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Respiratory Responses of Oribatid Mites to Temperature Changes

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The present paper presents results on the metabolic activity of adults of three oribatid species (*Scheloribates* cf. *latipes*, *Pilogalumna allifera* and *Achipteria oudemansi*), inhabiting the upper soil layers of a mediterranean pasture land, covered by evergreen-sclerophyllous shrubs. Oxygen consumption was recorded at six temperatures for three subsequent days to determine the respiration rate–temperature relationship and to describe the acclimation process to constant temperature conditions. The response of the animals to temperature changes was also determined. Low respiration rates and Q_{10} values, a relative thermal independence at temperature extremes and an acute response to temperature increase are the main metabolic characteristics of the animals. These results are discussed in relation to the life cycle characteristics of the species in the field.

Respiration rate Acari Oribatids Temperature Acclimation

INTRODUCTION

Over the last two decades, oxygen consumption of microarthropods has been used as a reliable activity index, in order to link the individual performance of the animals with environmental variables (Wood and Lawton, 1973; Block and Young, 1978; Vannier and Verdier, 1981; Argyropoulou and Stamou, 1993; among others). Most relevant studies focus on the dependence of the metabolic activity on temperature, which is considered one of the major determinants of the life cycle development of poikilotherms.

Oribatid mites are one of the most important groups of soil arthropods involved in litter breakdown, and have been found to dominate among Acari in the majority of soil types studied (Luxton, 1975; Petersen, 1981). Most of the studies on their metabolic activity, mainly deal with polar (Block, 1977; Block and Young, 1978; Young, 1979a, b; Young and Block, 1980) and temperate species (Berthet, 1964; Wood and Lawton, 1973; Luxton, 1975; Webb, 1975; Mitchell, 1979; Stamou, 1986).

Scheloribates cf. *latipes* (C. L. Koch), *Pilogalumna allifera* (Oudemans) and *Achipteria oudemansi* (Van der Hammen) are three characteristic species of the oribatid fauna in a mediterranean evergreen–sclerophyllous formation in northern Greece (Asikidis and Stamou, 1992). Within this formation, which is dominated by *Quercus coccifera* L. shrubs, these species occupy a variety of microhabitats, from sheltered sites, under the *Q. coccifera* canopy, to exposed ones in the areas between the *Q. coccifera* stands (Asikidis and Stamou, 1991). Apart from the spatial heterogeneity, mainly induced by grazing, the animals have to encounter the strong seasonality of the mediterranean climate, facing a wide temperature range, which can exceed 40°C on an annual basis (Argyropoulou *et al.*, 1993). Furthermore, diurnal temperature fluctuations of 15 or even 20°C are not exceptional. Under such conditions, a regulation of energy dissipation through respiration would be of crucial importance for the population development of these oribatids.

In the present study, we present data on oxygen consumption of the above mentioned species. Our purpose was to determine the metabolic characteristics of the animals, which allow them to overcome the strongly fluctuating thermal environment of the study area.

MATERIALS AND METHODS

The metabolic activity of single oribatid mites was determined by means of the gradient diver technique. This microgasometric method described by Lovlie and Zeuthen (1962) and modified by Petersen (1981), has been successfully used in terrestrial micro- and macroarthropods by Stamou (1986), Argyropoulou and Stamou (1993) and Stamou and Iatrou (1993). The method involves the sinking of a small glass ampula diver (about 12 μl gas volume) containing the experimental animal in a linear density gradient made of Na_2SO_4. The lower part of the diver contains an alkali

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solution for the absorption of the released CO_2. The animal's respiratory activity causes the diver to sink, and its successive positions are photographically recorded over regular time intervals.

The animals used were collected in the field a few weeks before respirometry. They were extracted from soil samples by means of a Berlese–Tullgren apparatus and stored outdoors under naturally fluctuating temperature conditions. Oxygen consumption was determined at 7, 11, 15, 19, 24, 29°C for three successive days at each temperature. At 11 and 24°C, measurements were continued for a fourth day, after changing the temperature. In the case of 11°C, after the 72nd hour we raised the temperature at 24°C, while in the case of 24°C we lowered the temperature at 11°C. Five divers, each containing a single adult oribatid, and a control diver were introduced in each gradient. Equilibration time was 20 min. Hourly photographs of the downward migration of the divers were taken over the following time intervals: 1–5, 20–24, 44–48, 68–72 h. After the temperature change, measurements were taken over 73–77 h and over 92–96 h. This procedure was adopted in order to describe the acclimation process of the oribatids to constant temperature conditions and to assess their response to short term temperature changes.

