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Intrapopulational variation in the standard metabolic rate of insects: repeatability, thermal dependence and sensitivity (Q_{10}) of oxygen consumption in a cricket

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Summary

Studies focusing on physiological variation among individuals, and its possible evolutionary consequences, are scarce. A trait can only be a target of natural selection if it is consistent over time, that is, a trait must be repeatable. In ectotherms it has been suggested that standard metabolic rate (MR) is related to Darwinian fitness, since it reflects energy usage and expenditure. The metabolic rate of the cricket *Hophlosphyrum griseus* was determined at three ambient temperatures. Repeatability of MR was estimated by product–moment correlation on residuals of body mass, as well as the thermal sensitivity of MR on an individual basis (individual Q_{10}). The MR of *H. griseus* was significantly repeatable (r=0.53) and highly dependent on ambient temperature, and its sensitivity (Q_{10}) was dependent on the temperature range. Our estimation of MR repeatability was high in comparison to published studies in vertebrates. Ours is the second report of repeatability (i.e. consistency over time of an individual's performance ranking within a population) of any aspect of energy metabolism in an insect, and also the first study to report significant repeatability of MR.

Individual Q_{10} values revealed important interindividual variation, which reflects the existence of intrapopulational variability in the thermal sensitivity of MR. In addition, individual Q_{10} values were negatively correlated between temperature ranges. This means that crickets having low Q_{10} at low temperatures, presented high Q_{10} at high temperatures, and *vice versa*. Our results suggest that MR could be of selective value in insects, showing consistency over time and intrapopulational variability in its thermal dependence. Nevertheless, its heritability remains to be determined.

Key words: standard metabolic rate, cricket, *Hophlosphyrum griseus*, Q_{10}, oxygen consumption, repeatability, ectotherm, evolution.

Introduction

Temperature has profound effects on ectothermic animals (Cossins and Bowler, 1987). It controls nearly all physiological and biochemical processes, thus determining a great deal of animal life histories (Huey and Berrigan, 2001). On the long-term (i.e. evolutionary) scale, temperature has important consequences for ectotherms, determining patterns of daily activity (Alexander, 1999), movement (Gibert et al., 2001), adult size (Sibly and Atkinson, 1994), reproduction (Madsen and Shine, 1999), and feeding and digestion (Blouin-Demers and Weatherhead, 2001). An organism's pattern of energy usage is reflected in measurements of energy expenditure, the most common being the rate of metabolism. In animals, metabolic rate (MR) can be determined by either the rate of CO_2 production, or the rate of O_2 consumption.

The most immediate determinants of MR in insects are body mass and ambient temperature (T_a). Secondarily, MR changes with mode of locomotion (Rogowitz and Chappell, 2000), gender (Rogowitz and Chappell, 2000), altitude (Rourke, 2000), parasitic infestation (Kolluru et al., 2002), water scarcity (Davis et al., 1999), climate (Nielsen et al., 1999), and reproduction (Prestwich and Walker, 1981). Several adaptive hypotheses have been proposed to explain general patterns and magnitudes of MR in insects. Two of the most popular, but at the same time highly debated, are discontinuous gas exchange and metabolic cold adaptation. The former makes use of a known respiratory pattern in insects (i.e. a burst of CO_2 release between periods of low CO_2 production) to explain water economy or adaptations to hypoxia (Lighton, 1996). The second hypothesis states that insects inhabiting geographic areas with low mean T_a will present elevated MR (after controlling for body mass, temperature and phylogeny), as a thermoregulatory adaptation to confront heat loss (Reinhold, 1999; Addo-Bediako et al., 2002). These studies make it clear that the ecological and physiological patterns and processes that account for observed

variation in MR in insects are not yet fully understood, especially in regard to its adaptive significance.

