

Elevational variation in adult body size and growth rate but not in metabolic rate in the tree weta *Hemideina crassidens*

these studies are conducted across a single elevational or latitudinal gradient (reviewed by [Chown and Gaston, 1999](#)). Here, we explore MCA in the context of multiple, independent, high-elevation populations of the same species, predicting a consistent replicated response between contrasting elevations.

Evidence suggests that a larger body and slower growth is adaptive in colder environments (see below, [Angilletta et al., 2004](#)), and might be coupled with elevated metabolic rates to sustain activity and allow for completion of life cycles in the shorter growing seasons characteristic of high-elevation environments. Intraspecific variation in body size has been reported for elevational gradients with a strong relationship between individual size and environment ([Angilletta and Dunham, 2003](#)). In general, animals found in colder climates tend to be larger as adults than their conspecifics in warmer climates. This pattern holds when either altitude or latitude is a proxy for environmental temperature ([Ashton, 2002](#); [Ashton and Feldman, 2003](#)).

Models of ectotherm life-history evolution predict larger adult size in cold environments that retard growth ([Atkinson, 1994](#); [Berrigan and Charnov, 1994](#)). Furthermore, individuals from colder environments are often larger at maturity than those from warmer environments when reared in common garden conditions; e.g., *Drosophila melanogaster* reared at lower temperatures were larger than high-temperature lines (reviewed by [Partridge and French, 1996](#)). To reach larger body sizes in cold environments, individuals must prolong growth and delay reproduction relative to those in warm environments. Such delayed maturation is adaptive when a colder environment enables an increase in fecundity or higher survival rates ([Stearns, 1992](#); [Angilletta et al., 2004](#)).

The Wellington tree weta, *Hemideina crassidens* (Orthoptera: Anostostomatidae), is a large, flightless, nocturnal insect endemic to New Zealand. It is found in the southern third of the North Island and on the west coast of the South Island ([Bulgarella et al., 2014](#)). Some populations are isolated on mountaintops or in low-elevation areas while others are continuously distributed from sea level to 1500 m a.s.l. ([Trewick and Morgan-Richards, 1995, 2014](#)). Tree weta hide in tree holes during the daytime, emerging at night to feed mainly on the leaves of trees and shrubs ([Wehi et al., 2013](#)). Adult *H. crassidens* are sexually dimorphic: males have enlarged heads and mandibles that they use to compete for harems of 1–13 females ([Asher, 1977](#); [Field and Deans, 2001](#); [Kelly, 2005](#)). Individuals of this species from one high-elevation population had longer tibiae and larger body mass than individuals from a low-elevation site, whether collected as adults, or raised from the 3rd or 4th instar in captivity ([Minards et al., 2014](#)).

Studies of the physiology of New Zealand montane insects have centred on the alpine weta *Hemideina maori* and the alpine cockroach *Celatoblatta quinque maculata* (reviewed by [Wharton, 2011](#)). In contrast to *H. maori*, *H. crassidens* features in only two thermal biology studies so far ([Sinclair et al., 1999](#); [Minards et al., 2014](#)). New Zealand sits on the continental boundary of the Pacific and Indo-Australian plates the activity of which resulted in the formation of the Southern Alps and the first widespread alpine habitats (about 5 Ma; [Trewick and Bland, 2012](#)). North Island mountains are of volcanic origin and more recent (<1 Ma). About 75% of New Zealand is >200 m a.s.l. with 19 peaks exceeding 3000 m a.s.l. ([Wallis and Trewick, 2009](#)). Consequently, there are records of repeated invasions of alpine zones in multiple taxa (reviewed by [Buckley et al., 2014](#)) and therefore New Zealand provides an excellent opportunity to explore the consequences of adaptation to the alpine zone.

We hypothesise that local selection at high elevations leads to MCA. Thus we expect to find consistently elevated metabolic rates in high-elevation populations when compared to conspecific weta from low elevations. Another hypothesis holds that larger adult body size is an advantage at higher elevations, leading to selection

for faster growth rates (perhaps because of increased growth efficiency; [Angilletta and Dunham, 2003](#)). If this phenotypic pattern is controlled by genetically-determined differences we predict that high-elevation individuals will grow faster when reared under common-garden conditions at a constant temperature (reviewed by [Arendt, 1997](#); [Angilletta et al., 2002](#)).

