

# Respiratory Activity of the Collembolan *Onychiurus meridiatus*

M. D. ARGYROPOULOU,\* G. P. STAMOU\*†

Received 29 March 1992; revised 8 September 1992

Oxygen consumption of *Onychiurus meridiatus* (Collembola: Onychiuridae) at six experimental temperatures was determined by means of the gradient diver technique.  $\log_{10}$  respiration rate was linearly related to  $\log_{10}$  live weight, with a mean regression coefficient of 0.64. Asymmetry at thermal optimum characterized the metabolic response to the elevation of temperature. Respiration rate rose sigmoidly up to 26°C and decreased exponentially beyond this point and up to thermal maximum. Acclimation at constant temperature conditions resulted in a depression of oxygen consumption. As regards mature individuals, this depression was significant throughout the whole temperature range studied, while regarding immatures it was significant only at high temperatures. The above results are discussed in relation to the special characteristics of the life cycle development of the species in the laboratory and in the field.

Respiratory activity Collembola *Onychiurus* Mediterranean ecosystem

## INTRODUCTION

Energy allocation is the basic determinant of the life-history strategy of an organism. Considering respiration as the most important path of energy loss, the estimate of an animal's respiration rate provides a measure of the rate at which the animal uses its resources to meet the demands placed on it by the environment (Peters, 1983). Thus, the study of metabolic activity could advance the understanding of the autecology of a species, linking individual performance to population dynamics.

Over the last two decades, the respiratory metabolism of microarthropods has been used for production and assimilation estimates. (Turner, 1983), for studies on cold adaptation (Block and Tilbrook, 1975; Block, 1977, 1979; Block and Young, 1978; Young, 1979), for comparison between populations of the same species and different geographical origin (Block and Tilbrook, 1978) or between different taxonomic groupings (Wood and Lawton, 1973), for distinction between euedaphic, hemiedaphic and epedaphic species (Petersen, 1980; Vannier and Verdier, 1981) or between micro-, macro- and panphytophages (Luxton, 1975). Furthermore, Testerink (1983) related respiration to seasonal changes in humidity and temperature, while Stamou (1986) used respirometry for estimating other parameters of biological activity and demography.

The work presented here is part of a wider project, concerning the dynamics and activity of soil arthropods

in a Mediterranean ecosystem. The study site is located on a gentle hill at the foot of Mt Hortiatis (Macedonia, Greece), and is covered by evergreen sclerophyllous *Quercus coccifera* shrubs. The climate is considered transient from mediterranean to temperate and is characterized by strong seasonal humidity and temperature fluctuations. Minimal and maximal temperatures recorded in the soil organic layers within a 2 yr period were -0.5 and 39°C, respectively (Argyropoulou *et al.*, 1993).

*Onychiurus meridiatus* (Gisin, 1952) is one of the main representatives of the collembolan fauna in the study area, exhibiting an annual life cycle with one population peak in autumn, while the population aestivates during summer in the form of eggs (Stamou *et al.*, 1993). Within the framework of a study concerning the life-strategy of this species, this paper deals mainly with its metabolic response to temperature variations, normally experienced in the field. This is considered an important task, closely related to population dynamics. Furthermore, we consider the metabolism-weight relationship and discuss the effect of fluctuating temperatures on the animal's oxygen consumption.

## MATERIALS AND METHODS

Oxygen consumption rates of single specimens of *O. meridiatus* were measured by means of the gradient diver technique (Lovlie and Zeuthen, 1962; Lints *et al.*, 1967; Petersen, 1981a). The technique is based on the gradual sinking of a small ampulla (diver), containing the experimental animal, in a linear density gradient made of

\*Department of Ecology, School of Biology, Faculty of Sciences, University of Thessaloniki, U.P. Box 119, 540 06 Thessaloniki, Greece.

†To whom all correspondence should be addressed.

Na<sub>2</sub>SO<sub>4</sub>-solution. At constant pressure over the gradient, the method assumes that a given migration of the diver corresponds to a given change in gas volume, caused by the animal's respiratory activity.