After the end of the experiment, the animals were removed from the divers, their length and width were measured, and their weight was estimated according to the formulae suggested by Lebrun (1971). Mean weights of the animals used here were 13.52 μg, 27.2 μg and 36.98 μg for *S.* cf *latipes*, *P. allifera* and *A. oudemansi* respectively.

RESULTS

The three oribatid species studied exhibited comparable respiration rates ranging from 0.56 μl $O_2 \times 10^{-3}$/ind/h in *S.* cf. *latipes* at 7°C to 4.54 μl $O_2 \times 10^{-3}$/ind/h in *A. oudemansi* at 29°C (Table 1). These values represent mean rates over the first three days of the experiment. Mean respiration rate over the whole temperature range was 1.83, 2.5 and 3.09 μl $O_2 \times 10^{-3}$/ind/h for *S.* cf. *latipes*, *P. allifera* and *A. oudemansi* respectively, corresponding to a mean weight specific metabolic rate of 135.40, 91.92 and 83.55 μl O_2/g/h respectively.

Within the temperature range examined, mean respiration rate does not change linearly with temperature. In the three species studied, it increases up to 19°C. From this threshold and up to 29°C metabolism remains more or less stable. This is reflected in the Q_{10} values (Table 1). In the upper temperature range (19–29°C), they are very close to unity, varying from 1.05 to 1.21.

The Q_{10} coefficient is the most common way of describing temperature dependent metabolic processes in arthropods. Occasionally, equations such as the exponential, the logarithmic, the Krogh-Jorgensen or the Arrhenius have been introduced in order to simulate the entire phenomenon (Block and Tilbrook, 1975, 1978; Young, 1979; Stamou, 1986; Stamou and Iatrou, 1993). However, all these equations presuppose a continuous increase of the metabolic activity with temperature, and are thus inadequate in the present case, where respiration plateaux are recorded.

In the present paper, the respiration rate–temperature relationship is expressed by the analytic model introduced by Logan *et al.* (1976) to describe the temperature dependence of life history parameters in a spider mite:

$$F = a[(1 + k\mathrm{e}^{-pT})^{-1} - e^{(T - Tm)}]$$

where F: respiration rate, T: temperature in °C, p: rate of increase of metabolism up to the optimal temperature, Tm: maximal lethal temperature, a: maximal respiration rate and k: constant. We should note that, according to the terminology used by Logan *et al.* (1976), optimal temperature is the point where the maximal respiration rate is recorded, and is not necessarily identical to the optimal temperature for the animal's long term survival.

As suggested by these authors, the model has a broad application in temperature depended biological processes, extrapolating responses beyond the limits where actual data are available. It has already been used to describe the respiration–temperature relationship in another soil arthropod (Collembola) by Argyropoulou

TABLE 1. Mean (±SE) respiration rate ($\mu lO_2 \times 10^{-3}$/ind/h) and Q_{10} values of adults of the three oribatid species at six experimental temperatures

	S. cf. *latipes*			*P. allifera*			*A. oudemansi*		
T (°C)	n	Respiration rate	Q_{10}	n	Respiration rate	Q_{10}	n	Respiration rate	Q_{10}
7	20	0.56 ± 0.06		18	0.88 ± 0.09		23	1.29 ± 0.24	
			9.50			2.13			1.16
11	24	1.37 ± 0.12		25	1.19 ± 0.09		24	1.37 ± 0.10	
			1.06			3.71			5.06
15	23	1.41 ± 0.08		20	2.01 ± 0.06		18	2.61 ± 0.21	
			3.70			4.00			3.5
19	28	2.39 ± 0.08		22	3.47 ± 0.16		19	4.33 ± 0.16	
			1.11			1.16			1.05
24	22	2.51 ± 0.18		21	3.73 ± 0.24		24	4.40 ± 0.15	
			1.21			1.19			1.05
29	23	2.76 ± 0.14		23	4.12 ± 0.24		23	4.54 ± 0.14	

