Convergent local adaptation in size and growth rate but not metabolic rate in a pair of parapatric Orthoptera species

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Local adaptation is inferred for many morphological and physiological traits but determining the role of natural selection in shaping geographical variation relies on evidence such as provided by fitness estimates or transplantation experiments. In addition, habitat-specific convergent (or parallel) evolution provides a powerful means of testing adaptive hypotheses. In the present study, we contrast size, growth rate, and metabolic rate (as inferred by oxygen consumption) in a pair of Orthopteran species collected from high and low altitude locations and raised in identical environments. We find that two related insects (tree wētā: *Hemideina crassidens* and *Hemideina thoracica*) have the same (convergent) pattern of larger adults and faster growth rates in populations from a high altitude location compared to conspecifics from low altitude. However, variation in metabolic rate was detected only between species and not among altitudes. The high and low altitude populations of each species were collected from the same location; therefore, selection pressures on the two species are likely to be similar. Thus, the independent detection of larger adults and faster growth rate of wētā derived from high altitude suggests an adaptive role for both these traits in tree wētā.   © 2014 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2014, **113**, 123–135.

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INTRODUCTION

Environmental pressures result in the adaptation of organisms to local conditions and the observed outcome is conspecific geographical variation in morphological and physiological traits (Endler, 1977). For example, size clines within species often correspond to environmental gradients. In many ectotherm species, individuals grow to a larger size at higher elevations and higher latitudes (Bergmann's rule; Angilletta Jr, Steury & Sears, 2004; Blanckenhorn & Demont, 2004; Joyce, Jamieson & Barker, 2004). Orthoptera exhibit both Bergmann's clines and converse Bergmann's clines (Bidau & Marti, 2007; Chown & Gaston, 2010). It has been suggested that the inter-

action of size, time to maturity, growth rate, temperature, and season length result in the range of clines and counter-gradient clines observed (Blanckenhorn & Demont, 2004; Walters & Hassall, 2006; Hayden, Parkes & Arthur, 2012). Phenotypic variation is the rule rather than the exception. Phenotypic plasticity to the environment can be differentiated from genetic adaptation by comparison of traits expressed under constant conditions, allowing inference about population differentiation (Stillwell, 2010). Geographical variation itself is not proof of local adaptation because patterns of variation may also be shaped by genetic drift. However, when separate species show similar responses to the same local conditions, then confidence that the differences are adaptations resulting from selection rather than drift is enhanced. Habitat-specific convergence provides a powerful means for testing adaptive hypotheses.

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Morphological and physiological traits of insects may be expected to vary with latitude and altitude as populations respond to local environments. Three traits that are of fundamental importance to an organism's fitness and often vary with altitude are growth rate (Angilletta Jr *et al*., 2004), adult size (Fielding & DeFoliart, 2008), and metabolic rate (Addo-Bediako, Chown & Gaston, 2002). Evolution of these traits might be influenced by many selection pressures, including season length, temperature, juvenile and adult mortality rates, and food quality and quantity (Chown & Gaston, 1999; Bale *et al*., 2002; Case *et al*., 2005; Hodkinson, 2005; Fielding & Defoliart, 2007). Smaller individuals are generally assumed to be less fit in evolutionary terms as a result of lower fecundity and lower competitive ability. However, evolutionary trade-offs may sometimes counter this; smaller individuals may be less susceptible to predation for example. The trade-off between adult size and development time can be circumvented by shifts in growth rate. The generally assumed advantages of large size and rapid development led to the expectation that growth rates in most organisms should be maximized (Arendt, 1997), although empirical evidence suggests that growth rate is seldom at its potential maximum (Margraf, Gotthard & Rahier, 2003; Tammaru *et al*., 2004). Rapid development potentially increases fitness by reducing generation time and by reducing the risk of mortality before reproduction (Fielding & Defoliart, 2007). Rapid maturation can be achieved by some combination of maturation at a smaller size (less growth) or more rapid weight gain (faster growth). Growth in colder environments can be enhanced by modifying rates of consumption, digestion, and respiration (Merila, Laurila & Lindgren, 2004; Oufiero & Angilletta, 2006). However, warm environments might select against rapid growth, if it imposes a cost, such as an elevated risk of predation with increased feeding activity. Natural selection can produce genetically induced variation (adaptation) in growth and development that counteracts thermally-induced variation, resulting in plasticity and counter-gradient variation in many organisms (Arendt, 1997).

In the present study, we compare and contrast the size, rate of growth, and metabolic rate of a pair of nocturnal Orthopteran (tree wētā *Hemideina*) to test an adaptive hypothesis for size and growth rate variation. In a related species, *Hemideina maori* (Pictet and Saussure), altitudinal size variation has been documented on one mountain range, with wētā at higher altitudes (1450 m a.s.l.) being larger than low altitude wētā (at 1100 m a.s.l.) (Koning & Jamieson, 2001; Joyce *et al*., 2004). Although *H. maori* at high altitudes are larger and faster growing (under common garden conditions; Joyce, 2002), survival is similar,

suggesting this size variation is adaptive (Joyce *et al*., 2004). The two wētā species in the present study are members of the same genus, *Hemideina* (White), and each was collected from the same two locations (contrasting high and low altitude). *Hemideina crassidens* (Blanchard) (Wellington tree wētā) has a more southerly distribution than *Hemideina thoracica* (White) (Auckland tree wētā), which is found in (warmer) northern New Zealand. Both of these *Hemideina* species are widely distributed and span latitudes in the range 35–44° south, encompassing a wide climatic envelope (Bulgarella *et al*., 2014).