The divers, made from glass capillaries of specific weight 2.04, consisted of two separate pieces: the respiration chamber, with a gas volume of about 12  $\mu$ l, containing the experimental animal, and a capillary with both ends narrowed, containing an alkali solution for the absorption of the released carbon dioxide. The two pieces were glued together by means of paraffin wax and colophony mixture (Stamou, 1986). Each diver was tagged with waterproof ink and weighed.

The density gradients were prepared in glass tubes 23 cm in height and 2 cm in diameter. Density ranged from 1 g/ml at the top of 1.04 g/ml at the bottom of the tube. Each gradient was used for one experiment only.

Four divers and a control, charged with 10% sodium hydroxide solution, were introduced into each gradient. A battery of five gradients was placed in a water bath of transparent plexiglass. The temperature in the bath was thermostatically controlled ( $\pm 0.01^\circ\text{C}$ ).

The animals used for respirometry were collected from culturing jars, which were stored outdoors for at least 1 month before the experiment, so that animals could experience ambient temperature fluctuations. Measurements of oxygen consumption were made at 6 temperatures (5, 10, 15, 20, 25 and  $30^\circ\text{C}$ ). Each experiment lasted for about 48 h.

Photographical recordings of changes in the divers' positions were taken at regular time intervals during the first and the last 6 h of each day of the experiment. Measurements were made on a negative film, by means of a stereo-microscope. A computer programme, based on the formulae presented in Lovlie and Zeuthen (1962), was used for the transformation of the divers' migrations into oxygen consumption of the experimental animals.

After the end of the experiment, gradients were calibrated in order to test their linearity and establish a relationship between divers' movement and pressure. Afterwards, animals were removed from the divers, their length was measured and their weight was estimated according to the relationship  $\log W = 0.7 + 2.5 \log L$ , where  $W$  = weight in  $\mu\text{g}$  and  $L$  = length in mm, suggested by Petersen (1975) for two Onychiuridae species. The weights of the animals used in each experimental temperature ranged from about 1 to 3.9  $\mu\text{g}$  and 4 to 19  $\mu\text{g}$ , for immatures and matures respectively, covering almost the whole size range of *O. meridiatus* recorded in the field.

## RESULTS

### Respiration and weight

In order to describe the relationship between respiration and live weight, we used the power function  $RR = a W^b$ , where  $RR$  is respiration rate in  $\mu\text{l O}_2/\text{ind.}/\text{h}$ ,

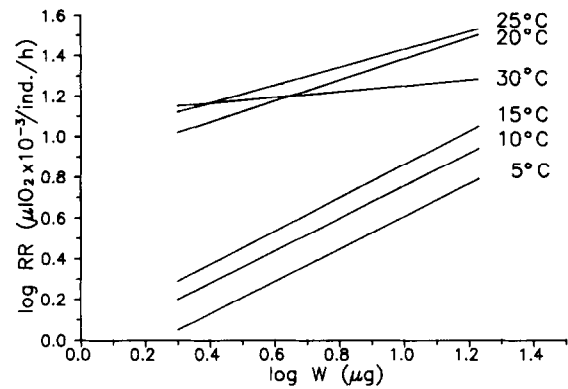


FIGURE 1. Relationship between respiratory rate and weight of *Onychiurus meridiatus*, on a double logarithmic scale, at six experimental temperatures. The regression line of  $30^\circ\text{C}$  concerns only mature individuals.

$W$  is animal's live weight in  $\mu\text{g}$  and  $a, b$  are constants. The former ( $a$ ) stands for the level of metabolism and depends either on endogenous factors, mainly activity, or on exogenous factors, i.e. climatic or chemical (Vannier and Verdier, 1981). The latter ( $b$ ) describes the dependance of the individual's oxygen consumption on its live weight.

All the regression lines of  $\log RR$  against  $\log W$ , in the six experimental temperatures (Fig. 1, Table 1), were statistically significant ( $P < 0.05$ ), except for the one of  $30^\circ\text{C}$ , where only data concerning mature individuals of *O. meridiatus* were used, because immatures could not survive. Analysis of covariance showed no statistically significant differences between the slopes of the regression lines ( $P > 0.05$ ). Yet, they cannot be replaced by a single line, due to significant differences in elevation ( $P < 0.01$ ). Thus, they should be considered parallel with a common  $b$  value equal to 0.64.

