

The effect of acclimation to constant temperatures, pollution of food by heavy metals and short-term fasting on the metabolic activity of *Glomeris balcanica* (Diplopoda: Glomeridae)

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Changing temperature regime has an important effect on the respiratory metabolism of *Glomeris balcanica*. A left skewing response of animals to increasing temperature is revealed and modeled. Acclimation from fluctuating to constant temperatures depresses metabolism through a three-step process. Short-term acclimation results in strongly depressed metabolism, mid-term acclimation induces metabolic recovery, whereas long-term acclimation results in an irreversible decline of metabolic activity. Heavy metal burdens of food do not affect the left skewing thermal response of animals, although they depress metabolic levels at the high temperature range, shorten tolerance ranges by shifting down the upper tolerance threshold, enlarge optimal temperature range (metabolic constancy) and stimulate the faster activation of the metabolic compensatory mechanism. Finally, no effect of short-term fasting on respiration was detected.

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The strategy of an organism is the outcome of a multivariate process involving growth, demographic and physiological features (Stamou 1998). Concerning physiological parameters, the rate of oxygen consumption is generally considered a reliable index of arthropod activity (e.g. Prosser 1973, Stamou and Iatrou 1993 among others). Although respirometry data reflect multivariate processes, and their interpretation should be very cautious (Šustr 1996a), studies on respiratory responses of arthropods to environmental factors may elucidate aspects of the ecological significance of these animals in the field.

This study concerns the respiratory response of the diplopod *Glomeris balcanica* to changing temperature regimes, heavy metal pollution of food and fasting, following and integrating previous papers on the metabolic activity of this animal (Stamou and Iatrou 1990, 1993). *G. balcanica* is among the most important agents of litter breakdown in Mediterranean type ecosystems of northern Greece (Iatrou 1989, Iatrou and Stamou 1989), which are characterized by spatial and temporal heterogeneity of habitats and consequently by pronounced variability in the availability of limited resources (Stamou 1998). The main

component of this heterogeneity is temperature, exhibiting strong diurnal, seasonal and interannual fluctuations (Argyropoulou et al. 1993, Stamou and Iatrou 1993). Hence the study of the strategic response of the ectotherm *G. balcanica* to varying temperature regimes is of crucial importance for a thorough understanding of its capacity for maintenance and even dominance in the unfavourable mediterranean soils. As regards soil pollution, although it is stated that it affects growth rate (Abdel-Lateif et al. 1998), demographic traits (e.g. Joosse and Verhoef 1983, Kooijman and Metz 1984, Van Straalen 1996, Butovsky 1996) or life history tactics (Steiner 1990, Siepel 1994, Posthuma and Janssen 1995) of soil arthropods, studies on the metabolic response of terrestrial arthropods to soil pollution are scanty (Janssen and Bergema 1991, Weigmann 1995, Laskowski et al. 1996). Finally, fasting was taken into account in our study, because it is considered important for the synchronization of the life cycle development of arthropods inhabiting Mediterranean areas (Stamou 1998).

Materials and methods

A Varian 3350 gas chromatograph was used for respirometry. The apparatus was equipped with a 1040/41 Universal Injector, a Thermal Conductivity Detector and fitted with a pre-packed column Haysep N 80/100 (6' ¥ 1/8'' SS). The temperature of the injector and the column was adjusted to 80 and 130°C respectively, whereas the temperature of the filaments of the detector was 270°C. The carrier gas was He with a flow rate about 20 psi. To estimate peak areas, a Varian 4290 integrator was used. Prior to each measurement, 0.6 ml of a standard gas mixture (0.1% CO₂, 424 ppm) was injected twice to determine the time at which the CO₂ peak occurs.

The experiments were conducted according to Šimek and Šustr (1995) and Šustr (1996b). *G. balcanica* specimens were incubated singly in 5 ml plastic syringes, on the bottom of which a wet small piece of Whatman paper was placed for atmosphere saturation. The plunger was adjusted to 2.1 ml. To avoid gas outflow, the needle of the syringe was inserted into a rubber stopper. The experimental syringes along with identical control ones were incubated for 5 h at 4, 13, 20 and 25°C. Then, 0.6 ml of the air in the syringe was injected into the gas chromatograph. In addition, two injections were made to estimate the CO₂ concentration of ambient air, and the measurements were subtracted from the amount of CO₂ measured for test and control syringes. We must note that oxygen consumption values estimated for *G. balcanica*, using gas chromatography, are comparable to those recorded using gradient diver techniques (Stamou and Iatrou 1993).