Where the distributions of *H. crassidens* and *H. thoracica* overlap, there are narrow regions of sympatry in which the two species will share daytime refuges in tree cavities (Trewick & Morgan-Richards, 1995), and two such locations were used as sources of both species for the present study. Reproductive isolation of the two species was inferred from diagnostic colour pattern differences and genetic analysis of tree wētā from Mt Taranaki where karyotypes and four nuclear loci show fixed differences (Morgan-Richards, Daugherty & Gibbs, 1995; Morgan-Richards, Trewick & Wallis, 2000). These two *Hemideina* species are not phylogenetically sister taxa, each being more closely related to other species (Trewick & Morgan-Richards, 2005). Little is known about the physiological and ecological differences between the two species and this is highlighted on Mt Taranaki where *H. crassidens* and *H. thoracica* form a narrow region of sympatry at their distribution junction, in the absence of any physical boundaries. On Mt Taranaki, *H. crassidens* is common at higher altitudes, completely surrounded by *H. thoracica* at lower altitudes. This pattern of parapatric altitudinal separation has also been observed on Mt Ruapehu where high altitude *H. crassidens* populations are entirely surrounded by *H. thoracica* (Trewick & Morgan-Richards, 1995).

Hemideina are hemimetabolous insects and therefore growth is achieved through a series of moults. Female tree wētā reach sexual maturity in their tenth instar, whereas male tree wētā may reach sexual maturity at the eighth, ninth or tenth instar (Spencer, 1995; Kelly & Adams, 2010) and have been termed 'trimorphic' (Kelly, 2008). Once sexual maturity is reached, allometric growth via moulting ceases but body mass may increase through an increase in body weight. In captivity, *H. crassidens* takes 12 months from hatching to maturity (Morgan-Richards *et al*., 2000), although there are no data available on how long it takes tree wētā in the wild to reach adulthood, nor are life-history data available for *H. thoracica*.

The present study aimed to investigate differences in the size, growth, and metabolic rate of tree wētā at a species level (*Hemideina crassidens* versus *H. thoracica*) and at a population level (high altitude

versus low altitude) to seek evidence for adaptive responses. Growth rates and metabolic rates were recorded under constant laboratory conditions to remove environmental variables and to ensure that differences observed were a result of genetic differences. The two species were collected from adjacent sites at high and low altitude locations; thus, if we detect local variation that is similar in the two species, this can be explained by convergent evolution, and we can infer a common selective force. We measured and compared eighth to tenth instar size, growth rate, and metabolic activity at two temperatures.

MATERIAL AND METHODS

STUDY ANIMALS

The animals used in these experiments were New Zealand tree wētā (Orthoptera: Anostostomatidae) *H. thoracica* and *H. crassidens* collected in the spring of 2009 when immature (instars 3 and 4), from two locations, and from similar latitudes (39°–40° south). The low altitude populations of the two wētā were collected from two sites in the Manawatu region, both at 150 m a.s.l. but 30km apart; Kahuterawa Valley (40°28′8.96′S, 175°36′36.80′E) and Waiopehu Reserve (40°38′21.41′S, 175°19′23.61′E). High altitude wētā were collected from Mt Taranaki between the altitudes of 500–1000 m a.s.l. on Manaia, Egmont and Pembroke Roads and Wilkie's Pools Loop track (39°21′S, 174°5′E) by extracting from natural tree cavities and collecting from previously positioned artificial roosts (New Zealand Department of Conservation permit WA-22197-RES). As a result of the low density of *H. thoracica* at 500–650 m a.s.l, three individuals were collected between 500–300 m a.s.l. The high altitude location for wētā collection has a broadleaf forest cover similar to that in the Manawatu sites, although it is both colder and wetter. Mean annual temperature at 800 m a.s.l on Mt Taranaki is 8.3 °C compared to 11.7 °C at 150 m a.s.l in Manawatu, and rainfall is considerably higher on Mt Taranaki (approximately 1500 mm per year) than in the Manawatu (approximately 1000 mm per year), based on climate data from the Land Environments of New Zealand database (Leathwick *et al*., 2003). Because tibia length provides a good estimate of overall body size (Spencer, 1995), this element was compared for female wētā collected as adults from the entire range of both species, including Manawatu and Mt Taranaki, to determine whether wild phenotype follows Bergmann's rule as seen in *H. maori* (Joyce *et al*., 2004).

Animals were kept individually in 2-L plastic containers with wire mesh fitted into the lids to allow ventilation, as well as damp paper towelling to provide moisture, and furnished with lengths of hollowed harakeke (*Phormium tenax*, Forster) flower stems as daytime refuge holes. All wētā were initially kept under a 12 : 12 h light/dark cycle that was gradually extended to a 14 : 10 h light/dark cycle after 1 month in captivity to match longer summer days. The wētā were allowed *ad libitum* access to food consisting of foliage of *Coprosma repens* (Rich) (taupata), *Coprosma robusta* (Raoul) (karamu), *Melicytus ramiflorus* (Forster) (mahoe), and *Prumnopitys ferruginea* (D. Don; De Laub) (miro); the fruits of these plants, as well as carrot tap root (*Daucus carota*-L) and soya protein (Thompson's Red 8 Protein Plus 80% nuggets), were provided weekly (Griffin, Morgan-Richards & Trewick, 2011).

SIZE AND GROWTH RATE

Immature tree wētā were collected from four populations: *H. crassidens* from high altitude and low altitude and *H. thoracica* from high altitude and low altitude. Each population sample was randomly divided into two equal groups and wētā were raised at constant temperatures of either 14 °C or 9 °C (Fig. 1). These temperatures were chosen after considering the temperatures that wētā are likely to be exposed to in their natural environments, tree wētā life expectancy in captivity, their likely rate of growth and the timing of maturity in the context of the time frame of the study, and the power to distinguish variation. Mean annual temperatures for the distribution of these two species are between 7.5 and 14.5 °C (Minards, 2011). Higher temperatures are likely to accelerate growth but might also increase death rate, and no data exist on optimal captive regimes. A difference of 5 °C was considered sufficiently large to result in growth rate variation and 14 °C and 9 °C straddled the mean annual natural conditions.