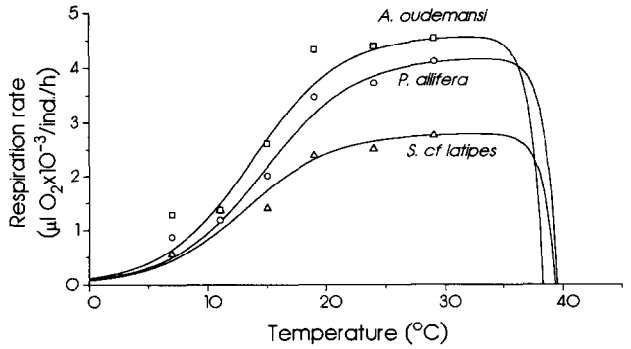

FIGURE 1. The model of Logan *et al.* (1976) fitted to respiratory rate–temperature data sets of the three oribatid species.

and Stamou (1993). In our case, it fitted our data well ($P < 0.05$) (Fig. 1). The derived parameters are given in Table 2. In addition, we estimated the following :

- The point where the first derivative of the function equals zero (Topt), corresponding to the optimal temperature, where respiration rate is maximum.
- The point where the first derivative of the function is maximum, corresponding to the inflection point of the curve (IP).
- The point where the second derivative of the function is maximum (Tcrit).
- Furthermore, we provide the optimum temperature range (OTR) for each species, which was arbitrarily defined as the temperature range where the first derivative of the function exhibited minimal fluctuations between -0.09 and $+0.09$.

As shown in Table 2, no marked differences are recorded between the three species. Maximum lethal temperature varied between 38–40°C, while maximum respiratory activity is recorded at about 32°C for all species. The inflection point of the curves lies between 13–15°C. Above these temperatures the increase of respiration rate per degree slows down. Critical temperatures (Tcrit) up to which the animals are relatively insensitive to temperature changes were low, lying between 8–9°C. Finally, *P. allifera* and *A. oudemansi* exhibit a similar optimum temperature range (23–36°C), while that of *S.* cf. *latipes* is wider, ranging from 19.5 to 36°C.

The animals' reaction to their transfer from the fluctuating acclimation temperatures to the constant experimental ones was identical in all temperatures and