Comparative physiological ecology is a discipline that largely focuses on inferring adaptations (McNab, 2002). Physiological ecologists analyse morphological, physiological and behavioural traits patterns, in order to explain how such traits originated, and whether or not their presence increases survival and reproduction. However, probably for historical reasons, only the first two tasks have been successful (Bennett, 1987). New physiological adaptations are currently occurring in populations, but interest in studying evolutionary processes at this level has only just begun (Kingsolver et al., 2000; Hoeckstra et al., 2001). Such processes need to be addressed in the context of natural selection and intraspecific variability. A trait can be the target of natural selection only if it is consistent over time, that is, the trait must be repeatable (Hayes and Jenkins, 1997). In fact, quantitative geneticists have demonstrated that repeatability is related to heritability, in the sense that the former sets the upper limit of the latter (Falconer and Mackay, 1997; Dohm, 2002). Hence, the demonstration of significant repeatability in a trait necessarily precedes any attempt to demonstrate its selective significance. Metabolic rate has been shown to be repeatable in vertebrates, both in endotherms (Hayes et al., 1998; Bech et al., 1999) and ectotherms (Garland and Else, 1987; Garland and Bennett, 1990), and recently, Rogowitz and Chappell (2000) have reported significant repeatability in activity metabolism of a beetle. However, although MR appear to be closely related to fitness in crickets (Crnokrak and Roff, 2002), as far as we know there is no published study that reports repeatability of MR in an insect, which is the first aim of this paper.

Our second aim concerns the thermal sensitivity of MR, termed Q_{10} (i.e. the magnitude of change in MR for a 10°C change in T_a) (Schmidt-Nielsen, 1995). There is a great deal of information on the Q_{10} of MR in insects, values ranging from 1.5 to 3, with a mode of 2.5 (Prestwich and Walker, 1981; Ashby, 1997; Davis et al., 1999; Rourke, 2000; Rogowitz and Chappell, 2000). However, Q_{10}, like MR, can be considered to be an individual attribute. Since it reflects the capacity of change in MR relative to changes in temperature, it could also be considered a measure of organismal performance. Hence, it is interesting to explore how much variability exists in Q_{10} within a population, and how this variability is related to the same variables that determine MR: temperature and body mass. As far as we know, this approach has been never attempted. We chose for our study model a small cricket species from central Chile, *Hophlosphyrum griseus*, since these insects are naturally exposed to a wide range of environmental temperatures, are available in large numbers and are easy to handle and measure.

Materials and methods

Animals and study site

Crickets *Hophlosphyrum griseus* Phillipi 1863 were collected during austral spring 2002. The species is widely distributed in central Chile, from La Serena (29°54′S, 71°16′W) to Valdivia (39°27′S, 73°49′W) (Lamborot, 1985). Studied individuals were obtained at San Carlos de Apoquindo (33°23′S, 70°31′W), near the Andean Range, at 800 m altitude. The climate in the study area is Mediterranean, with an annual mean of 376.4 mm rainfall, concentrated (65%) during the austral winter months, from June to August (Jaksic, 2001). Mean annual temperatures are 6.0 and 28.7°C. San Carlos de Apoquindo is covered by sclerophyllous vegetation which, physiognomically, may be described as an evergreen scrub (for a complete description of the study site see Jaksic, 2001). The crickets were collected by hand net, from underneath stones, pieces of wood and soil litter. Specimens were transferred to plastic containers and moved to the laboratory on the same day as capture.

Maintenance and acclimation

All specimens were kept in individual containers (i.e. perforated plastic Petri dishes) to ensure uniformity of acclimation conditions prior to measurements. Water was periodically added to a cotton swab placed at the end of the cage to provide a source of moisture. Food was supplied weekly, in the form of rabbit food pellets. The photoperiod was kept at 12 h:12 h dark:light. After an initial 1 week period of acclimation to laboratory conditions, and prior to each metabolic measurement, crickets were maintained for 2 weeks at either 7±1°C, 17±1°C or 27±1°C in environmental chambers. These temperatures were offered in a random order to avoid sequential training. We chose these acclimation temperatures since they are close to the average extremes of the natural temperature range in the habitat where the sample organisms were captured (see Di Castri and Hajek, 1976; Jaksic, 2001). Following each thermal acclimation, metabolic rate was measured at the same temperature as acclimation.

We collected additional individuals to increase sample size for the repeatability analysis. All of these specimens were maintained at 17°C since at this temperature mortality was minimal. Both metabolic measurements were performed 1 month apart (see below).

