



Field studies on the annual activity and the metabolic responses of a land snail population living in high altitude



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ABSTRACT

In the context of the metabolic cold adaptation hypothesis (MCA), we investigated a) the life and activity cycle characteristics and b) the metabolic responses of the endemic land snail species *Cattania trizona olympica* living at 1100 m altitude in Olympus mountain (Greece). Field observations on the annual activity cycle of *C. trizona olympica* revealed that snails' activity was restricted mainly between the end of May and September, when the higher temperatures were recorded, while first matings were recorded in July and the last ones in mid September indicating a restricted favorable time period for reproduction. The activities of enzymes of intermediate metabolism showed a periodic seasonal pattern of change which seems to be closely related to the pattern of annual changes of air temperature and most of them exhibited higher activities during the coldest and warmest periods of the year. Moreover the data indicate a distinct differentiation of fuel oxidation during arousal and reproductive periods with lipid oxidation, apart from carbohydrates, contributing significantly to ATP turnover during reproductive activity. The higher enzymatic activities, determined in the tissues of *C. trizona olympica* than the corresponding ones determined in the tissues of the land snail species living at low altitudes, might indicate higher sensitivity of the intermediate metabolism and ATP turnover in *C. trizona olympica* to changes in environmental factors. Although the latter seems to be in line with the MCA hypothesis, it needs further investigation on metabolic rates to support it.

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1. Introduction

Ambient temperature is an important environmental factor that affects species distribution, influencing at the same time all life functions of organisms through changes in the rates of physiological and biochemical processes (Johnston and Bennett, 1996; Pörtner, 2002; Somero, 2010). According to metabolic cold adaptation hypothesis (MCA), ectotherm species from colder environments (higher latitudes or altitudes) may have elevated metabolic rates, ATP turnover and growth rate compared to those from warmer climates allowing them to accelerate physiological processes in environments that feature shorter periods of optimal conditions (Chown and Gaston, 1999; Lardies et al., 2004). Moreover, MCA hypothesis predicts that higher latitude and altitude populations should be more sensitive (i.e., higher slopes of temperature–metabolic rate reaction norms) to changes in environmental temperature as this would allow for a more rapid response to increasing temperature (Nielsen et al., 1999; Lardies et al., 2004; Terblanche et al., 2009). This aspect of the MCA is not well tested and fails to examine metabolic responses and rates across a range of ecologically relevant temperatures which may be contributing to the varied support for the MCA (Gaitán-Espitia and Nespole, 2014).

Land snails in temperate regions undergo annual cycles of activity and dormancy (aestivation and/or hibernation) in response to environmental stimuli like high or low temperature, and humidity (Bailey, 1981, 1983; Riddle, 1983; Bailey and Lazaridou-Dimitriadou, 1986). During winter hibernation land snails have to deal with low and sometimes subzero temperatures. Metabolic depression and hypometabolism are common responses to low temperature and enable land snails to survive under unfavorable environmental conditions such as the cold, frost, heat and drought (Storey and Storey, 1990; Guppy and Withers, 1999). Winter hypometabolism is evoked in land snails by changes in ambient temperature, humidity and decrease in photoperiod and it is associated with molecular changes such as gene expression, selective inhibition of protein synthesis and changes in activities of enzymes of intermediate metabolism (Storey and Storey, 2004, 2010).

In Greece, land snails are distributed from the sea level to high altitudes up to 2500 m. In Mediterranean type climates severe drought coupled with high temperature during summer has been considered as the major factor that shape the activity cycles and metabolic responses of land snail populations. In this context several studies, examining metabolic responses of land snail species in Mediterranean habitats have been conducted (Michaelidis and Pardalidis, 1994; Michaelidis et al. 2008; Kotsakiozi et al. 2012). On the contrary, very little attention

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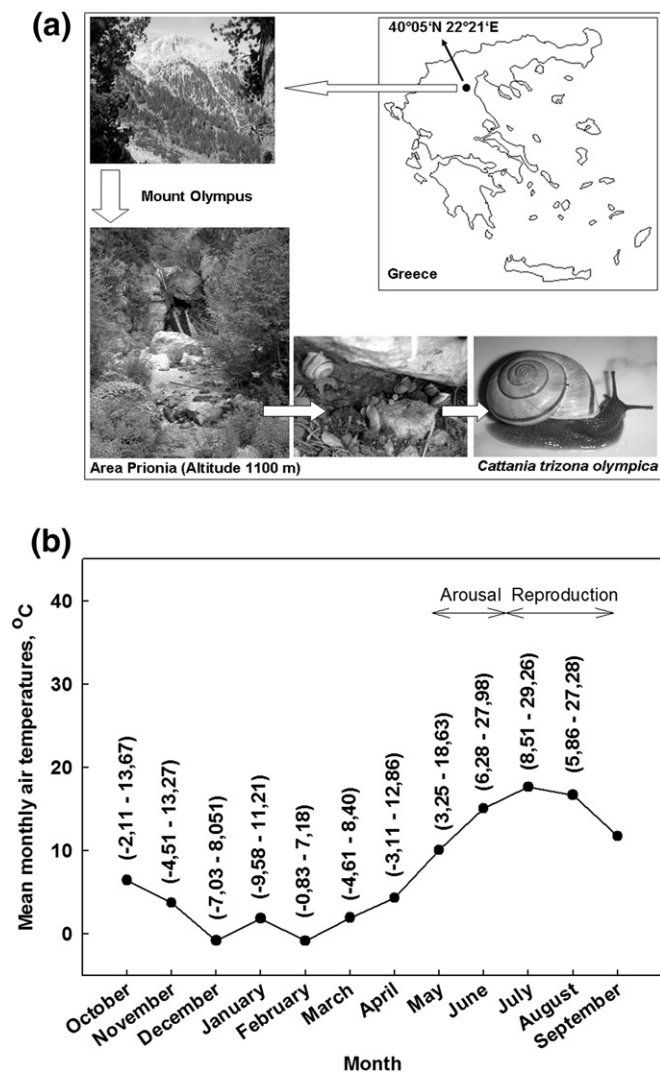