According to the above considerations, the effect of weight upon the respiration level of *O. meridiatus* does not differ significantly between temperatures. Differences between elevations are due to different levels of metabolism at various temperatures. Further analysis of covariance, applied to the pairs of successive lines of Fig. 1, showed that two successive lines can be replaced by a single one, because no significant difference either in

TABLE 1. Linear regression of log respiration rate against log live weight in *Onychiurus meridiatus*, at six experimental temperatures

$T(^\circ\text{C})$	$a$	$b$	$n$	$df$	$F$ -test
5	-0.19	0.80	17	1,15	5.43*
10	-0.04	0.80	10	1,8	5.55*
15	0.04	0.82	17	1,15	30.90**
20	0.86	0.52	9	1,7	11.33*
25	0.98	0.45	9	1,7	19.46**
30	1.11	0.14	12	1,10	0.99
Pooled	0.33	0.64		1,67	50.72**
Covariance analysis					
Within $b$ 's				5,60	0.89
Among $a$ 's				5,67	55.71**

\* $P < 0.05$ , \*\* $P < 0.01$ .

elevations or in slopes was recorded ( $P > 0.05$ ). There is an exception regarding the transition from 15 to 20°C, where a pronounced increase of mean respiration rate was recorded.

*Respiration and temperature*

Mean oxygen consumption rates of immature and mature individuals of *O. meridiatus*, at the six experimental temperatures, are presented in Table 2. Oxygen consumption does not change linearly with temperature. It increases up to 25°C, with a sharp rise between 15–20°C. Further temperature increase up to 30°C reduces the respiration rate of matures, while immatures die.

The most commonly used index of an organism's response to increasing temperature is the  $Q_{10}$ -coefficient, estimated from Van't Hoff's formula:  $Q_{10} = K_2/K_1^{(10/T_2-T_1)}$ , where  $K_2$  and  $K_1$  the respiration rate at temperatures  $T_2$  and  $T_1$ . Mean  $Q_{10}$  value of *O. meridiatus*, for the temperature range 5–25°C, is 2.45. However,  $Q_{10}$  is temperature dependent and unable to describe the entire phenomenon. Therefore, it is a mathematically unsatisfactory way of expressing variations of activity or reaction rate with temperature (Howard, 1971). Furthermore, the exponential, the logarithmic, the Krogh–Jorgensen or the Arrhenius equation, used by several authors (Block and Tilbrook, 1975, 1978; Young, 1979; Stamou, 1981, 1986), for the description of the metabolism–temperature relationship, assume a linear increase in respiratory activity with temperature, which is not the case with *O. meridiatus*.

Therefore, in order to describe the relationship between oxygen consumption and temperature, the analytical model proposed by Logan *et al.* (1976) was used:

$$F = a [(1 + ke^{-pT})^{-1} - e^{(T-T_M)}]$$

where  $F$  = respiration rate,  $T$  = temperature in °C,  $p$  = rate of increase of metabolism up to optimal temperature, which according to the terminology used in Logan *et al.* (1976) is the temperature where the maximal rate of the animal's reaction is recorded,  $T_M$  = maximal lethal temperature,  $a$  = maximal observed respiration rate, i.e. rate at thermal optimum,  $k$  = constant. This model provides biologically meaningful parameters and

TABLE 2. Mean respiration rate ( $\mu\text{l O}_2 \times 10^{-3}/\text{ind./h}$ ) of mature and immature individuals of *Onychiurus meridiatus*, at six experimental temperatures

T(°C)	Matures		Immatures	
	n	Respiration rate $\pm$ SE	n	Respiration rate $\pm$ SE
5	16	3.88 $\pm$ 0.66	9	2.09 $\pm$ 0.18
10	12	4.17 $\pm$ 0.71	6	2.21 $\pm$ 0.4
15	13	6.55 $\pm$ 1.06	11	3.38 $\pm$ 0.32
20	11	23.54 $\pm$ 2.84	12	10.75 $\pm$ 2.8
25	6	24.19 $\pm$ 2.05	13	13.25 $\pm$ 3.17
30	12	17.75 $\pm$ 0.66		