Each week, body weight was measured using an electronic scale (Avery Berkel FB711; accuracy ± 0.1 g) and left and right hind-tibiae length were measured with digital calipers (Q1382; digital Dick Smith Electronics; accuracy ± 0.03 mm). This provided total data from which we could calculate growth (mass) and allometric growth (tibia length). Allometric growth in hemimetabolous insects has a linear relationship, increasing in size by a specific ratio each moult (Whitman, 2008) that varies between orders and the structure measured. Spencer (1995) found tibial and femoral growth in *H. crassidens* to be consistent and tibial growth linear, allowing us to meet the assumptions required in the statistical analyses. A linear regression of tibia length or body mass against time (in weeks) provided the slope used as our estimate of growth rate. The growth rate at each instar was compared with all other instars to test for linearity and
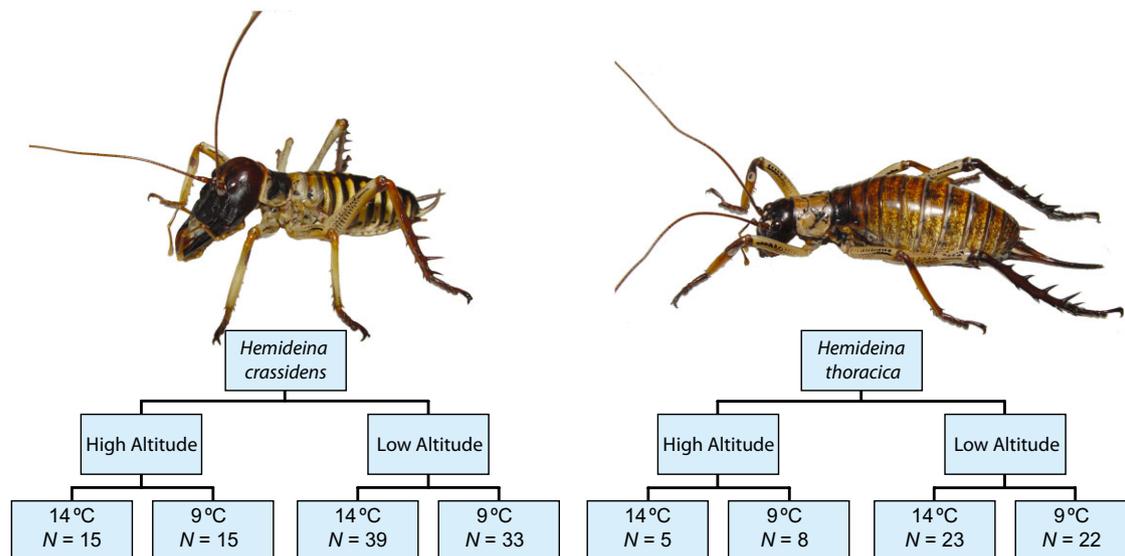
Figure 1. Treatment groupings and group sizes of two species of tree wētā (*Hemideina crassidens* and *Hemideina thoracica*) collected from two locations where they are locally sympatric and tested for growth rate and adult body size.

confirmed that there were no significant variations in rate estimates among instars. Individuals continued to be measured weekly until they reached their final, adult instar. Sexual maturity was determined by continuous morphological characteristics of a long, sharp, curved, dark ovipositor in females and by long, curved cerci in males. Additionally, expected adult leg measurements were derived from Spencer, (1995) and any irresolute individuals were tested for sexual behaviour against known adults of the opposite sex (Spencer, 1995). Once wētā reached maturity, weight measurements were taken for an additional 2 weeks to allow the weight to equilibrate after moulting. Whether measured allometrically or by weight, tree wētā in the present study were consistent in their growth and all treatment groups showed significant differences at the same points with respect to both weight and tibial growth. This suggests that either weight or length characteristics can provide an indication of both growth rate and life stage for any given *Hemideina* individual.

DETERMINATION OF LOWER TEMPERATURE LIMITS FOR ACTIVITY

We made observations of activity at a range of temperatures (5 °C–8 °C) to establish the lowest temperature threshold at which these two species of tree wētā were active. Wētā were kept at constant temperatures for 5 days and checked daily for evidence that they had left their day-time refuge (thread across the entrance hole) and/or feeding (a single intact *Coprosma repens* leaf). If the thread was disturbed

and the foliage was eaten, the study was reset to detect activity over the next 24 h.

MEASUREMENT OF OXYGEN CONSUMPTION

Oxygen consumption of adult wētā was measured at both 14 °C and 6 °C as a proxy for metabolic rate. Before experimentation, the wētā were allowed to acclimate to the study temperature for 10 days and all wētā used were starved for 24 h prior to use in the present study to reduce potentially complicating digestive effects. All metabolic trials were performed in dark cuvettes during the day, which corresponds to resting conditions for this nocturnal species. A closed circuit respirometry system was chosen for the present study as a result of the size of the animals and the relative simplicity of the set-up. The software used to record the oxygen metabolism was OOISENSOR, version 1.05 (Ocean Optics Inc.). This system uses an LED light (approximately 475 nm) in an optical fibre that excites a sol-gel formulation at the tip to fluoresce at approximately 600 nm. When this complex encounters an oxygen molecule, the excess energy quenches the fluorescent signal, resulting in a reading that correlates with the partial pressure of oxygen within the chamber. This 'oxygen lifetime' can then be transformed into partial pressure of oxygen (pO_2) using the Stern–Volmer equation (Carraway *et al.*, 1991). The software was first calibrated at each temperature with gas containing a high pO_2 (air ≈ 20.95% oxygen) and low pO_2 of oxygen (100% nitrogen gas ≈ 0% oxygen). These lifetime standards were then used to calculate the

Stern–Volmer constant (k). Once calibrated, and with k established, a single wētā was placed in an open ended glass tube (30.4 cm^3) covered with dark plastic to stimulate resting by reproducing a natural roosting space, which is essential for removing any chance of anaerobic metabolism (Schmidt-Nielsen, 1998). The open end of the tube was closed with the recording probe inserted into a rubber bung to ensure an air-tight seal. The O_2 probe was connected via a bifurcated fibre optic cable to a fibre optic O_2 sensing system (Tau Theta Instruments LLC), which recorded O_2 partial pressure at 2-s intervals over each 4-h run. The O_2 sensing system was calibrated for multiple temperatures and the environmental temperature was monitored continuously to ± 0.5 °C accuracy with DS1921K Thermochron iButton (Maxim). Once the wētā began resting, the recordings began. The data were collected for approximately 4 h or until a 3% drop in pO_2 was observed.

