

Respiration of *Abax ater* (Coleoptera, Carabidae): a complex parameter of the energy budget

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Summary. Respiration is quantitatively the most important element in the energy budget of the ground beetle *Abax ater*. It was measured in a Gilson respirometer for all developmental stages (except for the eggs), taking as many parameters as possible into account.

The standard metabolic rate (SMR) increased exponentially with *temperature* in the range 5–15 °C but *no metabolic acclimation* to temperature was observed.

A single relationship was found between *body mass* and respiration for all the active stages. Adult males regularly had a SMR slightly higher than did females, but the difference was seldom significant and may be explained by differences in body mass.

At constant temperature SMR exhibited a *daily cycle* with two peaks occurring in the first half of the night and in the morning. It also exhibited an *annual cycle* with a maximum in the summer.

SMR was up to twice higher than the *basal metabolic rate* (BMR), and the *activity metabolic rate* (AMR) of running individuals was two to three times higher than SMR.

Respiration increased to twice SMR the day after a full meal owing to *digestion*, and then decreased for three days.

The respiratory quotient (RQ) of 0.72 suggested that mainly lipid molecules were oxidised in *A. ater* respiration.

Measurements of respiration by gravimetry gave results that were close to BMR.

Besides the classical relationships of respiration with temperature and body mass, this work showed the significant influences of digestion and mobility on respiration : taking them into account realistically required multiplying SMR by a factor 2.3 during the active part of the annual cycle of *A. ater*. This correction allowed balanced energy budgets to be obtained.

Key words: Carabid beetles, *Abax ater*, respiration, standard metabolic rate, basal metabolic rate, activity metabolic rate, digestion, mobility, stage, body mass, temperature, acclimation

Introduction

Respiration is one of the most important parameters of an energy budget (Petrušewicz & Macfadyen 1970), and this is also the case for *Abax ater* (Chaabane et al. 1996). But it is also the parameter that is the most sensitive to both natural and artificial conditions. Respiration metabolism depends on intrinsic biological factors such as body mass, sex, nutritional state,

physiological state, locomotion, circadian rhythm and annual cycle. It also depends on laboratory induced conditions such as temperature acclimation, stress linked to space availability in the respirometer (mainly for thigmotactic organisms), stress induced by water vapour deficit (mainly for soil animals), and low CO₂ concentration in the respirometer if KOH is used (Zinkler 1972). Therefore the energy budgets published in the literature are rarely balanced and most generally respiration is considered to be responsible for the discrepancy (Wightman 1981).

Respiration frequently accounts for more than 50 % of insect energy budgets, especially in long-lived species. This work was performed to provide appropriate and flexible data on respiration in the ground beetle *Abax ater* and its dependence on the most important biotic and abiotic factors, with the goal of establishing a complete energy budget for both laboratory kept individuals and a natural population of this species (Chaabane et al. 1996).

Materials and Methods

1. Rearing

Collecting of beetles. Adults and third-instar larvae of *Abax ater* (Villers 1789) were caught in a near-climax beechwood set up as a natural reserve at Lembeek, south of Brussels, Belgium, where *Abax ater* is strongly dominant (Loreau 1984). They were collected by funnel traps as described in Loreau & Nolf (1993). These traps also served to catch some earthworms used mainly for feeding the larvae. Subsequently, these animals were kept either in the laboratory or under semi-natural conditions.

First- and second-instar larvae as well as pupae were obtained in laboratory rearing. Some first- and second-instar larvae were also collected by quadrat sampling (25 × 30 × 10 cm) in the beechwood at Lembeek and extracted in a size-adapted Tullgren extractor.

Rearing in the laboratory. Insects were reared in the laboratory in climatic chambers equipped with an automatic system controlling temperature and photoperiod and ensuring a continuous ventilation. Standard (summer) conditions were set at 18°C during daytime 16 h per day, 15°C during night-time 8 h per day, and humidity always near saturation. These conditions are very close to those that can be experienced in the top layer of the beechwood soil in July (Loreau 1984). Winter conditions for hibernation were set at 3°C during daytime 8 h per day and 1°C during night-time 16 h per day. These conditions are close to those which can be experienced in the top layer of the beechwood soil in January.