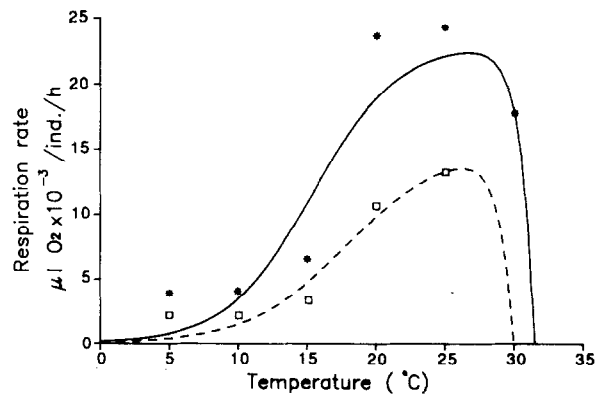


FIGURE 2. The fitting of the model on the respiratory rate–temperature data sets in (—) mature and (---) immature individuals of *Onychiurus meridiatus*.

accounts for asymmetry about optimal temperature, being based on the decomposition of the phenomenon into two distinct phases. The first phase is characterized by a sigmoid metabolic increase up to the thermal optimum and the second phase, occurring once optimal temperature has been exceeded, is characterized by a precipitous metabolic decline until thermal maximum is reached. The model fitted the data well ( $P < 0.05$ ), including the respiration rate of both mature and immature individuals of *O. meridiatus* (Fig. 2). The derived parameters are presented in Table 3. Furthermore, we also estimated the following arithmetically:

- (i) The point where the first derivative of the equation equals zero, that is the point where respiration rate is maximum, corresponding to optimal temperature ( $T_{opt}$ ). This was found to be 26°C, for both mature and immature individuals. Further rise of temperature results in a reduction in oxygen consumption. At this point, we should note that the term “optimal temperature”, as used in this paper, is not necessarily identical to the optimal temperature for the animal's long term survival.
- (ii) The inflection point of the curve (I.P.) is the point where the first derivative of the equation is maximum. It corresponds to 15.5 and 18°C for matures and immatures, respectively. Above these temperatures, the per °C increase in respiration rate slows down. Up to this point, the Arrhenius or any other exponential equation could describe the respiration–temperature relationship.

TABLE 3. Parameters derived from the function fitted to respiration rate–temperature data sets in mature and immature individuals of *Onychiurus meridiatus*

	$a^1$	$p$	$k$	°C			
				$T_M$	$T_{opt}$	I.P.	$T_{crit}$
Matures	23.11	0.32	141.5	31.5	26	15.5	11.5
Immatures	15.15	0.28	147.1	30	26	18	13

For parameters meaning see text.

<sup>1</sup>  $\mu\text{l O}_2 \times 10^{-3}/\text{ind./h}$ .

- (iii) The point where the second derivative of the equation is maximum ( $T_{crit}$ ). It corresponds to 11.5 and 13°C for matures and immatures, respectively. Up to these critical temperatures, the per °C increase of metabolism is relatively slow.

#### Acclimation at constant temperatures

The changes in the respiration rate of *O. meridiatus* with time, at 5 and 10°C, are shown in Fig. 3. In all experimental temperatures, the result was the same, that is a decline in oxygen consumption within the first day of the experiment.

In Fig. 4 the oxygen consumption of mature and immature individuals of *O. meridiatus* at the six experimental temperatures, during the first and second day, is presented. As regards matures, the metabolism-temperature curve shifts during the second day of the experiment, without changing slope, while regarding immatures, shifting is coupled with a change in slope, reminiscent of the two acclimation types, described by Prosser (1973), that is translation and translation with rotation, respectively. As far as immatures are concerned, one-way Analysis of Variance and LSD test, showed that the differences between the first and second day of the experiment were statistically significant only at 20 and 25°C ( $P < 0.05$ ). On the contrary, as regards the mature individuals, statistically significant differences ( $P < 0.05$ ) between the 2 days of the experiment were recorded at all temperatures. Thus, while reduction of metabolism is significant through the whole tempera-