Fig. 1. (a) The land snail *Cattania trizona olympica* and the area Prionia at Mount Olympus where the experiments were conducted and (b) seasonal changes of monthly mean air temperature at the area Prionia in Mount Olympus. The minimum and maximum air temperatures recorded are given in parentheses.

has been drawn to land snail species inhabiting high altitude mountainous habitats, where environmental stressful factors differ from the ones at lower Mediterranean type habitats and almost nothing is known on how snails respond metabolically to such factors. *Cattania trizona olympica* is an endemic subspecies in Olympus (2918 m) mountain. Its vertical distribution is not exactly known but populations have been found from several locations from an altitude of 300 m and up to 2600 m (unpublished data). At high altitudes, populations of this species face subzero temperatures for a long time of year, while higher optimal for activity temperatures are restricted to late spring and summer, thus leaving a short period of favorable conditions for snails' growth and reproduction. The life and activity cycle of populations of this species are completely unknown. Additionally almost nothing is known about their physiological and biochemical responses during seasonal hibernation and whether they have evolutionary adopted different mechanisms to compensate for the short periods of favorable conditions as it is predicted by the MCA hypothesis. We carried out a

field study on a population of *C. trizona olympica* living at 1100 m altitude. The aim of the study was to investigate a) the life and activity cycle characteristics of this population and b) compared to land snail species at sea level, whether this population might respond metabolically as it is predicted by the MCA. For the later we examined the seasonal responses and sensitivity of enzymatic activities of intermediate metabolism in the tissues of snails sampled from the field.

2. Materials and methods

2.1. Field study site

The population studied was situated at the area of Prionia (40°05'N, 22°21'E) on the east facing slope of Olympus mountain at an altitude of 1100 m above sea level (Fig. 1a). The snails were found within a traditional woodland-shrub habitat around the springs of the mountain stream Enipeas. Meteorological data for the region were obtained from the Department of Meteorology and Climatology, School of Geology, AUTH. During the study period, temperature in the region ranged from a minimum of -9.58°C recorded in January to a maximum of 29.26°C recorded in July (Fig. 1b).

2.2. Field study

The characteristics of the annual activity cycle of the snails were monitored during monthly visits at the study site. An initial survey to detect populations of the species was carried out during summer months while monitoring of the selected population activity cycle and sampling for biochemical analysis of snails' tissues lasted for one year. To secure snail sampling during hibernation, four field cages were constructed and placed at the study site. Adult snails (40–50) were collected in autumn (late October–early November) and put in each cage. Upon placement in the cages, an initial sampling was performed for the determination of $V_{\max}$ of the enzymes studied. During monthly sampling, lasting from early December until April snails were removed from the cages, and immediately dissected. Sampling was performed during morning hours and always started after 10:00 a.m. Foot and mantle tissues were separated, frozen in liquid nitrogen and transferred to the lab where they were ground under liquid nitrogen. Tissue powders were stored at -80°C until measurements of enzymatic activities. During activity period (from May to October) snails were sampled from the active population outside the cages, as well.

2.3. Preparation of tissues homogenates for the determination of enzymatic activities

Glycolytic enzyme assays were adapted from those described elsewhere (Storey and Storey, 1984; Brooks and Storey, 1991; Stuart et al., 1998; Michaelidis et al., 2008). CS and HOAD were adapted from Stuart and Ballantyne (1996). Briefly, samples of frozen tissue powders (200–500 mg) were rapidly weighed and homogenized (1:5 w/v) in ice-cold 50 mM imidazole-HCl (pH 7.0) containing 100 mM sodium fluoride (NaF), 5 mM EDTA, 5 mM EGTA, 15 mM 2-mercaptoethanol and 0.1 mM PMSF added just prior to homogenization, using a Polytron PT10 homogenizer (3 periods, 20 s each time). After centrifugation (15,000 g, 4 min, 4°C), the supernatant was removed and passed through a 5-ml column of Sephadex G-25 equilibrated in 40 mM imidazole-HCl buffer (pH 7.0) containing 5 mM EDTA, 15 mM 2-mercaptoethanol, and 20% glycerol to remove metabolites of low molecular mass (Helmerhorst and Strokes, 1980). The column was centrifuged in a desktop centrifuge at 2000 g for 1 min, and the supernatant was used for the determination of enzyme activity. Enzyme

Fig. 2. Seasonal changes in the enzymatic activity of (a) hexokinase (HK), (b) phosphofructokinase (PFK), (c) aldolase (Ald), (d) phosphoglycerokinase (PGK), (e) pyruvate kinase (PK), (f) D-lactate dehydrogenase (D-LDH), (g) citrate synthase (CS), (h) β -hydroxyacyl coenzyme A dehydrogenase (HOAD) and in the ratio (i) D-LDH/CS and (j) CS/HOAD in the foot muscle of *Cattania trizona olympica*. Values are given as means $\pm$ S.E.M., $N = 10$ preparations from different animals. * $P < 0.05$ compared to the initial sampling in December.

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