STATISTICAL ANALYSIS

Sizes of wētā were tested with a linear mixed effects model. Growth rate and oxygen consumption of tree wētā were tested using analysis of variance for the incomplete factorial experimental design. Both analyses cater to the varying number of observations for treatment combinations and were conducted using R statistical software (The R Project for Statistical Computing). We assumed that the growth rate of the wētā (measured by tibia length or weight) was linear and therefore equivalently well-established regardless of the number of instars used to estimate growth rate (this was supported by a test for linearity). We also assumed that each mean in each category is an accurate reflection of the mean response for that treatment combination, despite the different number of replicates for each combination.

RESULTS

MATURATION OF TREE WĒTĀ

Of the 160 weta in the present study (Fig. 1), only 65 tree wētā reached maturity in the time available. Thirty-seven were females that matured in their tenth instar. Fifteen males matured at their ninth instar (54% of males) and 13 males matured at their tenth instar (46% of males). Of the early maturing males, 11 of 15 were *H. crassidens* (73%; two high altitude and nine low altitude) and four (27%; low altitude) were *H. thoracica*. These proportions of early maturing males from each population are in keeping with our sample sizes (χ^2 = 2.22, d.f. = 1, $0.5 < P < 0.10$). The temperature at which wētā were raised had no effect on rate of early maturing (χ^2 = 1.807, d.f. = 3, $P > 0.5$). Instar duration in cap-

tivity varied between 5 and 41 weeks, depending on instar, temperature, and weta.

SIZE OF WĒTĀ

Size variation of adult females has been noted within the range of both species. A weak latitudinal gradient is observed (see Supporting information, Fig. S1; r^2 = 0.239, $P < 0.0001$) over more than 800 km, confounded by altitude effects with larger tree wētā at higher elevations (M. Morgan-Richards, pers. observ.). Female tree wētā collected as adults from the Manawatu region generally have slightly shorter legs than wild caught adult females from Mt Taranaki: *H. crassidens* – Manawatu (N = 25) tibia length = 21.50 mm; Taranaki (N = 22) tibia length = 22.60 mm (*t*-test; P = 0.0001); *H. thoracica* – Manawatu (N = 46) tibia length = 21.92 mm; Taranaki (N = 15) tibia length = 23.17 mm (*t*-test; P = 0.0003). These data indicate that wild populations follow Bergmann's rule as seen in *H. maori* (Joyce *et al.*, 2004).

To determine what factors influence size of captive weta (Table 1), a mixed-effect model for tibia length incorporating the three final instars, sex, species, altitude of collection, and temperature at which the insect was raised was used. We incorporated instar into the analysis to deal with the trimorphic nature of adult males, although this resulted in non-independence of some data points. When species was found to make no significant improvement to model fit (likelihood ratio = 5.2187; P = 0.074), a reduced linear mixed-effects model was used (Table 2). Naturally, instar was a significant factor with respect to determining size, and we also found that females were significantly smaller than male wētā; however, no significant effect of species was found on tibia length. The warmer temperature (14 °C) resulted in wētā with longer tibia than the cooler constant temperature of 9 °C, and the wētā of both species from low altitude had shorter tibia than wētā from the higher altitude. There was significant interaction between the traits: instar and sex; instar and temperature; instar and altitude; and temperature and altitude. An interaction between instar, temperature, and altitude was the only significant higher level interaction (Table 2). Overall, *H. crassidens* were heavier than *H. thoracica*, although they have similar length tibia. Both species collected from the same high altitude region reached larger size than conspecifics from the low altitude location (Fig. 2).

GROWTH RATE OF TREE WĒTĀ UNDER CONTROLLED CONDITIONS

Growth rate was estimated using tibia length and weight and these two measures produced identical

Table 1. A comparison of size (tibial lengths) and body weight for two species of tree weta from high and low altitude locations raised at two temperatures, at the eighth, ninth, and tenth instars