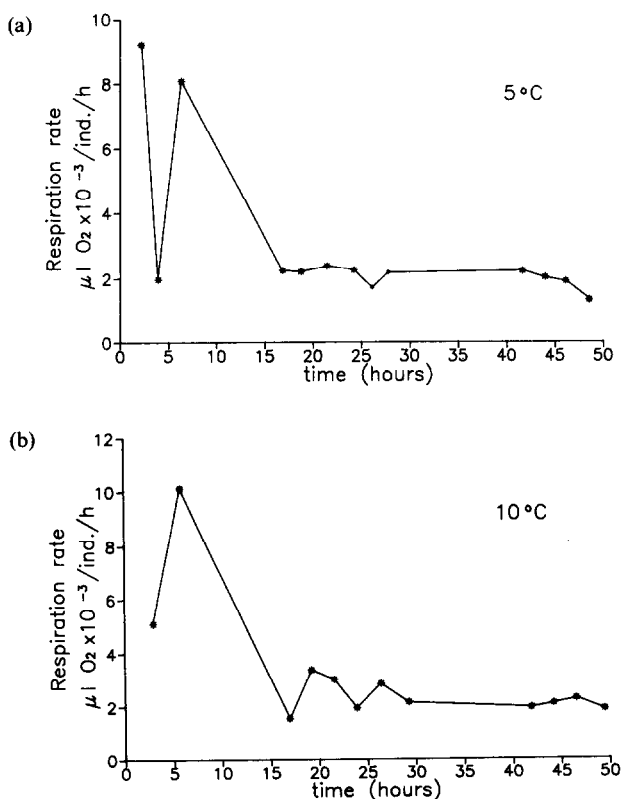


FIGURE 3. The effect of time on the respiratory rate of *Onychiurus meridiatus* at (a) 5 and (b) 10°C. Data are average values for matures and immatures, grouped every 2.5 h.

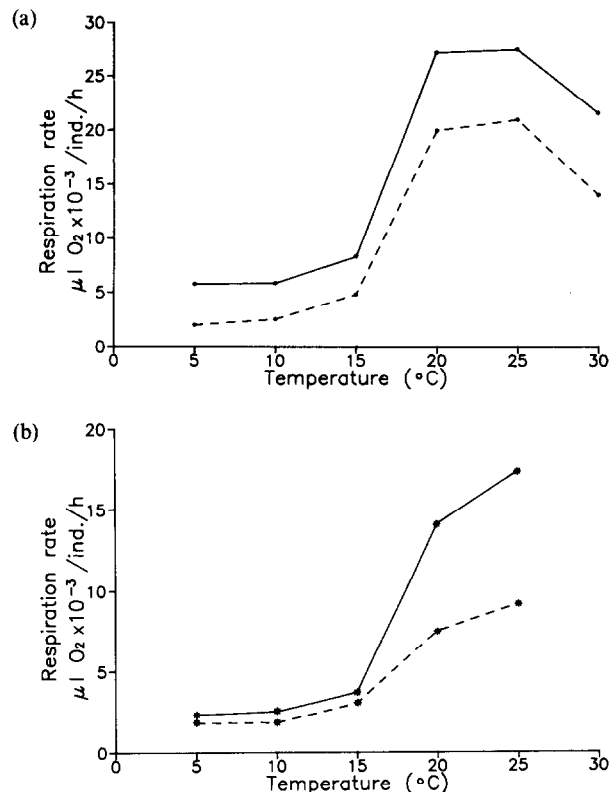


FIGURE 4. Changes of respiratory rate with temperature in (a) mature and (b) immature individuals of *Onychiurus meridiatus*, at the (—) first and (----) second day of the experiment.

ture range for matures, this is not the case with immatures. At the low temperature range, where oxygen consumption is low, differences in level of metabolism between the 2 experimental days are not significant. In contrast, at 20 and 25°C, where oxygen consumption is much higher, metabolic depression is more pronounced.