Respiration measurements (in each occasion 5-10 replicate recordings) were made on adult specimens, from 138 to 471 mg live weight, sampled by hand from a non-con-

taminated *Pinus brutia* formation nearby the city of Thessaloniki. In the laboratory, animals were reared in darkness, in plastic vessels 10 cm in diameter, regularly watered to maintain ambient air humidity near 100%. Food was a pulverized 9:1 mixture of non-contaminated litter and humus from the field (Iatrou and Stamou 1990). Every 3 days food was renewed and culture vessels were cleaned from animal excrements for preventing mycelia development.

To assess the effect of acclimation to constant temperatures, measurements were made on animals reared at constant temperatures for 5, 43 and 63 days, as well as on animals stored outdoors under naturally fluctuating temperatures. To assess the pollution effect, measurements were also made on animals fed on food to which a fivefold higher amount of polluted litter from different green urban areas was added (data on heavy metal concentration of litters from Panagiotopoulos unpublished). In each occasion a second set of measurements was made three days later on animals isolated from food resource.

Results

Respiration and temperature

In soil arthropods, the respiration-temperature relationship is generally discussed either upon Q₁₀ coefficients of Van't Hoff or upon parameters of empirical models fitted to data, such as the exponential, the logarithmic, the Krogh-Jorgensen or the Arrhenius equation. However, these methods have been criticized for mathematical limitations, inadequacy to describe temperature depended phenomena, and for not providing ecologically meaningful parameters (Howard 1971, Young 1979, Argyropoulou and Stamou 1993, Stamou and Iatrou 1993, Abdel-Lateif et al. 1998).

In this study, the analytical model proposed by Logan et al. (1976) was numerically fitted to data:

$$MR = \alpha [(1 + ke^{-pT})^{-1} - e^{(T-T_1)}]$$

where MR: metabolic rate in µl O₂ g⁻¹ h⁻¹, T: temperature in °C, *p*: rate of increase of metabolism up to optimal temperature, T₁: upper tolerance threshold, *a*: maximal metabolic rate recorded at optimal temperature and *k*: constant. The model accounts for asymmetric responses to temperature changes, as is the case with *G. balcanica*, and it fitted data significantly (P<0.05). Further critical temperature points were estimated arithmetically by elaborating the first and second derivative of the equation (T_{opt}: optimal temperature, i.e. the point where the 1st derivative equals zero and MR is maximum, T₁: the point where the 2nd derivative is maximum, T₂: the inflection point of the curve, i.e. the point where the 1st derivative is maximum). Optimum temperature range (OTR) is arbitrarily defined