Metabolic rate measurements

All metabolic trials were performed during the day, which corresponds to the rest phase in this species. Rates of oxygen consumption ($\dot{V}_{O_2}$) were used as a measure of MR. $\dot{V}_{O_2}$ was determined using ‘closed system’ metabolic chambers (Vleck, 1987), consisting of disposable 10 ml hermetic syringes fitted with three-way valves (see also Chappell, 1983; Ashby, 1997; Chown, 1997). All measurements were made during the day, when crickets are inactive, and thus they serve as measures of ‘standard rates of metabolism’ (MR) (Schmidt-Nielsen, 1995; McNab, 2002). Animals were weighed (body mass = M_b) to the nearest mg in an analytical balance and then placed, individually, inside the syringes. Small granules of CO_2-absorbent Baralyme™ and Drierite™ were added to each syringe in a compartment isolated from the cricket. The syringes were sealed from the atmosphere and placed in a

temperature controlled, dark incubator for the duration of the measurement period (ca. 3–6 h, depending on the T_a at which measurements were made). In no case did the O_2 within the syringe decrease by more than 10% (usually less than 5%) between the start and the end of each measurement period. Three blank syringes served as controls for each series of measurements. We injected the air of the syringe into a Tygon™ tube (1.5 m long) connected to the O_2 analyzer after passing through CO_2-absorbent granules of Baralyme™ and Drierite™. At the end of the measurement interval, O_2 concentrations were determined using a Fox Field Oxygen Analysis System (Sable System International, Henderson, NV, USA) supplied with barometric pressure compensation. Output from the O_2 analyzer was recorded by a computer using the DATACAN program. Rates of oxygen consumption (in $\mu l\, O_2\, h^{-1}$) were calculated for each syringe, using the following equation modified from Vleck (1987):

$$\dot{V}_{O_2} = V(F_{1,O_2} - F_{E,O_2}) / (1 - F_{E,O_2})t\,, \qquad (1)$$

where V is the initial volume of dry, CO_2-free air in the syringe at STP; F_{1O_2} and F_{EO_2} are the O_2 fractions within the syringe at the start and end of incubation, respectively; and t is the duration of incubation in h.

This system was not intended to measure the instantaneous rate of metabolism, nor to resolve discontinuous gas exchange (e.g. Chappell and Rogowitz, 2000), since each measurement is an average of oxygen consumption over several hours. However, technical errors associated with this measurement method are small (see Anderson et al., 1989), and its simplicity allows simultaneous measurements of a large number of individuals, which are needed for statistical analyses of repeatability.

Statistics

Our design included three predictor variables: two categorical variables (sex and T_a), and one continuous variable (M_b). Dependent variables were MR and Q_{10}. We performed an analysis of covariance (ANCOVA), with M_b as the a covariate, to test the effects of each categorical variable on $\dot{V}_{O_2}$. We checked analysis of variance (ANOVA) assumptions using Kolmogorov–Smirnov and Cochran tests for normality, and Hartley and Bartlett tests for homogeneity of variances. The parallelism assumption (i.e. interaction with the covariate) was checked using an ANCOVA homogeneity-of-slopes model (Statistica 6.0), and was found to be significant in all cases. Consequently, we performed a separate slopes model ANCOVA (Statistica 6.0), which accounts for the absence of parallelism. Common linear regressions of M_b and MR were performed between each temperature. Although, formally repeatability is the intraclass correlation coefficient between two measurements (Lessels and Boag, 1987), several authors have adopted the Pearson product–moment correlation (Huey and Dunham, 1987; Chappell et al., 1995) since it is statistically easier to manage, and theoretically it represents the same quantity (Lynch and Walsh, 1998). We then used the Pearson product–moment correlation (residuals from M_b) performed on the same individuals, 1 month apart. Values of Q_{10} were computed for each individual as $MR(T_2)/MR(T_1)$, where T_2 and T_1 were either 17°C and 7°C, or 27°C and 17°C, respectively. Since MR strongly covaries with M_b, a prerequisite to treating individual Q_{10} as independent data points (and using them in statistical analyses) is that the ratio of $M_b(T_2)$:$M_b(T_1)$ must be approximately equal to unity (i.e. M_b does not change between T_a values). We tested this assumption prior to any statistical treatment of individual Q_{10} values [$M_b(17°C)/M_b(7°C)$=0.97±0.10 and $M_b(27°C)/M_b(17°C)$= 1.08±0.16 (mean ± S.E.M.)].

We obtained two samples of individual Q_{10} values at different temperatures (low: 7–17°C and high: 17–27°C, T_a). These values were compared by ANCOVA, using mean M_b, $[M_b(T_2)+M_b(T_1)]/2$ as the covariate. To explore the effect of T_a on individual Q_{10} values, we correlated residuals of Q_{10} with M_b, between T_as (i.e. Q_{10} residuals from low T_a *versus* Q_{10} residuals from high T_a), in those crickets where $\dot{V}_{O_2}$ could be measured at the three T_as (N=38 individuals).