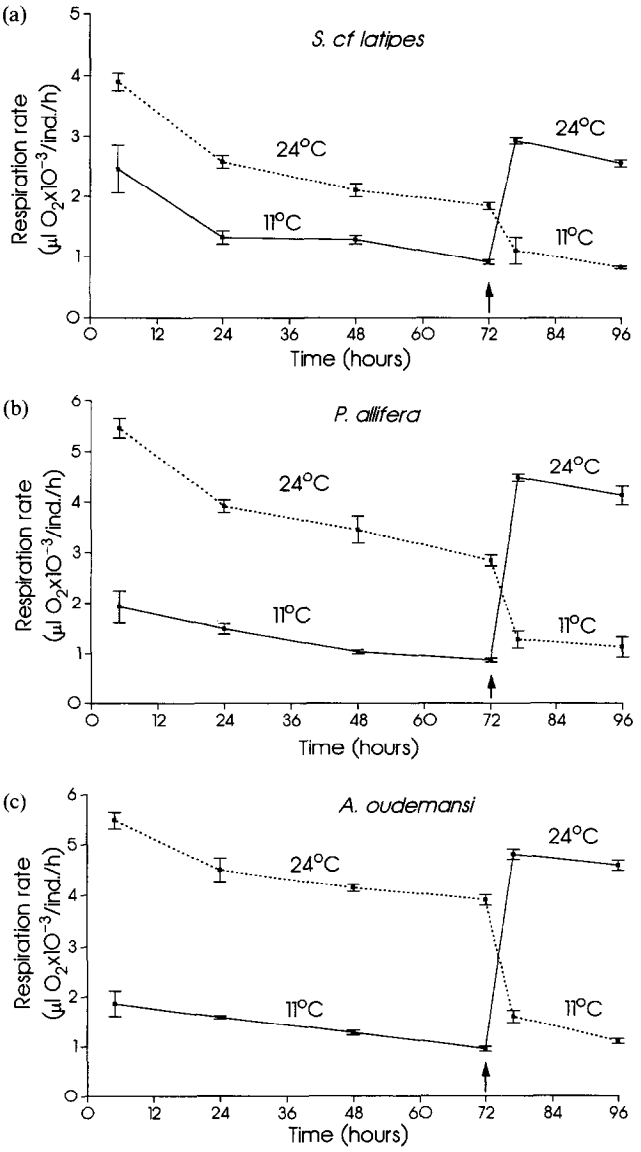

FIGURE 2. The acclimation of three oribatid species to constant temperature conditions. Each dot represents mean values of five successive measurements. The arrow indicates the moment of temperature change.

independent from the instant temperature the animals experienced just before the beginning of the experiment. Figure 2 shows representative graphs of this process at 11 and 24°C, where temperature was changed after the third experimental day. In all cases the respiration rate declines with time. Analysis of variance (ANOVA) and LSD-test showed that in most cases there is a statistically

TABLE 2. Parameters of the model of Logan *et al.* (1976) fitted to respiration rate–temperature data in three oribatid species. The optimum temperature range (OTR) for each species is also given

	a*	*p*	*k*	*Tm*	Topt	Tcrit	IP	OTR
S. cf. *latipes*	2.8	0.27	34.80	39.33	32.50	8.25	13.25	19.50–36.00
P. allifera	4.2	0.26	45.86	39.50	32.25	9.25	14.75	23.25–35.75
A. oudemansi	4.6	0.27	40.58	38.30	32.00	8.50	13.75	22.50–34.50

*In μl $O_2 \times 10^{-3}$/ind/h.
For parameters meaning see text.

TABLE 3. Comparison between mean respiration rates of three oribatid species exhibited at constant temperature conditions (RR_1) and those recorded after temperature change (RR_2, RR_3)

	T (°C)	RR_1	RR_2	RR_3	P
S. cf *latipes*	24	2.11 ± 0.09	2.65 ± 0.08		< 0.05
	11	1.16 ± 0.06		1.00 ± 0.14	> 0.05
P. allifera	24	3.24 ± 0.15	4.22 ± 0.15		< 0.01
	11	1.05 ± 0.06		1.21 ± 0.12	> 0.05
A. oudemansi	24	4.12 ± 0.09	4.71 ± 0.08		< 0.05
	11	1.22 ± 0.07		1.41 ± 0.12	< 0.05

RR_1: Mean respiration rate at constant temperature conditions.
RR_2: Mean respiration rate after temperature increase from 11°C.
RR_3: Mean respiration rate after temperature decrease from 24°C.
P: probability level.

significant decrease of the respiratory activity of about 30% by the end of the first day, which does not exceed the levels of 40% after 72 h. The high metabolic activity recorded during the first five hours of the experiment should be considered as the closest to the one normally exhibited by the animals in the field, since it may still reflect to an extent the metabolic levels at fluctuating temperature conditions. The low metabolic activity exhibited after the fifth hour may be considered as the animals' resting metabolism at constant temperature conditions.

As shown in Fig. 2, temperature increase caused a remarkable metabolic response of the animals. In all species, the transfer from 11 to 24°C resulted in an immediate increase in respiratory activity, by 400% in *A. oudemansi*. On the contrary, the temperature decrease from 24 to 11°C did not have such a pronounced result; metabolic depression ranged between 30 and 60%. It should also be noted that the mean respiration rate recorded during the last 24 h of the experiment, after transferring the animals to 24°C was significantly higher than that of animals acclimated for three days (the 5 first hours excluded) at the same temperature (t-test, $P < 0.05$). The transfer of the animals to a lower temperature (from 24 to 11°C) did not have an analogous effect (Table 3).

DISCUSSION

The adversity of the mediterranean environment, as regards the soil mesofauna, consists of the wide temporal oscillations of the climatic variables and the fragmentary structure of the habitats, resulting from management practices (grazing, wood removing), as is the case with the study area (Argyropoulou *et al.*, 1994). According to Asikidis and Stamou (1992) and Stamou *et al.* (1993), oribatids respond to these constraints by adjusting their demography to the seasonally oscillating environment. In these papers, the authors argue that the basic determinants of the life strategy of soil microarthropods are the demographic characteristics of adults, and that, on this basis, the life cycles of the three oribatids studied here are quite similar.