2. Materials and methods

2.1. Animal collection and care

We collected weta by searching tree holes during daytime between March and December 2011 (New Zealand Department of Conservation collection permits WE-31465-FAU, NM-32444-FAU, TW-32116-FAU and WA-22197-RES, where appropriate). Adult weta ($n = 55$, 33 female and 22 male) from seven populations were included in the metabolic rate trials ([Fig. 1](#)). Juvenile weta ($n = 138$, 60 female and 78 male) from nine localities were included in the growth trials, and their adult size compared after their final moult. Our sampling represented populations with different elevational (9–1171 m a.s.l.) distributions ([Fig. 1](#)). Two pairs of weta populations in our study are continuously distributed from low to high elevation. On the North Island of New Zealand, the weta from Nga Manu (low elevation) and Mt. Hector (high elevation) are part of a contiguous population, as are those from Graham river (low elevation) and Flora (high elevation) in the South Island. All other populations studied are located on the North Island of New Zealand ([Fig. 1](#)).

We used previously-published 480 bp mitochondrial DNA (mtDNA) cytochrome b sequences ([Bulgarella et al., 2014](#)) to determine the extent of haplotype sharing among 92 individuals from the nine sampled populations by constructing a haplotype network using the median-joining algorithm in the software Network 4.1 ([Bandelt et al., 1999](#); [Fig. 1](#)).

Weta were transported to the laboratory where they were kept in individual plastic containers (17 × 17 × 9 cm) with wire mesh in the lids in a temperature-controlled room at 14 ± 1 °C with a 14:10-h light:dark cycle. The weta were provided with a roost hole made from hollowed bamboo stalk (*Phormium tenax*), and moisture via damp paper-towel. Food was leaves of mahoe (*Meliccytus ramiiflorus*), taupata (*Coprosma repens*) and miro (*Prumnopitys ferruginea*) provided ad libitum. These three plant species are browsed by tree weta in the wild ([Griffin et al., 2011](#); [Dewhurst, 2012](#); [Wehi et al., 2013](#)).

The oxygen levels in the testing cylinder did not drop below 19 kPa. The O₂ sensing system was calibrated for multiple tem-

trial temperature. Most intraspecific studies of MCA lack information about population differentiation (it might indicate the direction of evolved trait changes), and fail to examine whether phenotypic plasticity could explain the observed patterns ([Clarke, 1991, 1993](#); [Terblanche et al., 2009](#)). In our study, mitochondrial

energy for maintenance during physical inactivity ([Lindgren and Laurila, 2009](#); [Gaitán-Espitia and Nespolo, 2014](#)).

H. crassidens presented low Q_{10} values that might be related to their nocturnal habits. Tree weta are active and forage at night when microclimate temperatures are cooler and more homoge-

IAE technicians: Paul Barrett, Tracy Harris, Shaun Nielsen and Cleland Wallace. Karen Smillie from Naturalac Nutrition Ltd (Auckland, New Zealand) donated the protein we used to supplement the diet of our captive weta. Dr. Gabe Redding helped set up the respirometry experiments. Gareth Boyt and Pete Shaw allowed and helped us to collect weta at Pohokura, and Rhys Mills allowed us to sample in the Nga Manu Nature Reserve. Milan Plečáček helped obtain the climate data. The following offices and staff of the New Zealand Department of Conservation helped us: Gareth Boyt (Rangataiki), Jeanine Bishop (Wellington), Beverley Freer and Ian Millar (Nelson Marlborough), and Robyn Ellis (Tongariro Wanganui Taranaki). We are grateful to several anonymous referees for critical comments on an earlier version of the manuscript. This work was supported by a Massey University Research Grant (MURF...2010: What limits a weta?) and the Royal Society of New Zealand (Marsden PVT...601).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.jinsphys.2015.02.012>.

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