Results

Metabolic rate was significantly correlated with body mass for all T_a (Fig. 1, Table 1). There were significant differences in the slopes of the $\dot{V}_{O_2}/M_b$ relationship, at different T_a values, which is demonstrated by the significant interaction between temperature and M_b in the parallelism test ($F_{2,286}$=23.5, P<0.0001, ANCOVA, homogeneity-of-slopes model). The slope of $\dot{V}_{O_2}$ and M_b increased with T_a (Fig. 1). Additionally, T_a had a significant effect on $\dot{V}_{O_2}$ after controlling for M_b ($F_{2,286}$=62.1, P<0.0001, ANCOVA, separate slopes model). Although sex was not significant as a main factor, it had an effect on $\dot{V}_{O_2}$ through interaction with T_a and the covariable ($F_{1,290}$=16.5, P=0.0006, one-way ANCOVA, Table 2, Fig. 2). This effect is probably due to the sexual dimorphism presented by this species, and the fact that females became significantly larger than males at high T_a (27°C; see Fig. 2).

Residuals of $\dot{V}_{O_2}$ were significantly repeatable between

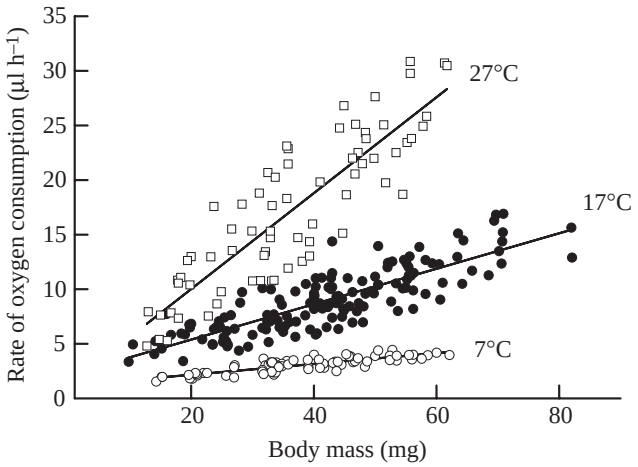

Fig. 1. Oxygen consumption and body mass in crickets acclimated to and measured at 7°C, 17°C and 27°C. For means and regression statistics, see Table 1.

Table 1. *Means (± S.E.M.) and regression statistics between* $\dot{V}_{O_2}$ *and* M_b

T_a (°C)	$\dot{V}_{O_2}$ (µl O_2 h^{-1})	M_b (mg)	Slope	Intercept	r^2	N
7	3.07±0.69	38.4±11.7	0.05±0.004***	1.18±0.15***	0.70***	75
17	8.99±2.94	42.2±15.0	0.162±0.009***	2.13±0.40***	0.70***	147
27	17.14±6.83	36.2±10.0	0.440±0.03***	1.22 NS	0.76***	70

T_a = ambient temperature; $\dot{V}_{O_2}$ = rate of oxygen consumption; M_b = body mass; N = number of individuals.
***P<0.001.

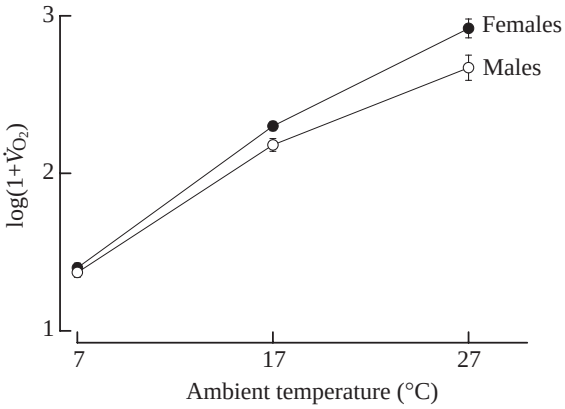

Fig. 2. Interaction plot (see Table 2) from an ANCOVA, with body mass M_b as the covariate, showing the relationship between sex and ambient temperature T_a on $\dot{V}_{O_2}$. Data were transformed to log+1 to meet ANOVA assumptions. Values are adjusted means ± S.E.M. (N=75, 147 and 70 for 7°C, 17°C and 27°C, respectively).