		Hemideina crassidens				*Hemideina thoracica*			
		High altitude		Low altitude		High altitude		Low altitude	
Instar		9 °C	14 °C	9 °C	14 °C	9 °C	14 °C	9 °C	14 °C
Tibia length, mean ± SE (mm)									
10	Male			21.75 ± 0.94	21.085	21.52 ± 0.12	23.08 ± 0.51		23.88 ± 0.35
	Female		23.00 ± 0.36	21.36 ± 0.19	22.02 ± 0.39	23.52 ± 1.1	22.95	21.25 ± 0.38	22.29 ± 0.27
9	Male	18.18 ± 0.03	19.76 ± 0.28	18.19 ± 0.39	18.15 ± 0.29	20.153	19.41 ± 0.29	18.67 ± 0.57	19.62 ± 1.24
	Female		18.87 ± 0.37	17.68 ± 0.16	18.35 ± 0.40		18.376	18.26 ± 0.35	18.84 ± 0.28
	EM Male	20.14 ± 0.38		18.89 ± 0.47	19.60 ± 0.37				19.20 ± 0.18
8	Male	17.75 ± 0.04	17.44 ± 0.29	17.33 ± 0.45	16.76 ± 0.31	18.53 ± 0.49	15.167	16.13 ± 0.42	17.54 ± 0.03
	Female							15.99 ± 0.25	16.05 ± 0.2
	EM Male	17.23 ± 0.02	15.17 ± 0.37	16.28 ± 0.17	16.60 ± 0.16				16.21 ± 0.11
Weight, mean ± SE (g)									
10	Male			4.25 ± 0.41 (4)	3.45 (1)	3.66 ± 0.17 (3)	3.87 ± 0.29 (4)		3.06 ± 0.21 (4)
	Female		4.92 ± 0.23 (5)	3.46 ± 0.1 (3)	3.37 ± 0.37 (3)		5.19 (1)	3.27 ± 0.37 (8)	3.24 ± 0.17 (3)
9	Male	4.33 ± 0.35 (5)	4.35 ± 0.06 (3)	3.47 ± 0.31 (7)	2.58 ± 0.11 (6)	3.39 ± 0.29 (3)	3.17 ± 0.06 (3)	3.35 ± 0.19 (4)	2.78 ± 0.06 (4)
	Female		4.19 ± 0.26 (5)	2.97 ± 0.09 (5)	2.80 ± 0.14 (6)		3.72 (1)	2.63 ± 0.16 (8)	2.46 ± 0.09 (5)
	EM Male	3.82 ± 0.29 (6)		2.86 ± 0.27 (4)	3.21 ± 0.2 (4)				2.68 (1)
8	Male		3.82 ± 0.39 (3)	2.74 ± 0.17 (12)	2.19 ± 0.1 (12)	2.77 (1)	2.46 ± 0.39 (2)	2.73 ± 0.17 (5)	1.97 ± 0.05 (3)
	Female		2.34 ± 0.24 (4)		1.98 (1)			2.29 ± 0.17 (3)	1.94 ± 0.08 (6)
	EM Male		2.69 ± 0.25 (3)	2.65 ± 0.16 (4)	2.51 ± 0.03 (4)			1.99 ± 0.11 (7)	1.94 ± 0.21 (3)

EM, early maturing males. Sample sizes (in brackets) for weight are the same for tibia except where moulting damage required removal.

Table 2. A reduced linear mixed-effects model to explain variation in tibia length of two tree weta species (*Hemideina crassidens* and *Hemideina thoracica*) collected from high and low altitude and raised at either 14 °C or 9 °C

	Value	SE	d.f.	t	P
(Intercept)	−2.4993	1.2605	156	−1.9828	0.0491
Instar	2.4938	0.1541	156	16.1834	< 0.0001
Sex – female	−6.3163	1.3125	147	−4.8125	< 0.0001
Sex – male	1.8054	1.1226	147	1.6082	0.1099
Temperature	−8.2552	1.1190	147	−7.3776	< 0.0001
Altitude	−1.4728	0.8142	147	−1.8090	0.0725
Instar × Sex – female	0.6473	0.1487	156	4.3543	< 0.0001
Instar × Sex – male	−0.1884	0.1321	156	−1.4265	0.1557
Temperature × Altitude	7.3392	1.3195	147	5.5622	< 0.0001
Instar × Temperature	0.9084	0.1367	156	6.6457	< 0.0001
Instar × Altitude	0.0582	0.1090	156	0.5341	0.5941
Instar × Temperature × Altitude	−0.7862	0.1598	156	−4.9197	< 0.0001
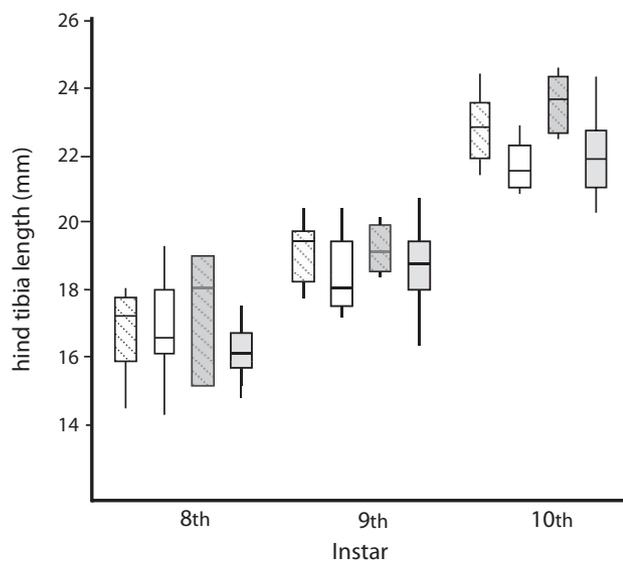
Figure 2. Size (tibia length) of tree wētā in their final three instars, which originated from different locations but were raised in captivity. *Hemideina crassidens* (white), *Hemideina thoracica* (grey), high altitude (hatched), low altitude (not hatched), mean, SE, and range indicated. Data for the two temperature regimes are combined for simplicity of presentation but considered separately in the model.

results; therefore, the results are shown for allometric growth (tibia length) only (Table 3).

Temperature (14 °C and 9 °C) and collection location were shown to have a significant effect on growth rate. Tree wētā grew faster at 14 °C than at 9 °C (Tables 3, 4). When raised under identical conditions, wētā from the high altitude location (Mt Taranaki) grew faster than those from the low altitude location (Manawatu; $P < 0.012$). This was the case for both

species of tree wētā and was observed at both captive temperatures (Table 4). High altitude wētā show a mean growth rate at 14 °C, which is over double that at 9 °C, whereas the low altitude wētā increased their growth rate only slightly from 9 °C to 14 °C (Fig. 3). Sex alone was tested for importance as a predictor of growth rate (see Material and methods) but was not found to be significant ($P = 0.3239$). The two species did not differ significantly in growth rate when tested alone; however, interactions were detected between sex and species, and temperature and altitude (Table 4). Female *H. thoracica* grew faster than any other group [sample size from low altitude, 14 °C ($N = 15$), 9 °C ($N = 14$); high altitude 14 °C ($N = 1$), 9 °C ($N = 4$)]. By contrast, early maturing males from the same species ($N = 6$) showed the slowest rate of growth of all groups (Fig. 3). Although high altitude wētā grew faster than low altitude wētā, this difference was more pronounced at the higher laboratory temperature (Fig. 3). To test for the significance of higher interactions, residual sum of squares values were calculated for both the full factorial model (0.26633, d.f. = 141) and for the reduced model (0.27846). The difference between these values (0.012132) represents the extra variability associated with all interactions within the model, which proves to be insignificant ($P = 0.6255$); therefore, higher interactions for growth rate are not detected in the present study.