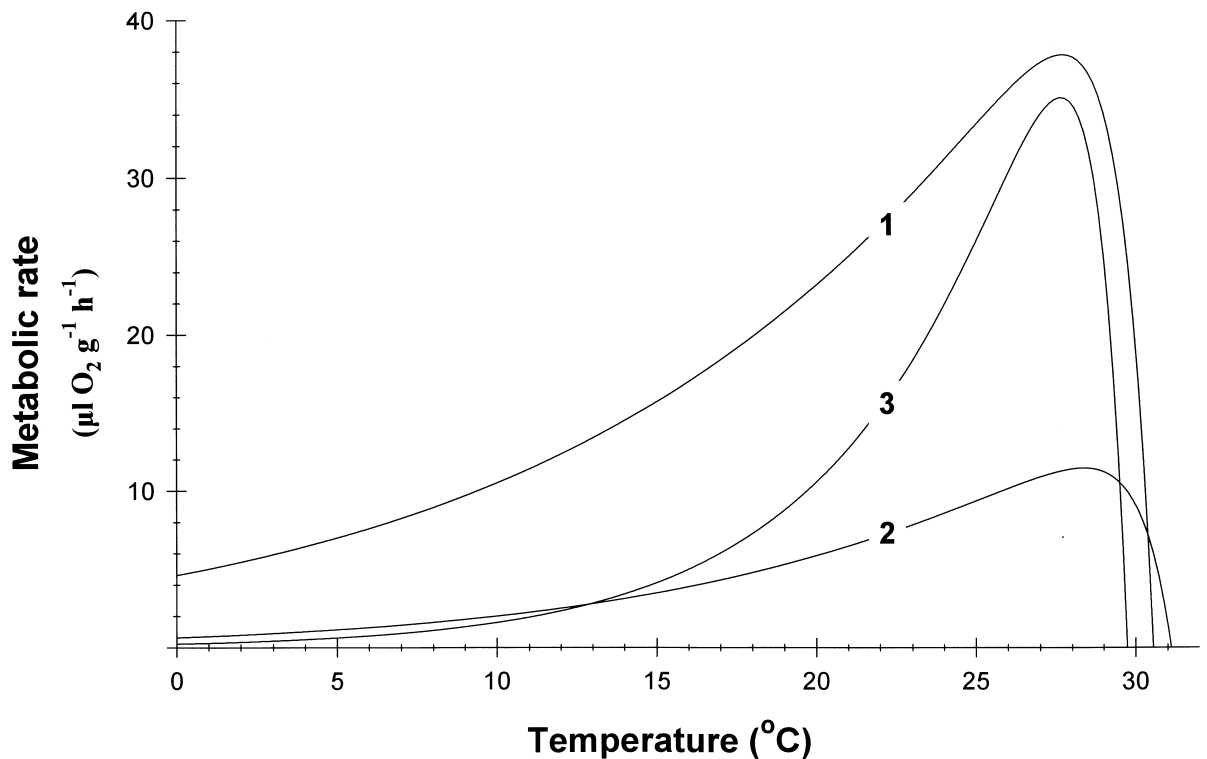


Fig. 1. Relationship of metabolic rate to temperature in adult *G. balcanica*. 1: specimens acclimated to fluctuating temperatures, 2: specimens short-term acclimated to standard temperatures (up to 5 days), 3: specimens mid-term acclimated to standard temperatures (43 days).

as the range where MR exhibits minimal fluctuations (less than 10% of maximal MR), while T_3 is the lower limit of this range.

The fitting of the model to data sets of different acclimation regimes is given in Fig. 1, while the derived parameters are given in Table 1, along with mean values of oxygen uptake and Q_{10} values. The metabolic activity of *G.*

balcanica increases slowly until the critical temperature T_1 , which lies between 12–20°C. Then, respiration increases exponentially up to the inflection point of the curve (T_2). Above T_2 the rate of increase of oxygen consumption slows down until the optimal temperature, which lies between 25 and 29°C. Beyond T_{opt} a precipitous decline in respiration occurs and the upper tolerance point is about 30°C.

Table 1. Temperature critical points in °C (for explanations see text) and corresponding metabolic rates in $\mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$ of adult *Glomeris balcanica* at different acclimation regimes. Metabolic rate at 0°C is also given, along with optimal temperature range (OTR), Q_{10} values for several temperature ranges and overall Q_{10} (0°C to T_{opt}).

Acclimation regime		T_1	T_2	T_3	T_{opt}	T_T	OTR	Q_{10} overall
Short-term (5 days)	TEMP	0	15	21	25	28	32	2.74
	MR	0.7	3.6	6.6	9.7	11.8	25–30	
	Q_{10}	2.98	2.74	2.61	1.92			
Mid-term (43 days)	TEMP	0	21	23	25	27.5	30	6.54
	MR	0.2	11.3	18	26	35	25–29	
	Q_{10}	6.83	10.2	6.29	3.28			
Fluctuating temperature	TEMP	0	17	21	24	28	30.5	2.11
	MR	4.6	18.2	24.8	31	37.2	24–29	
	Q_{10}	2.24	2.17	2.1	1.58			

Acclimation at constant temperatures, food pollution and fasting

Acclimation to constant temperatures does not affect the respiration-temperature relationship (Fig. 1). However, changing temperature regime has a highly significant effect on the level of respiratory metabolism. A strong decline in respiration of animals transferred from fluctuating to constant temperatures was recorded after 5 days. Further acclimation of animals to constant temperatures (up to 43 days) results in a recovery of respiratory metabolism. This recovery is more pronounced in higher temperatures and results in higher Q_{10} values.

In Table 2, average oxygen consumption of animals fed on material from 9 different stations as well as the Pb, Cu and Zn concentrations of this material are given. No statistically significant correlation between metabolic rate and metal burdens of food was detected. However, further analysis of variance and LSD test showed that oxygen consumption of animals fed on litter gathered in stations 1-5 is significantly lower than that of animals fed on litter from stations 7-9. No significant difference was recorded in respiratory activity of the latter specimens and those fed on non-contaminated food. Hence, for further analyses, only stations 1-5 were considered polluted and were treated together.

In Fig. 2, the relationship of metabolism to live weight is plotted on a double Log scale, for animals fed on polluted and not polluted food. A covariance analysis revealed statistically significant differences in the elevation of the regression lines, but not in slope. Thus, food contamina-

tion depresses significantly the level of metabolism, without changing the metabolic dependence on live mass. The same holds for the metabolism-temperature relationship as well (Fig. 3). Nevertheless, contaminated food depresses metabolism only in the high temperature range (above 16°C) and lowers all critical temperature points. Thus, metabolic rate rises more rapidly up to thermal optimum. Moreover, the optimum temperature range is wider.

The metabolic response to increasing temperature of animals fed on contaminated food, for two acclimation regimes is presented in Fig. 4. The comparison of these curves with the corresponding ones of Fig. 1 (curves 2 and 3) shows that the response to acclimation of specimens fed on contaminated and non-contaminated food is analogous.

