw SMR data was measured in ml O_2/h and body mass was measured in grams.

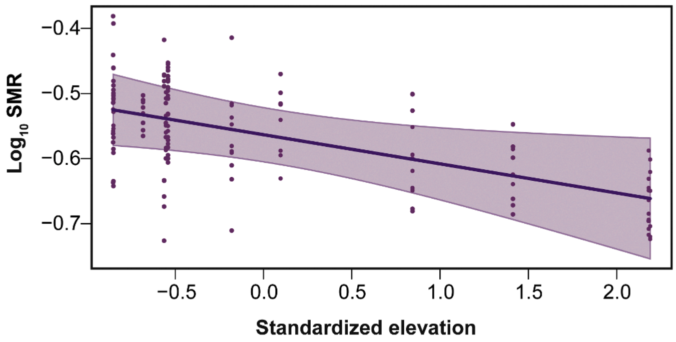

Fig. 3. Partial residual plot of $\log_{10}$-transformed standard metabolic rate (SMR) for the explanatory variable standardized elevation. The purple band indicates the 95 % confidence interval for the conditional expected value of SMR. See Supplementary File S1 for summary output of the selected linear mixed effects model.

values of 1.0 and 4.6 (reviewed by Nespolo et al., 2003). The Q_{10} values calculated at 4–14 °C, ranged from 1.19 to 2.36, with variation in individual Q_{10} values likely reflecting both intra- and interspecific variability in the thermal sensitivity of SMR. In a different study, the cricket *Hophlosphyrum griseus*, presented mean Q_{10} values of 2.43 when measured at 7–17 °C and 2.63 when measured at 17–27 °C, with individual Q_{10} values negatively correlated with the temperature of measurement (Nespolo et al., 2003). The relatively low Q_{10} values obtained for most species in our study might be related to their nocturnal habits. Ambient and body temperatures are lower at night than during the day, and most of these species are active and forage at night. Thus, reduced thermal sensitivity might help preserve a relatively high nocturnal metabolic rate (cf. Chappell, 1983). One individual ground wētā *Hemiandrus pallitarsis*, a Hawkes Bay tree wētā *Hemideina trewicki* and a tusked wētā *Motuweta riparia* presented the highest values of Q_{10} measured. These species are nocturnal and restricted to the North Island of New Zealand. In general, the species we studied with the highest metabolic sensitivity to temperature change were those with northerly (warmer) distributions. Two of the New Zealand species we studied with high thermal sensitivity of metabolic rate estimates are localised, declining species (*Deinacrida rugosa* and *Motuweta riparia*). Climate change will elevate the average temperatures these organisms experience (Dean and Stott, 2009), resulting in increased metabolic rates in thermally sensitive individuals, thus requiring greater energy expenditure. This will be an added challenge to species already facing threats from habitat loss and introduced predators.

We present novel physiological data for the rare and endangered Cook Strait giant wētā *Deinacrida rugosa*, a flagship species for insect conservation in New Zealand (Watts et al., 2008; Pennisi et al., 2017). Giant wētā have a life cycle of >3 years, body length of up to 7 cm, are nocturnal and mainly herbivorous. Adults live primarily on the ground, lay their eggs in soil and roost in dense low-lying vegetation or under piles of sticks or leaf litter. Juveniles are arboreal but generally found within 1 m of the ground (Watts et al., 2017). This study represents, to the best of our knowledge, the first metabolic rate data for this species, and we hope it will inspire more physiological research.

5. Conclusions

Our study does not support the MCA hypothesis. Indeed, we found evidence of co-gradient variation in SMR, with insects from higher elevations and latitudes presenting lower SMR. This finding opens an avenue for further research. The physiological data presented will aid in