However, the life strategy of an organism should be viewed as the outcome of a number of co-adopted characteristics, which are detected on both the demographic and the physiological level. The results presented in this paper concern the second response level of the oribatids, i.e. that of physiology.

All three species studied display low metabolic activity and low Q_{10} values, compared with other temperate and polar species (Wood and Lawton, 1973; Luxton, 1975; Block, 1977; Young, 1979; Stamou, 1986). These features hold also for other soil arthropod groups in the study area (Argyropoulou and Stamou, 1993; Stamou and Iatrou, 1993), indicating a great capacity to regulate respiratory activity, a characteristic of animals living in variable environments (Prosser, 1973).

Phenological features (e.g. duration of activity in the field and/or habitat selection) have been used in order to interpret differences in metabolic level and temperature dependence in soil arthropods (Byzova, 1971; Gromysz-Kalkowska, 1974; Wooten and Crawford, 1974). In our case, *S.* cf. *latipes* displays the lowest mean respiration rate and the widest optimum temperature range compared to *P. allifera* and *A. oudemansi*. These metabolic characteristics are compatible with the longest activity period the animal is displaying compared with the other two oribatids (Asikidis and Stamou, 1992), as well as with its broader habitat selection (Asikidis and Stamou, 1991).

The fitting of the model to the respiration rate–temperature data showed that, apart from the above mentioned differences, the three oribatid species display similar metabolic characteristics, implying a more or less common mode of life. More specifically, the animals display a relative thermal independence at temperature extremes, that is up to 8°C and from 20 to 35°C, while at intermediate temperatures, the metabolic dependence is much more pronounced. Moreover, the acclimation experiment showed that, within this intermediate range, the metabolic response to temperature change is rapid, indicating a capacity of the animals to respond to short term diurnal fluctuations of temperature.

Another feature that emerged from this study is the stimulating effect of fluctuating temperatures. This was exemplified by the metabolic depression, recorded after transferring the animals from fluctuating to constant temperatures. Indeed, metabolic decline has often been reported as an adaptation to constant temperature conditions (Block and Tilbrook, 1977; Argyropoulou and Stamou, 1993; among others). It should be noted that the metabolic decline recorded in the present experiment cannot be attributed to the starved condition of the mites in the respirometer, since metabolic reductions of the same magnitude to the one recorded here after 24 h, are reported as a result of food deprivation of 1–4 week periods (Young and Block, 1980; Testerink, 1983). Young and Block (1980) also correlate metabolic decline with oxygen depletion in the diver. However, in our experiment the reduction of oxygen concentration in the diver is negligible, with respect to its gas volume, at least

within the first 24 h when the most pronounced metabolic depression occurs. Thus, any possible effect of animals' starvation or reduction of the oxygen content of the diver on the measured respiration rates is probably masked by the stronger effect of the transfer from fluctuating temperatures to the constant experimental condition. This fact is also reinforced by the metabolic levels reached after the instant temperature increase, which were higher than those recorded during temperature constancy.

Asikidis (1989) reports that when rearing these species at constant temperatures in the laboratory, 15°C was the threshold under which the life cycle development of these three oribatids was inhibited, a fact which does not hold under field (fluctuating) conditions. At low temperatures in winter and early spring the animals, despite their low respiration rate, may accomplish energy consuming activities such as egg synthesis and deposition (Asikidis and Stamou, 1992), exploiting even the slightest, hazardous temperature increase.

At high temperatures (summer, early autumn), when the animals pass through a number of stadia to complete their life cycle development, the metabolic activity is high but constant over a wide temperature range. This indicates the existence of an energy saving homeostatic mechanism, preventing an increase of metabolism and thus an increase of the maintenance cost during the unfavourable period of the year.

REFERENCES

Argyropoulou M. D. and Stamou G. P. (1993) Respiratory Activity of the Collembolan *Onychiurus meridiatus*. *J. Insect Physiol.* **39,** 217–222.

Argyropoulou M. D., Asikidis M. D., Iatrou G. D. and Stamou G. P. (1993) Colonization patterns of decomposing litter in a maquis ecosystem. *Eur. J. Soil Biol.* **29,** 183–191.