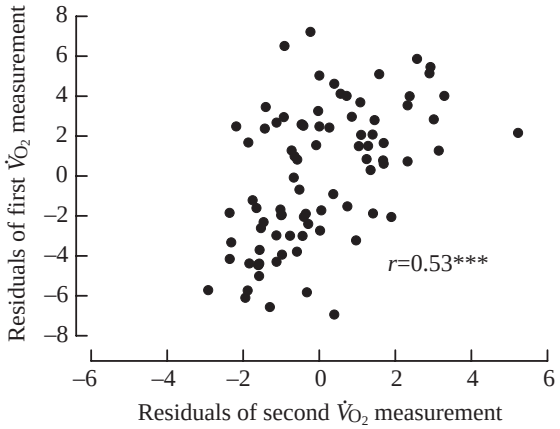

Fig. 3. Repeatability of the rate of oxygen consumption of 85 crickets measured twice (at T_a=17°C) before and after a 1 month interval. Data are residuals of body mass. ***P<0.001.

measurements made 1 month apart (r=0.53; P<0.0001, Fig. 3), which reflects trait consistency over time. Individual Q_{10} values were significantly correlated with M_b only in the low T_a range, but this correlation was weak (r^2=0.08, P<0.0001; high T_a: r^2=0.03, NS, Fig. 4). Individual Q_{10} presented substantial variability, with coefficients of variation of 22% and 30% in the low and high temperature range, respectively. However, Q_{10} values from the different temperature ranges were not significantly different ($Q_{10,7–17°C}$=2.43±0.53; $Q_{10,17–27°C}$= 2.63±0.80, t_{37}=–1.07, NS), although residuals of Q_{10} were significantly and negatively correlated between T_a values (r=–0.59, P=0.0001; Fig. 5).

Discussion

The standard metabolic rate of *Hophlosphyrum griseus* was repeatable and highly dependent on T_a, and the thermal sensitivity of MR (i.e. Q_{10}) was dependent on the temperature range. According to Rogowitz and Chappell (2000), this would be the second report of repeatability (i.e. consistency over time of an individual's performance ranking within a population) of any aspect of energy metabolism in an insect, and the first report of significant repeatability of MR. Another interesting outcome of this study was that individual Q_{10} values revealed important intrapopulational variation, which reflects the existence of interindividual variability in the thermal sensitivity of $\dot{V}_{O_2}$. More interestingly, individual Q_{10} values were negatively correlated between temperature ranges. This mean that crickets with low Q_{10} at low temperatures, present a high Q_{10} at high temperatures, and *vice versa*.

Metabolic rate

Our values of metabolic rate are very similar to those reported for other species of similarly sized crickets (Prestwich and Walker, 1981), or values that have been allometrically standardized by body size (Reinhold, 1999; see also Ashby, 1997). Assuming a respiratory quotient of 0.84 (Addo-Bediako et al., 2002), and taking into account each test temperature, our

Table 2. *ANCOVA, separate slopes model testing the effects of sex and* T_a *on log(1+*$\dot{V}_{O_2}$*), with* M_b *as the covariate*

Factor	SS	d.f.	MS	F	P value
Intercept	48.47	1	48.47	1758.9	<0.0001***
Sex × M_b × T_a	18.20	6	3.03	110.1	<0.0001***
Sex	0.03	1	0.03	1.02	0.314 (NS)
T_a	3.07	2	1.54	55.8	0.0001***
Sex × T_a	0.01	2	0.005	0.20	0.82
Error	7.72	280	0.03		

***P<0.001; *P<0.05; NS, not significant.
T_a = ambient temperature (°C); M_b = body mass (mg); SS = sum of squares; MS = mean squares.

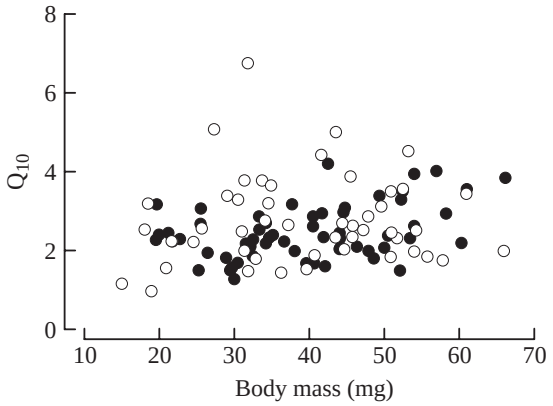

Fig. 4. Q_{10} computed for each individual, measured at two temperatures (open circles, 7–17°C; filled circles, 17–27°C), *versus* body mass. Only the regression between Q_{10} and body mass in the 7–17°C range was significant (see text for statistics).