METABOLIC RATE

The lower temperature limit of activity for both species of tree wētā was determined by testing for feeding and emergence from their daytime refuge holes at various temperatures. At 5 °C, although one wētā emerged from her refuge hole, no feeding activity was recorded ($N = 31$ observations). At 6 °C, four tree wētā emerged

Table 3. A comparison of growth rates (tibial lengths (mm week⁻¹) for two species of tree weta from high and low altitude locations when raised at constant temperatures (9 °C or 14 °C)

Tibia (mm week⁻¹), mean ± SE

| | *Hemideina crassidens* | | | | *Hemideina thoracica* | | | |
| | High altitude | | Low altitude | | High altitude | | Low altitude | |
	9 °C	14 °C	9 °C	14 °C	9 °C	14 °C	9 °C	14 °C
Male	0.014 ± 0.006 (11)	0.109 ± 0.024 (9)	0.025 ± 0.003 (23)	0.025 ± 0.003 (28)	0.048 ± 0.005 (6)	0.071 ± 0.019 (4)	0.006 ± 0.011 (8)	0.003 ± 0.008 (4)
Female		0.079 ± 0.011 (5)	0.054 ± 0.006 (5)	0.053 ± 0.011(7)	0.076 ± 0.033 (4)	0.063 (1)	0.038 ± 0.005 (14)	0.047 ± 0.004 (15)
EM Male			0.028 ± 0.007 (5)	0.054 ± 0.003 (4)	0.039 ± 0.003 (2)			0.010 ± 0.004 (4)

EM, early maturing males. Sample sizes in brackets.

from their refuge and one wētā was recorded as having eaten ($N = 39$ observations). From this, we infer that *H. crassidens* and *H. thoracica* can be active at 6 °C, making this a suitable lower limit for recording oxygen consumption.

OXYGEN CONSUMPTION OF TREE WĒTĀ

A weak positive correlation between mass and oxygen consumption was observed at 14 °C ($r^2 = 0.196$; $P < 0.001$); thus, we analyzed mass-specific oxygen consumption. Temperature had a strong positive effect on mass-specific oxygen consumption (Table 5). The rate of mass specific oxygen consumption was approximately 2.7-fold higher when wētā were tested at 14 °C than at 6 °C (Table 5). On average, *H. thoracica* has a higher mass-specific oxygen consumption than *H. crassidens* at both 14 °C and 6 °C, although the difference is small (0.032 mL O₂ g h⁻¹ at 14 °C; 0.019 mL O₂ g h⁻¹ at 6 °C) (Table 5). Mass specific oxygen consumption did not show significant differences among populations or sexes ($P = 0.346$ and 0.200) (Tables 6, 7). No significant higher interactions were detected for mass specific oxygen consumption.

DISCUSSION

We have demonstrated for the first time that *H. thoracica* males can reach maturity at either their ninth or tenth instar. Our sample sizes of wētā in each of the 24 categories varied. In particular, fewer *H. thoracica* individuals were collected from the high altitude location as a result of the low density of this species at the high altitudes where the ranges of *H. thoracica* and *H. crassidens* meet. It was necessary to broaden our sampling effort to lower altitudes to obtain sufficient wētā. Importantly, the uneven sampling did not prevent us demonstrating that several factors have a significant influence on the characters of interest (size and growth rate). Although we detected significant size variation between the sexes (females smaller), we failed to detect significant variation in either metabolic rate or growth rate to explain this size difference. However, our power to discriminate variation among the ninth-instar maturing males and the tenth-instar maturing males was low and thus we regard observations of variation among the sexes as preliminary.

Tree wētā of both species from high altitude (Mt Taranaki) showed greater weights and tibial lengths in their last three instars (eighth, ninth and tenth) than those collected from low altitude (Manawatu), consistent with observations of wild caught adult weta from these locations. Although most orthoptera species with interspecific size clines show a negative relationship with altitude or latitude, these species

Table 4. A reduced factorial model to explain variation in growth rates (tibia length) of two species of tree weta (*Hemideina crassidens* and *Hemideina thoracica*) from high and low altitude populations raised at two constant temperatures (14 °C or 9 °C)

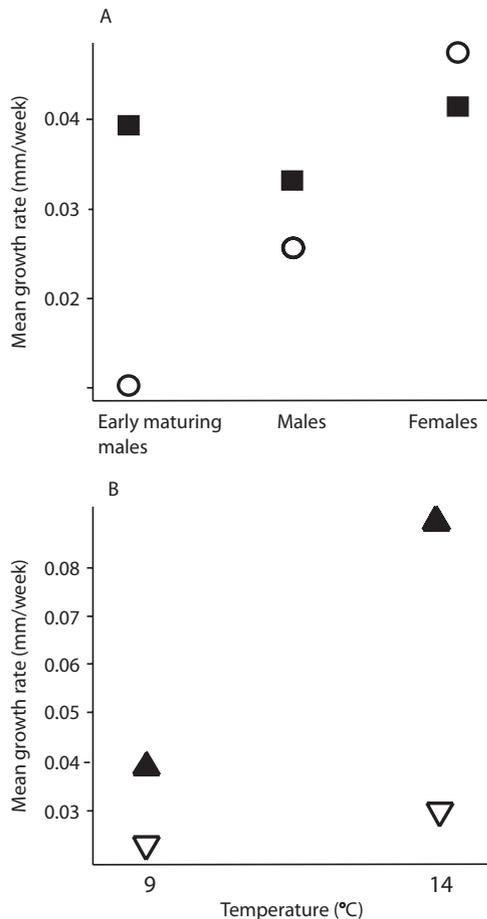|	d.f.	Sum of squares	Mean squared	F	$Pr(> F)$
Temperature	1	0.0122	0.0122	6.603	0.0112
Altitude	1	0.0462	0.0462	24.957	> 0.0001
Sex	2	0.0100	0.0049	2.6486	0.0740
Species	1	0.0001	0.0001	0.0433	0.8354
Temperature × Altitude	1	0.0131	0.0131	7.1019	0.0085
Sex × Species	2	0.0113	0.0056	3.0477	0.0504
Residuals	151	0.2794	0.0019		