Argyropoulou M. D., Stamou G. P. and Iatrou G. D. (1994) Temporal and spatial distribution patterns of Collembola in a patchy environment. *Eur. J. Soil Biol.* **30**. In press.

Asikidis M. D. (1989) Population dynamics and activity of oribatid mites from an evergreen–sclerophyllous formation (Hortiatis). (In Greek with English summary). Ph.D. Thesis. Univ. of Thessaloniki.

Asikidis M. D. and Stamou G. P. (1991) Spatial and temporal patterns of an oribatid mite community in an evergreen–sclerophyllous formation (Hortiatis, Greece). *Pedobiologia* **35,** 53–63.

Asikidis M. D. and Stamou G. P. (1992) Phenological patterns of oribatid mites in an evergreen–sclerophyllous formation (Hortiatis, Greece). *Pedobiologia* **36,** 359–372.

Berthet P. (1964) L'activite des Oribatides (Acari: Oribatidae) d'une Chenaie. *Mem. Inst. r. Sci. nat. Belg.* **152,** 1–152.

Block W. (1977) Oxygen consumption of the terrestrial mite *Alaskozetes antarcticus* (Acari: Cryptostigmata). *J. exp. Biol.* **68,** 69–87.

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*. *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.

Byzova J. B. (1971) Oxygen uptake and temperature in some millipedes (Julidae, Diplopoda). *Ann. Zool.* 193–195.

Gromysz-Kalkowska K. (1974) The effect of some exogenous factors and body weight on the oxygen consumption in *Glomeris connexa* (CL Koch) (Diplopoda). *Folia Biol.* **22,** 37–49.

Lebrun Ph. (1971) Ecologie et biocenotique de quelques peuplements d'arthropodes edaphiques. *Mem. Inst. r. Sci. nat. Belg.* **165,** 1–203.

Logan J. A., Wollkind D. J., Hoyt S. C. and Taniigoshii L. K. (1976) An analytic model for description of temperature dependent rate phenomena in arthropods. *Envir. Ent.* **5,** 1133–1140.

Lovlie A. and Zeuthen E. (1962) The gradient diver—A recording instrument for gasometric micro-analysis. *C. R. Trav. Lab. Carlsberg* **32,** 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.

Mitchell M. J. (1979) Energetics of oribatid mites (Acari: Cryptostigmata) in an aspen woodland soil. *Pedobiologia* **19,** 89–98.

Petersen H. (1981) Open gradient diver respirometry modified for terrestrial microarthropods. *Oikos* **37,** 265–272.

Prosser C. L. (1973) *Comparative Animal Physiology* 3rd edn. Saunders, Philadelphia, PA.

Stamou G. P. (1986) Respiration of *Achipteria holomonensis* (Acari: Cryptostigmata). *Oikos* **46,** 176–184.

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.

Stamou G. P. and Iatrou G. D. (1993) Studies on the respiratory metabolism of *Glomeris balcanica* (Diplopoda, Glomeridae). *J. Insect Physiol.* **39,** 529–535.

Testerink G. J. (1983) Metabolic adaptations to seasonal changes in humidity and temperature in litter-inhabiting Collembola. *Oikos* **40,** 234–240.

Webb N. R. (1975) Respiratory metabolism of *Steganacarus magnus* (Acari). *Oikos* **26,** 43–46.

Wood T. G. and Lawton J. H. (1973) Experimental studies on the respiratory rate of mites (Acari) from Beech-woodland leaf litter. *Oecologia* **12,** 169–191.

Wooten R. C. and Crawford C. S. (1974) Respiratory metabolism of the millipede *Orthoporus ornatus* (Garard) (Diplopoda). *Oecologia* **17,** 179–186.

Young S. R. (1979a) Respiratory metabolism of *Alaskozetes antarcticus*. *J. Insect Physiol.* **25,** 361–369.

Young S. R. (1979b) Effect of temperature change on the metabolic rate of an Antarctic mite. *J. Comp. Physiol.* **131,** 341–346.

Young S. R. and Block W. (1980) Some factors affecting metabolic rate in an Antarctic mite. *Oikos* **34,** 178–185.