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 weta: 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 weta derived from high altitude suggests an adaptive role for both these traits in tree weta. © 2014 The Linnean Society of London, Biological Journal of the Linnean Society, 2014, 113, 123–135.

ADDITIONAL KEYWORDS: geographical variation – growth rate – Hemideina – parallel evolution.

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 interaction of size, time to maturity, growth rate, temperature, and season length result in the range of clines and counter-gradient clines observed (Blanckenhorn

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 organismÕs Þtness 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 inßuenced 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 Þt in evolutionary terms as a result of lower fecundity and lower competitive ability. However, evolutionary trade-offs may some-times 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 develop-ment 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 Þtness 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 respi-ration (Merila, Laurila & Lindgren, 2004; OuÞero & Angilletta, 2006). However, warm environments

versus low altitude) to seek evidence for adaptive

conÞrmed that there were no signiÞcant variations in rate estimates among instars. Individuals continued to be measured weekly until they reached their Þnal, 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,

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

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

Tibia length, mean ± SE (mm)

Instar		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
10	Male		23.00 ± 0.36	21.75 ± 0.94	21.085	21.52 ± 0.12	23.08 ± 0.51	21.25 ± 0.38	23.88 ± 0.35
	Female			21.36 ± 0.19	22.02 ± 0.39	23.52 ± 1.1	22.95		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		15.17 ± 0.37					15.99 ± 0.25	16.05 ± 0.2
	EM Male	17.23 ± 0.02		16.28 ± 0.17	16.60 ± 0.16				16.21 ± 0.11

Weight, mean ± SE (g)

Instar		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
10	Male	4.33 ± 0.35 (5)	4.92 ± 0.23 (5)	4.25 ± 0.41 (4)	3.45 (1)		3.87 ± 0.29 (4)	3.27 ± 0.37 (8)	3.06 ± 0.21 (4)
	Female		4.35 ± 0.06 (3)	3.46 ± 0.1 (3)	3.37 ± 0.37 (3)		5.19 (1)	3.35 ± 0.19 (4)	3.24 ± 0.17 (3)
9	Male	3.82 ± 0.29 (6)	4.19 ± 0.26 (5)	3.47 ± 0.31 (7)	2.58 ± 0.11 (6)	3.66 ± 0.17 (3)	3.17 ± 0.06 (3)	2.63 ± 0.16 (8)	2.78 ± 0.06 (4)

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 signiþcant 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 signiþcant (P = 0.3239). The two species

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 O_2 g h$^{•1}$ at 14 ¡C; 0.019 mL O_2 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. roxi-

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		
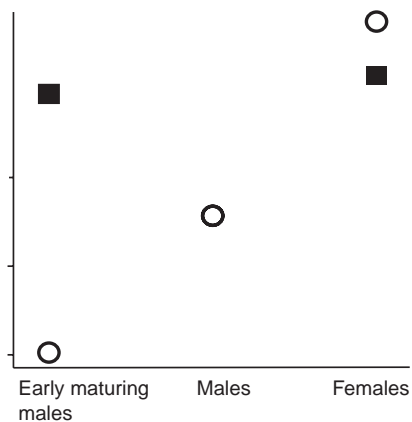
are not the Þrst to follow BergmannÕs rule (Atkinson, 1994; Bidau & Marti, 2008), which was observed in the weta H. maori (Koning & Jamieson, 2001; Joyce et al., 2004; Shelomi, 2012). The temperature at which the weta were raised inßuenced their adult size, with the warmer temperature resulting in slightly 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 weta, 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

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 we øta that originated from high altitude populations grew faster than the weøta 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 we øta 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.

make a cline, although convergence of these traits in two non-sister tree weøta 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 Þttest adult size is likely to be location dependent in tree weøta.

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