Figure 3. Interaction plots describing the relationship of growth rate (tibial growth) of tree wētā with variables examined. A, the effect of sex on growth rate depends on species; *Hemideina crassidens* (black squares), *Hemideina thoracica* (circles). B, the effect of the temperature at which raised on growth rate depends on the location from which the wētā were collected as nymphs; high altitude (black triangle) and low altitude (white triangle).

Table 5. A comparison of the effect of ambient temperature on the mean mass specific oxygen consumption of two species of tree weta (*Hemideina crassidens* and *Hemideina thoracica*)

	Mean mass specific oxygen consumption (mL O_2 g^{-1} h^{-1})	
Temperature (°C)	*Hemideina crassidens*	*Hemideina thoracica*
14	0.2177 ($N = 30$)	0.2501 ($N = 27$)
6	0.0751 ($N = 26$)	0.0938 ($N = 19$)

are not the first to follow Bergmann's rule (Atkinson, 1994; Bidau & Marti, 2008), which was observed in the weta *H. maori* (Koning & Jamieson, 2001; Joyce *et al.*, 2004; Shelomi, 2012). The temperature at which the wētā were raised influenced their adult size, with the warmer temperature resulting in slightly larger individuals. Thus, the naturally lower temperatures at high altitude would be expected to result in smaller individuals, via a purely plastic phenotype response. This is not what is observed in wild caught adult wētā, suggesting that genetic differences among populations produce larger individuals at high altitude, thus revealing counter-gradient variation (Conover & Schultz, 1995).

GROWTH RATES

Because *H. crassidens* and *H. thoracica* have parapatric ranges that only narrowly overlap in the region of our collecting locations, we expected physiological differences might be revealed when we compared growth rates. It is surprising, therefore, that none of the variation in growth rates observed could be attributed to species differences. Striking differences in growth rate are seen when the high altitude populations are compared with the low altitude populations

Table 6. A comparison of mass specific oxygen consumption (mL O_2 g^{-1} h^{-1}) of two species of tree weta collected from high and low altitude, measured at two temperatures, with sample size in brackets

Sex	*Hemideina crassidens* (14 °C)		*Hemideina thoracica* (14 °C)	
	High altitude	Low altitude	High altitude	Low altitude
Male	0.21 ± 0.025 (6)	0.24 ± 0.013 (11)	0.25 ± 0.021 (5)	0.25 ± 0.030 (4)
Female	0.21 ± 0.025 (6)	0.20 ± 0.026 (7)	0.19 ± 0.025 (2)	0.26 ± 0.029 (16)
	Hemideina crassidens (6 °C)		*Hemideina thoracica* (6 °C)	
	High altitude	Low altitude	High altitude	Low altitude
Male	0.08 ± 0.017 (4)	0.09 ± 0.011 (9)	0.11 ± 0.040 (2)	0.10 ± 0.048 (2)
Female	0.06 ± 0.010 (6)	0.07 ± 0.013 (7)	0.10 ± 0.028 (2)	0.09 ± 0.024 (12)

Table 7. A reduced factorial model to explain variation in mass specific oxygen consumption of two tree weta species (*Hemideina crassidens* and *Hemideina thoracica*) from high and low altitude, measured at two temperatures (14 °C and 6 °C)

	d.f.	Sum of squares	Mean squared	F	$Pr(> F)$
Sex	1	0.0079	0.0079	1.801	0.1827
Species	1	0.0452	0.0452	10.273	0.0018
Population	1	0.0043	0.0043	0.972	0.3267
Temperature	1	0.5523	0.5523	125.409	> 0.0001
Residuals	99	0.4360	0.0044		

and there is no interaction between location and species, although samples for high altitudinal *H. thoracica* were smaller ($N = 17$) than high altitudinal *H. crassidens* ($N = 25$). At both captive rearing temperatures (9 °C and 14 °C), the wētā that originated from high altitude populations grew faster than the wētā from the low altitude populations, although the difference was most pronounced at 14 °C. The more rapid growth rate is correlated with larger adults raised in captivity for both *H. crassidens* and *H. thoracica* from high altitude locations, and concordant with size differences of wild wētā from these two locations. Very few studies have shown counter-gradient variation at contrasting altitudes (Berven, 1982; Berner, Korner & Blanckenhorn, 2004). Especially interesting is that, for tree weta, the counter-gradient variation is for body size itself (which usually shows a co-gradient pattern), as well as growth rate.