In Fig. 5, the food pollution effect is shown for animals acclimated for 63 days at constant temperatures (long term acclimation) and transferred outdoors, i.e. to naturally fluctuating temperatures, for 2 days. Depression of respiratory metabolism due to pollution is again obvious, along with the wider optimum temperature range, rapid increase of metabolism up to thermal optimum and the lowering of critical temperature points. The comparison of curves 1 and 2 of Fig. 5 to the curves of Fig. 1 and Fig. 4, respectively, shows that although mid-term acclimated animals exhibit a metabolic recovery, they do not save this competence after long-term acclimation, even after their transfer to fluctuating temperatures, which are known to trigger metabolic activity (Stamou 1998 among others). On the contrary, respiration remains at levels which are comparable to those displayed by short-term acclimated specimens,

Table 2. Oxygen uptake ($\mu\text{l O}_2 \text{ g}^{-1}\text{h}^{-1}$) of *G. balcanica* specimens fed on litter contaminated by Pb, Cu and Zn. Data on metal concentration (mg.Kg^{-1} dry matter) refer to litter burdens before mixing with ordinary food from Panagiotopoulos (unpubl.).

Station	Replicates	Oxygen uptake	Pb	Cu	Zn
1	12	3.05±0.13	166	74	180
2	17	2.62±0.14	515	74	200
3	15	3.69±0.21	99	25	290
4	16	2.85±0.16	95	44	89
5	12	4.99±0.28	475	89	310
6	15	7.12±0.16	51	27	50
7	12	6.37±0.18	92	34	84
8	15	6.73±0.21	85	32	75
9	16	8.31±0.12	59	28	42

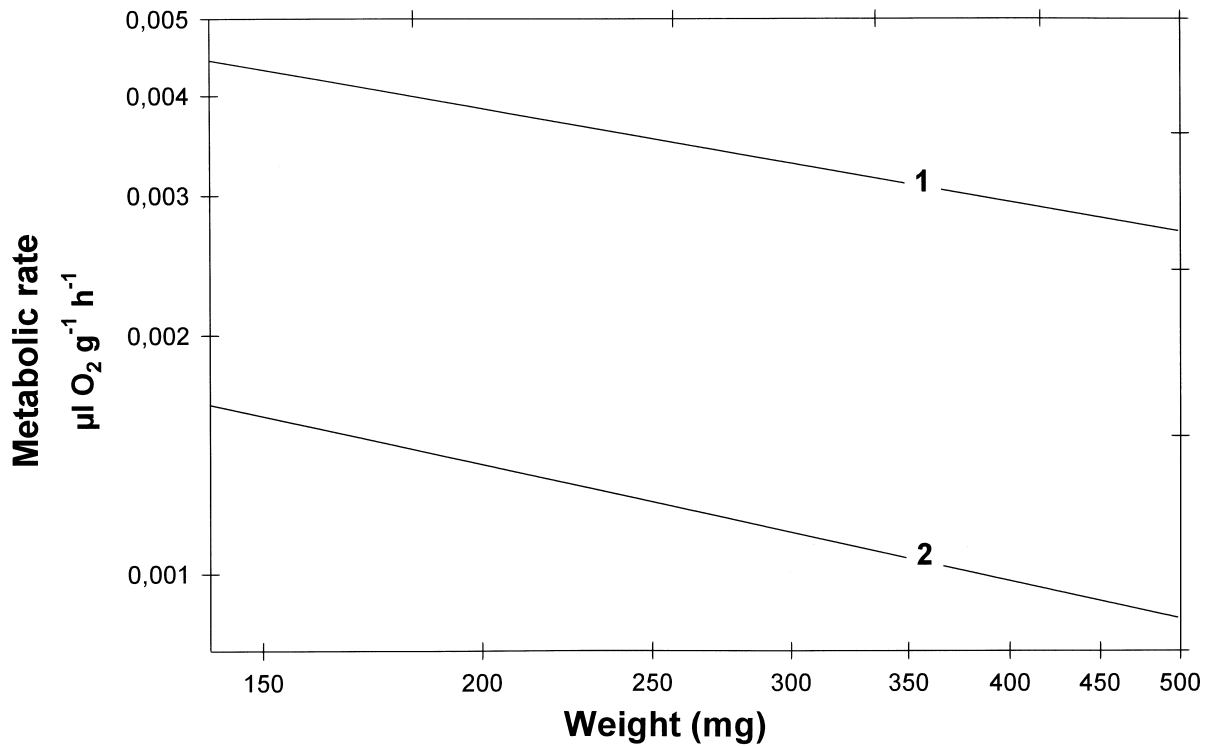


Fig. 2. Regression lines standing for the relationship of Log metabolic rate on Log live mass in specimens *G. balcanica* fed on non-contaminated (1) and contaminated food (2). Regression coefficients b are -0.39 ± 0.06 and -0.49 ± 0.04 for animals fed on non-contaminated and contaminated food respectively.