## DISCUSSION

### Respiration and weight

According to the results presented here, the weight of *O. meridiatus* influences its respiration rate moderately, since the mean value of coefficient  $b$ , from all experimental temperatures, is 0.64, which is lower than those reported for Collembola from temperate and even from polar regions (Zinkler, 1966; Block and Tilbrook, 1975, 1978; Block 1979; Petersen, 1981b; Vannier and Verdier, 1981). Many authors claim that the value of the regression coefficient characterizes, to an extent, the species (Gromysz-Kalkowska and Stojalowska, 1971) or at least larger taxonomic groupings, being related to growth patterns and type of respiratory organs (Bertalanffy, 1957), or levels of activity (Wood and Lawton, 1973). Yet, despite the intrinsic relation between metabolism and weight,  $b$ -values may vary within a single species, due to factors that act differentially among various life stages, such as food type, temperature acclimatization, diel rhythm, locomotory activity during the experiment (Petersen, 1981b), culture stress (Young, 1979) or different degree of exoskeleton sclerotization

(Block, 1977). In the case of *O. meridiatus*, *b*-values vary from 0.45 to 0.82, in the temperature range of 5–25°C, although the differences are not statistically significant. At 5, 10 and 15°C, where the metabolic level is low, weight seems to exert a greater effect on metabolism and *b* displays higher values. After the pronounced increase of metabolism, during the transition from 15 to 20°C, weight seems to become less important as a factor differentiating respiration rate within the species, probably due to a different response to the elevation of temperature between young and older individuals.

#### *Respiration and temperature*

As regards the  $Q_{10}$  value, it falls within the lower part of the range reported for polar and temperate Collembola (Tilbrook and Block, 1972; Block and Tilbrook, 1975, 1978; Petersen, 1981b; Vannier and Verdier, 1981; Turner, 1983; among others). *O. meridiatus* lives in a region where temperature fluctuates within a range much larger than that at polar or temperate regions. Thus the animal, experiencing large temperature fluctuations, displays a greater capacity for regulating its respiratory activity over a wide temperature range, than animals from relatively constant environments (Prosser, 1973).

According to the model fitted to the data, 11.5 and 13°C, for matures and immatures respectively, could be considered as "critical temperatures", below which a temperature increase does not result in a great increase of oxygen consumption. Thus, the animal displays a low thermal sensitivity up to this critical threshold. Beyond this and up to the inflection point of the curve—15.5 and 18°C for matures and immatures respectively—the organism exploits even the slightest increase of temperature, by increasing its respiration rate considerably. Thus, within this range, temperature exerts a great influence upon metabolism. For further increase in temperature, the corresponding increase in respiration rate slows down, probably indicating the existence of an energy saving compensation mechanism. In the laboratory cultures of *O. meridiatus* (Argyropoulou, unpublished), 15°C was the lowest temperature, where eggs were recorded, while at 5 and 10°C both fecundity and mortality rates equalled zero. Thus, the thermal compensation mechanism, within the range 15.5–26°C and 18–26°C for matures and immatures respectively, probably results in a gradually greater energy expenditure for production processes rather than respiration. Further elevation of temperature above 26°C, results in a reduction of respiratory activity and death. The range between the optimal temperature and the maximal lethal temperature is narrow—5.5 and 4°C for matures and immatures, respectively—indicating a great sensitivity of the animal to high temperatures. Indeed, *O. meridiatus* aestivates during summer as an egg, while activity begins with decreasing temperature in autumn, holding out to the end of spring (Stamou *et al.*, 1993). Thus, simulation of the results of this experiment to field conditions, provides an essential aid to the understanding of the dynamics of this species and the synchroniza-

tion of its biological cycle with the environmental constraints.