Significant variation in rates of growth and size of adults (when raised in identical conditions) suggests a genetic difference between intraspecific populations of both *H. crassidens* and *H. thoracica*. High altitude populations are likely to have a shorter growing season that might select for more rapid growth rate and this is observed in a number of orthoptera. For example, *Omocestus viridulus*-L (Acrididae) grasshoppers have a similar response to altitude; high altitude populations have a higher growth rate and attain sexual maturity faster than those from lower altitude when raised in a common environment (Berner *et al.*, 2004). Our results are consistent with the observations of faster growth in captivity of high altitude *H. maori* compared to low altitude conspecifics, and larger adults in wild populations of that species at high altitude (Joyce, 2002). The grasshopper *Melanoplus sanguinipes* (Fabricus) also shows a faster growth rate in individuals taken from a colder climate (Alaska, sub-arctic) but, in contrast to the present study, cold adapted individuals had a lower mature body mass than those from the temperate region of Idaho, regardless of the temperature at which they were raised (Fielding & Defoliart, 2007). This local adaptation may be a result of the shorter growing season in Alaska (106 growing days versus 187 days). Subarctic populations show sensitivity to a poorer quality diet, which leads to increased consumption and therefore a greater proportion of time feeding, which may lead to a greater chance of predation (Fielding & Defoliart, 2007).

In combination, the size obtained and growth rate under constant conditions allows us to infer the final

outcomes of the counter gradients observed. The genetic control of growth rate inferred from population variation retained in the laboratory suggests that high altitude wētā have an innate faster rate of growth than low altitude wētā. High altitude wētā were observed to attain longer tibia than low altitude wētā in captivity. In the wild, if there were no genetic difference, high altitude wētā are expected to experience lower temperatures (annual mean 8.3 °C) and thus grow more slowly and end up smaller than their low altitude counterparts. The counter-gradient variation is for body size as well as growth rate, and the expected result is wētā of optimal size in each location. However, for this data set, we cannot be sure that altitude and temperature are key factors because each species was collected from only two locations. The convergence of intraspecific variation of growth rate and adult size in the two species allows us to infer that both traits are adaptive.

METABOLIC RATE

A positive but weak correlation between mass and oxygen consumption was observed at 14 °C, as seen in other Orthoptera species (Ashby, 1997; Nespolo, Lardies & Bozinovic, 2003; Booth & Kiddell, 2007; Terblanche *et al.*, 2009). Mass specific oxygen consumption at the same temperature differed between the two species but not among high and low altitude populations. The species with a distribution in the cooler regions of New Zealand (*H. crassidens*) had a slight but significantly lower mean metabolic rate (as measured by mass specific oxygen consumption) than *H. thoracica*. This difference is not as expected because cold adapted ectotherms usually show an elevated metabolic rate in a counter-gradient pattern (Massion, 1983; Addo-Bediako *et al.*, 2002). Although high altitude conspecifics are larger and faster growing, they do not have elevated mass specific metabolic rates. The lower metabolic rate of *H. crassidens* compared to *H. thoracica* is in keeping with a body shape (heavier bodies but same sized tibia) suggesting that this species jumps less often than its congeneric counterpart.

The lack of variation in metabolic rate between populations is surprising because, in similar experiments involving Orthoptera, mass specific oxygen consumption was almost always elevated in high altitude populations compared to low altitude populations at the same temperature (Massion, 1983; Lachenicht *et al.*, 2010). For example, in the grasshopper, *Aeropedellus clavatus* (Thomas), collected from an altitudinal gradient, VO_2 increased with altitude, a positive correlation attributed to adaptation to lower temperatures at higher altitude. Tree wētā with faster growth rates and larger body size do not appear

to have gained this advantage from an increase in metabolic rate.

CONVERGENCE OF GROWTH RATES

Geographical variation within species is not uncommon but inferring the evolutionary processes involved in the production of patterns of differentiation is not always possible. Even when plastic responses to the environment can be ruled out, such as in the case for some of the observations in the present study where measurements were made under constant laboratory conditions, it is still possible that genetic drift is responsible for the observed variation. However, convergence of local adaptations in separate lineages provides strong evidence that natural selection is involved in the local differentiation. In these tree wētā, we found variation in growth rate and size when populations from high and low altitude were compared, and this variation was detected in two species, suggesting independent evolution and an adaptive role for growth rate and adult body size in these insects. We assume that the common ancestor of these two species did not contain the range of physiological diversity recorded within each species and, given the time and range changes that have occurred since the last common ancestor, this may be reasonable (Trewick & Morgan-Richards, 2005; Bulgarella *et al.*, 2014). Caution is needed when interpreting the present results because the wētā were collected as immature individuals from the wild and early environmental experience and maternal effects on growth could influence the growth-rate and size at maturity variation that we detected under controlled conditions (Ab Ghani, Herczeg & Merila, 2012). However, it cannot explain the variation that we found in growth rate and final body size of wētā from the same location that were grown at different temperatures.

Rapid development potentially increases fitness by reducing generation time and reducing the risk of mortality before reproducing (Fielding & Defoliart, 2007). However, empirical evidence suggests that growth rate is seldom at its potential maximum (Margraf *et al.*, 2003; Tammaru *et al.*, 2004). A change in growth rate can result from changes in quality and/or quantity of food eaten or more efficient absorption of nutrients. In this case, changes in metabolic rate do not appear to be involved in variation of growth rate.

It is possible that altitude and its concordant temperature gradient is not the principle selective force driving convergence in size and growth rate, although altitude and latitude have both been linked to such changes in ectotherms, (Berner *et al.*, 2004; Fielding & Defoliart, 2007). Furthermore, two locations do not

make a cline, although convergence of these traits in two non-sister tree wētā species in the same landscape comprises strong evidence for a role for natural selection. Growth rate might not be at its potential maximum to be at a selective advantage and the fittest adult size is likely to be location dependent in tree wētā.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Size cline over the latitudinal range of two species of New Zealand tree wētā, for tibia length (mm) of adult females (*Hemideina crassidens* (filled points) and *Hemideina thoracica* (open points)]. A simple regression analysis revealed a weak but significant relationship, with smaller (shorter tibia) wētā in the warmer north of the species' range compared to larger (longer tibia) in the cooler south, $r^2 = 0.239$ (adjusted $r^2 = 0.236$), $F_{1,230} = 72.36$, $P < 0.0001$.