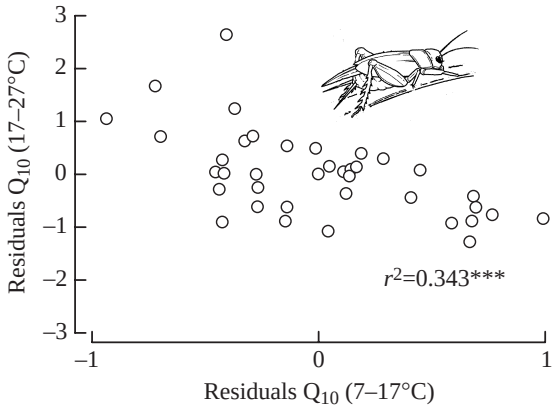

Fig. 5. Correlation (residuals from body mass) of individual Q_{10} values measured at two temperature ranges (7–17°C and 17–27°C). ***P<0.001.

MR values are above those reported by other authors using open flow-$\dot{V}_{CO_2}$ respirometry for crickets (4–6 μl O_2 h^{-1}, T_a=30°C; Kolluru et al., 2002), harvestmen (2.6 μl O_2 h^{-1},T_a=25°C; Lighton, 2002), and some beetle species (5.9 μl O_2 h^{-1}, T_a=28°C; Davis et al., 1999), and are similar to some grasshopper species (7.14–11.9 μl O_2 h^{-1}, T_a=25°C; Rourke, 2000). Metabolic rate increased with T_a, as expected in an ectotherm species. However, the rate of increase was different at different temperatures. Such a pattern has been described in crickets (Prestwich and Walker, 1981), grasshoppers (Rourke, 2000), beetles (Rogowitz and Chappell, 2000), ants (Nielsen et al., 1999), and several other species of terrestrial and aquatic invertebrates (Rao and Bullock, 1954). In addition to M_b and T_a, some authors have reported significant effects of sex on MR (Rogowitz and Chappell, 2000). This is not the case here since the main effects of sex on $\dot{V}_{O_2}$ were not significant when controlling for M_b.

Repeatability of metabolic rate

Our results suggest that standard MR in *Hophlosphyrum griseus* is significantly repeatable after controlling for M_b. A potential drawback of our estimation is that we did not control for activity, which influences MR, although individuals were measured during the rest phase. If the same individuals in the sample were more active during both periods of MR measurement, the repeatability result could be high since individuals conserve their activity ranking across measurements. However, this does not apply to the relationship between body mass and MR, where these were high and significant. This means that larger individuals consistently presented higher MR values than smaller individuals, which is clearly a biological effect and not an artefact. Activity would be 'noise' in the sense of residual error, which reduces the power of the analysis. In our case, this would yield a small and probably nonsignificant correlation, which was not the case. Another factor that could affect the repeatability analysis is that individuals were growing during the experimental period. This is very hard to avoid since *H. griseus* is a yearly species (i.e. individuals reproduce seasonally and live no more than a year; Lamborot, 1985). On the other hand, a shorter measurement period would have been less informative since repeatability is the consistency of a trait over relatively long periods of time. Thus, to minimize the effect of growth, we controlled by body mass by using residuals and excluded individuals that molted during this period (approximately three crickets).

Previous attempts to determine the repeatability of $\dot{V}_{O_2}$ or $\dot{V}_{CO_2}$ in insects suffer from serious biases. For example, Ashby (1997) reported a $\dot{V}_{O_2}$ product–moment correlation of 0.85 for a grasshopper, but N=6 and, furthermore, no significance value was provided, nor body size controlled for. This result is, therefore trivial, since apparent repeatability of MR without correction for M_b, or computed over mass-specific MR, would be very high, given that M_b is known to be a highly repeatable trait (Chappell et al., 1995). Actually, if we reanalyze our data using $\dot{V}_{O_2}$ values obtained per individual (i.e. ml O_2 h^{-1}), our repeatability would be 0.72 (P<0.01), compared with repeatability for mass-specific $\dot{V}_{O_2}$ (i.e. ml O_2 g^{-1} h^{-1}), where r=0.55 (P<0.01). These inflated values are only due to effects of M_b . On the other hand, Rourke (2000) concluded that repeatability of water loss rate is high because three measurements made 2 weeks apart in 15 individuals did not show significant differences. The problem with this reasoning is that statistical tests are designed to avoid type I error, but not type II. In other words, the absence of significant differences among means is not evidence for their similarity (Parkhurst, 2001). Thus, Rourke (2000) can only conclude that there is not enough evidence to decide whether the water loss rate is different between samples. The only study we found where accurate estimations of repeatability in an insect were provided was for the metabolic rate of forced terrestrial exercise in a beetle (Rogowitz and Chappell, 2000). These authors reported significant values of repeatability, some as high as 0.75 between trials, but with all measurements made over a time period of 5 days. This value was higher than our findings and, together, both studies report considerably higher