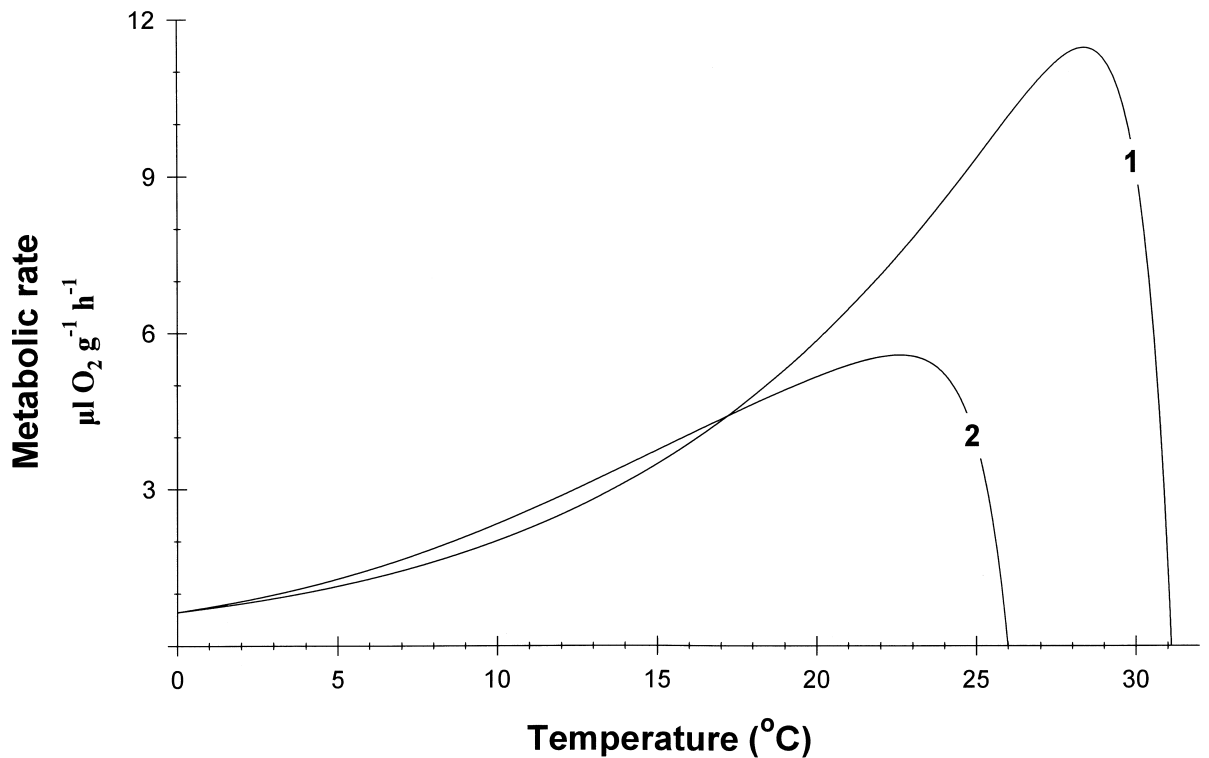


Fig. 3. Relationship of metabolic rate to temperature in adult *G. balcanica*. 1: specimens fed on non-contaminated food, 2: specimens fed on contaminated food.