#### *Acclimation at constant temperature*

According to our results, the oxygen consumption of *O. meridiatus* was reduced considerably within the first day of the experiment. Since reduction in oxygen concentration in the diver is negligible, with respect to its gas volume, this metabolic decline cannot be correlated with a depletion of oxygen, as reported by Young and Block (1980). Furthermore, metabolic depression is also reported as a result of starvation (Zinkler, 1966; Testerink, 1983), but these recordings refer to periods of at least 4 days. In addition, our laboratory cultures did not provide any evidence that a 1-day period of food deprivation can cause considerable changes in animals' activity. Thus, the decline in respiratory activity, recorded in the present study, is probably due to the transfer of the animals from the fluctuating acclimation temperatures to the constant experimental one. Indeed, metabolic decline is often reported as an adaptation to constant temperature (Block and Tilbrook, 1977; Stamou, 1986; Stamou and Iatrou, 1990; among others). Therefore, Block and Tilbrook (1975) stress the desirability of working with fresh animals rather than those cultured in constant temperatures. Yet, freshly collected animals undergo a considerable thermal shock when they pass through the extractor, and a second one when they are placed in the respirometer. This can cause appreciable modifications in metabolic activity (Berthet, 1971). In our case, the shock from the extractor was avoided, because we used animals cultured in fluctuating temperatures. Furthermore, metabolic depression was recorded irrespective of whether the animals have been previously acclimated at lower or higher fluctuating temperatures. Thus, any possible effect of the elevation or reduction in temperature on the respiratory activity was either not obvious within the 2 days of the experiment or masked by the stronger effect of the transfer from fluctuating temperatures to the constant experimental condition. From the above considerations we could infer that fluctuating temperatures have a stimulating effect on the animal's metabolism, as reflected in the high respiratory rate values recorded during the first hours of the experiment.

The stimulating effect holds throughout the whole temperature range in matures, while regarding immatures it is significant only in the high temperature range. This might be the reason of the delay in immatures' development into the adult stadia, during the low temperature season in the field (Argyropoulou, unpublished). More specifically, the last immature instar seems to be a barrier to further development, dominating the immature population throughout winter. On the contrary, matures continue to develop into later stadia, exploiting instantaneous temperature increases, and the population grows older. Furthermore, they continue to provide the population with new offspring, although in small numbers.