repeatability values than any previously reported values for physiological traits in vertebrates (Chappell et al., 1995; Berteaux et al., 1996; Bech et al., 1999). The fact that standard MR in insects is repeatable is interesting, since it suggests that this trait could respond to natural selection (Falconer and Mackay, 1997). To address this key question, which is a second step directed towards addressing adaptive hypotheses of physiological traits in insects, researchers should attempt to answer the more specific question: is standard metabolic rate heritable? Studies in vertebrates yielded mixed results (Calvo et al., 2002; Nespolo et al., 2003) but the fact that metabolic rate appear as important determinant of fitness in some species of cricket (Crnokrak and Roff, 2002) along with the results of this paper suggest that insect metabolism could be of selective importance.

Thermal sensitivity of metabolic rate

We assessed the metabolic response to T_a using Q_{10} values computed for each individual at two temperature ranges. There are plenty of studies reporting the Q_{10} of metabolic rate for insects, and for invertebrates in general. It appears that in most insects MR presents a Q_{10} ranging from 2.0 to 2.5, with extreme values of 1.0 and 4.6 (Forlow and MacMahon, 1988; Hadley and Massion, 1985; Cooper, 1993; Chown et al., 1997), which are in agreement with our results.

From thermodynamic considerations for general biochemical reactions, Q_{10} is predicted to be higher at lower temperatures (Schmidt-Nielsen, 1995). However, in insects this pattern is rather variable. For example, the results of Harrison and Fewell (1995) were in agreement with this theoretical prediction for a grasshopper, since Q_{10} values of digestive processes were always negatively correlated with temperature. These authors found that Q_{10} was quite variable, depending on the specific process being tested, with extreme values such as 5.3 for excretion rate. However, for MR, these authors found that Q_{10} did not change with temperature, and, in fact, reported remarkably high magnitudes (Q_{10}=3.6–3.7). Hadley and Massion (1985), on the other hand, found that altitude had inverse effects on Q_{10} and T_a. Low-altitude populations presented low Q_{10} at low T_a and high-altitude populations presented high Q_{10} over the same temperature range. However, the pattern was completely reversed at a higher temperature range: low-altitude populations presented high Q_{10}, and so on. Our results suggest a similar, but perhaps more surprising, outcome: first, there is intrapopulation variation in individual Q_{10} values of around 30%; second, this variation shows a significant dependence on T_a; third, the dependence is negative, which suggests a trade-off, where individuals with low Q_{10} at high T_a present high Q_{10} at low T_a, and the contrary for individuals with high Q_{10} at high T_a.

What could be the explanation for such an unusual outcome? We recomputed individual Q_{10} values several times and the results remained unchanged, so we believe that this finding is not an artefact. The following mechanism, modified from Heinrich (1977), and applied by Casey and Knapp (1987) to explain their results with caterpillars, provides a good explanation. Metabolic rate, as well as its thermal sensitivity, depends on biochemical reactions inside cells and tissues. These reactions are organized in metabolic pathways, whose efficiency depends primarily on limiting pathways which, in turn, depend on enzyme complexes. Enzymes in different individuals have different thermal optima. The point is that perhaps a polymorphism in such enzyme complexes could exist in a population. Then, if a key metabolic pathway is unique for an individual, it could be that such an animal with a low optimum would perform better (i.e. present higher Q_{10}) at low temperatures *but not* at high temperatures. Other individuals, stocked with an enzyme complex with a higher thermal optimum, would present higher Q_{10} at higher T_a, *but not* at low T_a. Such a trade-off polymorphism would produce a response to selection, if sensitivity to temperature influences fitness.

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