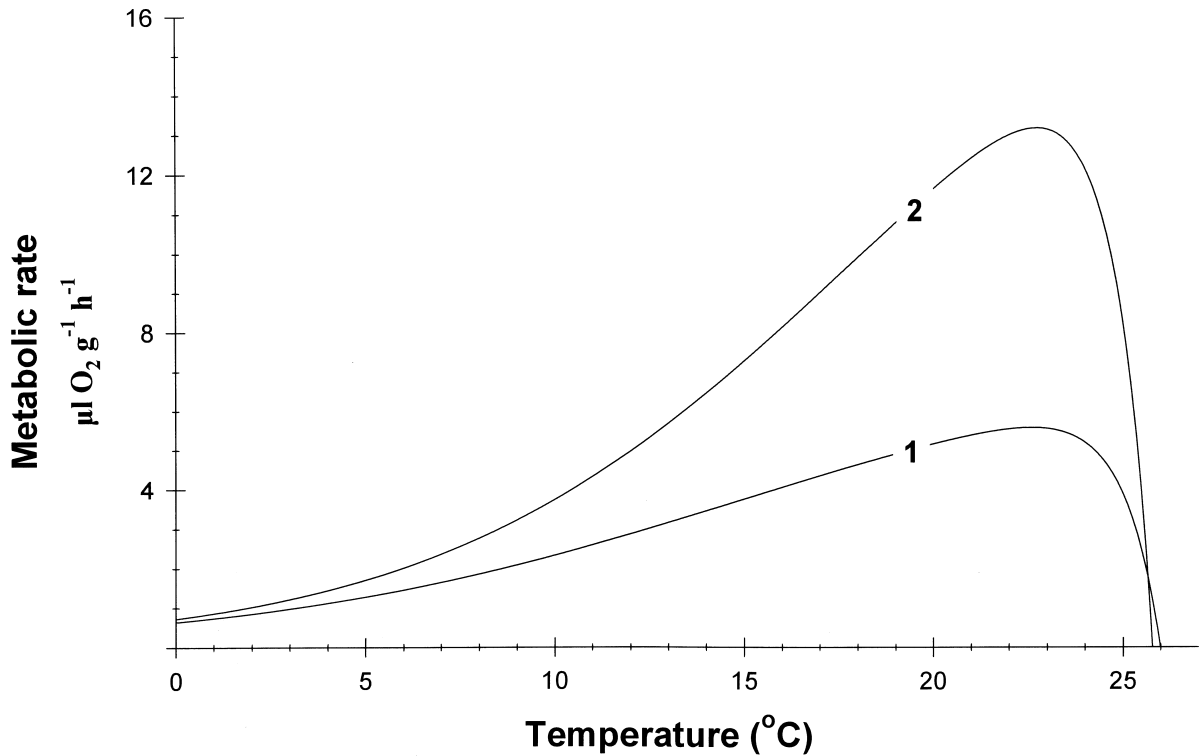


Fig. 4. Relationship of metabolic rate to temperature in adult *G. balcanica* fed on contaminated food. 1: specimens short-term acclimated to constant temperatures (up to 5 days), 2: specimens mid-term acclimated to constant temperatures (43 days).

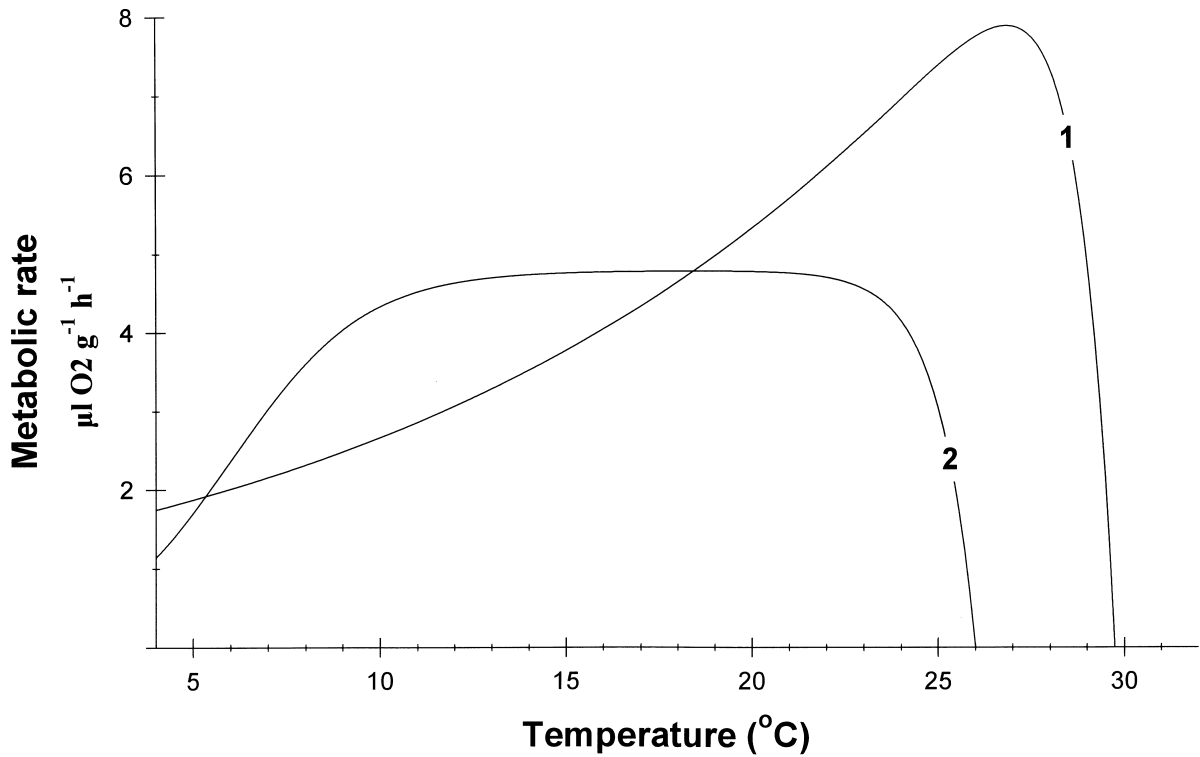


Fig. 5. Relationship of metabolic rate to temperature in adult *G. balcanica*. Specimens were long-term acclimated (63 days) at constant temperatures were stored for 48 h at fluctuating temperatures. 1: specimens fed on non-contaminated food, 2: specimens fed on contaminated food.

indicating that long-term acclimation to constant temperatures results in non-reversible metabolic decay.