## REFERENCES

- Argyropoulou M. D., Asikidis M. D., Iatrou G. D. and Stamou G. P. (1993) Colonization patterns of decomposing litter in a maquis ecosystem. *Pedobiologia*. In press.
- Bertalanffy L. von (1957) Quantitative laws in metabolism and growth. *Quart. Rev. Biol.* **32**, 217–231.
- Berthet P. (1971) Mites. In *Methods of Study in Quantitative Soil Ecology* (Ed. Phillipson J.), I. B. P. Handbook No. 18. 297 pp. Blackwell, Oxford.
- Block W. (1977) Oxygen consumption of the terrestrial mite *Alaskozetes antarcticus* (Acari: Cryptostigmata). *J. exp. Biol.* **68**, 69–87.
- Block W. (1979) Oxygen consumption of the Antarctic Springtail *Parisotoma octooculata* (Willem) (Isotomidae). *Rev. Ecol. Biol. Sol.* **16**(2), 227–233.
- Block W. and Tilbrook P. J. (1975) Respiration studies on the Antarctic collembolan *Cryptopygus antarcticus*. *Oikos* **26**, 15–25.
- Block W. and Tilbrook P. J. (1977) Effects of long-term storage on the oxygen uptake of *Cryptopygus antarcticus* (Collembola). *Oikos* **29**, 284–289.
- Block W. and Tilbrook P. J. (1978) Oxygen uptake by *Cryptopygus antarcticus* (Collembola) at South Georgia. *Oikos* **30**, 61–67.
- Block W. and Young S. R. (1978) Metabolic adaptations on antarctic terrestrial microarthropods. *Comp. Biochem. Physiol.* **61A**, 363–368.
- Gromysz-Kalkowska K. and Stojalowska W. (1971) Oxygen consumption level in *Glomeris connexa* C. L. Koch (Diplopoda) in different physiological states. *Folia Biol.* **19**(4), 457–472.
- Howard P. J. A. (1971) Relationships between activity of organisms and temperature and the computation of the annual respiration of microorganisms decomposing leaf litter. *Ct. rend. IVE Colloque Comite Zool. Assn. int. le Sci. Sol INRA, Paris*. Publ. 71–7.
- Lints C. L., Lints F. A. and Zeuthen E. (1967) Respiration in *Drosophila*. Oxygen consumption during development of the egg in genotypes *Drosophila melanogaster* with contribution to the gradient diver technique. *Co. r. Trav. Lab. Carlsberg* **36**, 35–66.
- Logan J. A., Wollkind D. J., Hoyt S. C. and Tanigoshi L. K. (1976) An analytic model for description of temperature dependent rate phenomena in arthropods. *Envir. Ent.* **5**(6), 1133–1140.
- Lovlie A. and Zeuthen E. (1962) The gradient diver—A recording instrument for gasometric micro-analysis. *C. R. Trav. Lab. Carlsberg* **32**(31), 513–54.
- Luxton M. (1975) Studies on the oribatid mites of a Danish beech wood soil II. Biomass, calorimetry, and respirometry. *Pedobiologia* **15**, 161–200.
- Peters R. H. (1983) *The Ecological Implications of Body Size*. Cambridge University Press.
- Petersen H. (1975) Estimation of dry weight, fresh weight, and calorific content of various Collembolan species. *Pedobiologia* **15**, 222–243.
- Petersen H. (1980) Population dynamic and metabolic characterization of Collembola species in a beech forest ecosystem. In *Soil Biology as Related to Land Use Practices* (Ed. Dindal D. L.) Proc. VII Int. Soil Zoo. Colloq. of the I.S.S.S., Syracuse, NY (1979); pp. 806–8330 EPA 560/13–80–038, Washington, DC.
- Petersen H. (1981a) Open gradient diver respirometry modified for terrestrial microarthropods. *Oikos* **37**, 265–272.
- Petersen H. (1981b) The respiratory metabolism of Collembola species from a Danish beech wood. *Oikos* **37**, 273–286.
- Prosser C. L. (1973) *Comparative Animal Physiology*, 3rd edn. Saunders, Philadelphia, PA.
- Stamou G. P. (1981) Population dynamics of *Achipteria* cf. *italicus* in the soil subsystem of an oakwood in Holomon Mt. (in Greek). Ph. D. Thesis, University of Thessaloniki, Thessaloniki, pp. 1–127.
- Stamou G. P. (1986) Respiration of *Achipteria holomonensis* (Acari: Cryptostigmata). *Oikos* **46**, 176–184.
- Stamou G. P. and Iatrou G. D. (1990) Respiration metabolism of *Glomeris balcanica* at a constant temperature. In *Proc. 7th Int. Congress of Myriapodology*. (Ed. Minelli A.), Leiden, The Netherlands, pp. 197–205.
- Stamou G. P., Asikidis M. D., Argyropoulou M. D. and Sgardelis S. P. (1993) Ecological time versus standard clock time: The Asymmetry of phenologies and the life history strategies of some soil arthropods from Mediterranean ecosystems. *Oikos* **66**, 27–35.
- Testerink G. J. (1983) Metabolic adaptations to seasonal changes in humidity and temperature in litter-inhabiting Collembola. *Oikos* **40**, 234–240.
- Tilbrook P. J. and Block W. (1972) Oxygen uptake in an Antarctic collembole *Cryptopygus antarcticus*. *Oikos* **23**, 313–317.
- Turner B. D. (1983) Annual respiration and production estimates for collembolan and psocopteran epiphyte herbivores on larch trees in southern England. *Ecol. Ent.* **8**, 213–288.
- Vannier G. and Verdier B. (1981) Criteres ecophysologiques (transpiration, respiration) permettant de separer une espece souterraine d'une espece de surface chez les Insectes Collemboles. *Rev. Ecol. Biol. Sol* **18**(4), 531–549.
- Wood T. G. and Lawton J. H. (1973) Experimental studies on the respiratory rates of mites (Acari) from Beech-woodland leaf litter. *Oecologia* **12**, 169–191.
- Young S. R. (1979) Respiratory metabolism of *Alaskozetes antarcticus*. *J. Insect Physiol.* **25**, 361–369.
- Young S. R. and Block W. (1980) Some factors affecting metabolic rate in an Antarctic mite. *Oikos* **34**, 178–185.
- Zinkler D. (1966) Vergleichende untersuchungen zur atemungsphysiologie von Collembolen (Apterygota) und anderen Bodenkleinarthropoden. *Z. vergl. Physiol.* **52**, 99–144.

---

*Acknowledgements*—We wish to thank Dr J. Rusek for the identification of the collembolan, Dr G. D. Iatrou for his instructive criticism and Mrs A. Karamanli-Vlachopoulou for typing the manuscript.