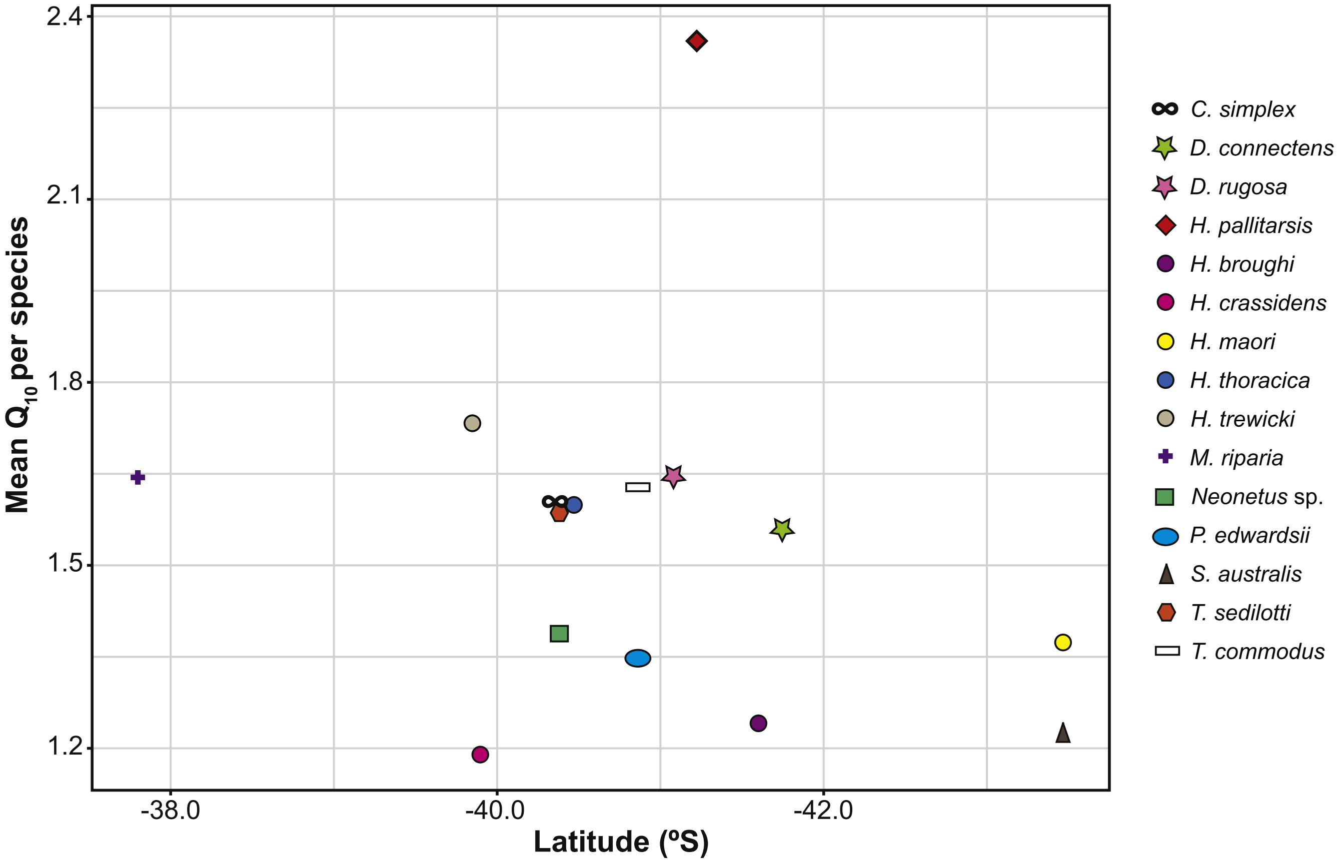

Fig. 4. Mean thermal sensitivity of metabolic rate, Q_{10} per species ($n = 15$) versus mean latitude where the specimens were collected. The values of SMR were obtained at 4 and 14 °C. Each symbol shape corresponds to a different insect genus with the species shown in different colours.

understanding potential responses of these unusual species to changing climatic conditions in Aotearoa/New Zealand (Dean and Stott, 2009; Hopkins et al., 2015).

CRediT authorship contribution statement

Mariana Bulgarella: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing – original draft, Writing – review & editing. **John Haywood:** Formal analysis, Writing – review & editing. **Eddy J. Dowle:** Formal analysis, Writing – review & editing. **Mary Morgan-Richards:** Funding acquisition, Project administration, Writing – review & editing. **Steven A. Trewick:** Investigation, Project administration, Visualization, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Raw data have been submitted to Zenodo, available at https://doi.org/10.5281/zenodo.12775613, and the ShareTrait Project, https://github.com/ShareTraitProject/ShareTrait.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.cris.2024.100092.

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