The respiratory activity of animals starving for 3 days was estimated for specimens previously fed on contaminated and non contaminated food (Fig. 6). Analysis of variance showed that there is no significant difference between fasting and non fasting animals irrespective of the food treatment.

Discussion

Respiration and temperature

The low oxygen consumption and Q_{10} values of *G. balcanica*, in comparison with other temperate diplopods (Byzova 1967, Penteado and Mendes 1977, Gromysz-Kalkowska and Tracz 1983, Šustr 1996b), indicate a low heat budget, which is of adaptive value for an animal experiencing the wide and sharp diurnal, seasonal and interannual temperature fluctuations of the mediterranean environment (Stamou and Iatrou 1993).

At low temperatures (up to T_1), corresponding to winter field conditions, *G. balcanica* displays relatively low respiratory metabolism and temperature independence. The rapid response to increasing temperature, from T_1 to T_3 , indicates a capacity of the animal to exploit episodic in-

creases in winter temperature, which are not exceptional in mediterranean regions, as well as diurnal temperature fluctuations, in order to accomplish part of its development. A relative thermal independence is displayed again in optimal temperatures (OTR), generally occurring during the oviposition period in late spring-early summer. During this period, strongly oscillating field temperatures are recorded, and *G. balcanica* seems to cope with them by maintaining a metabolic constancy. The precipitous decline of metabolic activity beyond T_{opt} indicates a lack of any metabolic compensation at high temperatures. Indeed, at these temperature levels *G. balcanica* switches rapidly from full activity to latent life, entering a pre-ecdysial phase, which results in negligible respiratory activity (Iatrou and Stamou 1990).

The type of the response of mediterranean arthropods to varying temperatures is considered an essential element of their adaptive strategy (Stamou 1998). The results of this experiment showed that thermal independence is exhibited by the animals at low temperatures, where maintenance priorities overwhelm, and at the optimal temperature level, when energy is invested mostly in production. The high thermal sensitivity exhibited in intermediate temperatures, as well as within $T_{opt}-T_1$, matches with developmental priorities. Apart from *G. balcanica*, analogous interpretations of respirometry data are made for collembolans and oribatids of the same region (Argyropoulou

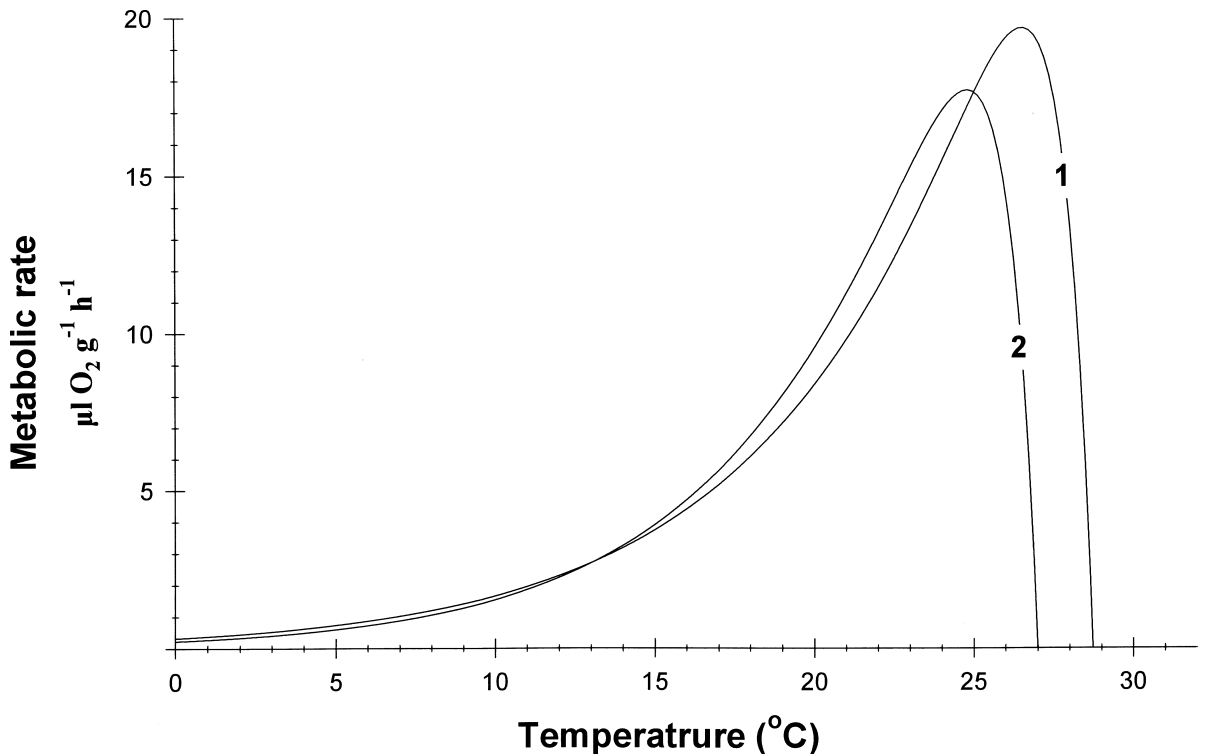


Fig. 6. Relationship of metabolic rate to temperature in fasting adult *G. balcanica*. 1: specimens fed on non-contaminated food, 2: specimens fed on contaminated food.

and Stamou 1993, Stamou et al. 1995). This indicates a more or less common strategic response of both micro- and macroarthropods to the peculiarities of the mediterranean environment.

Acclimation at constant temperatures, food pollution and fasting

The thermal history of arthropods is of great importance for their activity (Prosser 1973, Newell et al. 1974). More specifically, maintenance at constant temperature depresses the activity of some diplopods (Cloudsley-Thompson 1953), while other species appear unaffected (Snider 1981). As in many other arthropods, fluctuating temperatures stimulate the respiratory activity of *G. balcanica*. Stamou and Iatrou (1993) transferred animals from fluctuating to constant temperatures and recorded a metabolic depression of 30% and 50% after 5 and 24 h respectively. After 72 h, respiration remained at low levels, although at high temperatures it exhibited a small increase and stabilization, showing a Precht's 3rd type compensation (Stamou and Iatrou 1990).

In the present study, the effect of acclimation at constant temperature conditions was studied for longer time periods. According to our results, there is a three-step acclimation process, through short-, mid- and long-term periods. After 5 days, the metabolic depression due to the transfer of animals from fluctuating to constant conditions is still evident, being in agreement with our previous studies, while after 43 days metabolism tends to recover. However, this mid-term compensation mechanism does not hold after 63 days, where an irreversible depression in metabolic activity is observed. This irreversible decline of activity due to long-term storage at constant temperatures is in agreement with data concerning egg-laying rate of *G. balcanica* cultured in laboratory and semi-natural conditions (Iatrou and Stamou 1990). This correspondence between respiration and demographic features indicates that respiratory rate is a reliable index of animal activity, supporting statements of Lebrun and Van Ruybeke (1971) and Stamou (1986) that irrespective of the used parameter (physiological or demographic) similar Q_{10} values are estimated in certain arthropods.

As regards the effect of food pollution on respiratory metabolism, we must note that avoidance of contaminated food by *G. balcanica* is excluded, since no significant difference in food consumption (estimated by excrement production) of specimens fed on contaminated and non-contaminated food was revealed, at least during the first 3 days of the experiment (two-way ANOVA). Thus, differences in metabolism are attributed to metal intoxication.

Our results show that food pollution does not modify the type of the metabolic response of animals to varying temperatures, not changing thus profoundly their mode of life. However, pollution shortens tolerance ranges, lowers

critical temperature points and depresses respiratory levels at the high temperature range. Moreover, metabolism rises more rapidly up to thermal optimum and the optimum temperature range, i.e. the range of metabolic constancy, is wider. The lower respiratory levels reflect increased maintenance cost, while the broad optimal temperature range shows that activity remains at its highest for longer. Analogous observations were made for some above ground insects under low pollution conditions (Migula 1996). The same author postulates that elevated activity may result in intensified detoxification, smoothing thereby the harmful effect of pollutants, while Laskowski et al. (1996) report an initial respiratory decline, followed by metabolic recovery in the centipedes *Lithobius mutabilis* fed on Cu-contaminated food. It seems possible that although survival cost may be affected directly by stressful conditions, this can be counterbalanced by an earlier activation of the energy saving homeostatic mechanism, inducing rapid detoxification.

Regarding starvation, it has been reported that it induces a decline in respiration activity of millipedes and other soil arthropods (e.g. Gromysz-Kalkowska 1979, Testering 1983, Pentead and Hebling-Beraldo 1991). However, in all above cases animals starved for at least 4 days. The results of our experiment show that short term fasting (lasting for 3 days) does not affect the respiratory activity of *G. balcanica*. Presumably, it can be stated (following Block 1996) that metabolic depression due to fasting is the first step of a long-term metabolic adjustment against stressful conditions, such as prolonged drought and/or cold.

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