Larvae were reared separately in glass vials 5 cm in diameter, 3 cm high, and furnished with 1 cm of sieved soil. They were fed twice a week on pieces of earthworm of the species *Dendrobaena subrubicunda* and *Lumbricus eiseni*. Adults were kept separately in PVC vials 8 cm in diameter, 12 cm high, and furnished with 7 cm of moist sieved forest soil. They were fed twice a week on ground beef meat (as in Thiele 1968).

Rearing under semi-natural conditions. The beetles were reared under semi-natural conditions in four outdoor tubs sunk into the soil under a bush on the Solbosch campus of the Free University of Brussels. The tubs were covered by a glass sheet preventing rain from coming in while letting air circulate. Temperature and humidity were recorded continuously using a thermo-hygrograph placed in one of the tubs.

2. Respirometry

General methods. The differential compensated respirometer (Gilson 1963) was used in this study. First- and second-instar larvae were put in 7 ml vials; third-instar larvae, pupae and adults in 30 ml vials. Only one individual was used at a time in each vial furnished with a piece of wet filter paper in order to maintain a high atmospheric humidity and provide a substratum under which the individuals could hide. CO₂ was trapped by 0.3 ml of a 5% KOH solution.

The results are given (a) for respiration (R), in µl of O₂ per hour and per individual, and (b) for respiration rates (ρ SMR, BMR, AMR), in µl of O₂ per hour and per mg (fresh mass) under standard conditions (T = 273 °K, P = 1013 hPa).

The *Standard Metabolic Rate* (or SMR) is the respiration rate of an animal exhibiting a minimum level of movement (Mill 1972); in this paper it is the respiration of an isolated resting individual with an empty stomach. The measurements performed during daylight encouraged the individuals to stay hidden and at rest underneath the piece of wet filter paper.

Influence of stage, body mass and temperature. SMR was measured at 5, 10 and 15 °C in all the developmental stages (except for the eggs) kept under summer conditions. The group of third-instar larvae was heterogeneous: it was composed of a subgroup of younger larvae (100–115 mg) and a subgroup of older larvae (165–180 mg). Extra measurements were performed at 20 and 25 °C in third-instar larvae and adults. The measurements were performed for two hours after a 2-hour period of temperature stabilisation and habituation to the vial. Numbers of replicates are shown in Table 1. The individuals were weighed before and after the measurements.

The respiration ratio, Q_{10} , of an animal under the same conditions but at different temperatures is defined as:

$$Q_{10} = (R_1 / R_2)^{10 / (T_1 - T_2)}$$

where R_1 and R_2 are the respirations at temperatures T_1 and T_2 , respectively.

Influence of acclimation to temperature. Three groups, each of 12 male and 12 female adults kept under summer conditions, were first acclimated for 10 days at a constant temperature of 5, 10 or 15 °C.

If acclimated at 5 °C, their respiration was measured at 5, 10 and 15 °C successively, each time for two hours after a 2-hour period of temperature stabilisation.

If acclimated at 10 °C, their respiration was measured at 10, 5 and 15 °C successively.

If acclimated at 15 °C, their respiration was measured at 15, 10 and 5 °C successively.

Influence of digestion. Twelve male and 12 female adults kept under summer conditions were first starved for two weeks and subsequently fed ad libitum. They were then weighed and their respiration measured daily for six hours at 15 °C for five days.

The *Basal Metabolic Rate* (or BMR) is the respiration rate of an animal exhibiting no movement at all (Hill 1972); in this study it was considered to be the respiration of anaesthetised individuals with an empty stomach. Twelve male and 12 female adults kept under summer conditions were first anaesthetised in chloroform vapour and their BMR measured at 5, 10 and 15 °C. The measurements were interrupted after 60 to 90 minutes when the individuals recovered their movements.

The *Activity Metabolic Rate* (or AMR) is the respiration rate of an animal exhibiting some predetermined level of activity such as walking,... (Hill 1972); in this study it was considered to be the respiration of running individuals with an empty stomach. Twelve male and 12 female adults kept under summer conditions were introduced into respirometric vials, the bottom of which was covered with glass marbles (2 mm in diameter). During the measurements, the vials were shaken in a circular movement that made some of the marbles move, creating an instability and forcing the beetles to run. The measurements were performed at 5, 10 and 15 °C.

Influence of daily cycle (and oxygen partial pressure). The metabolic rate was measured at 15 °C in equal numbers of male and female adults kept under semi-natural conditions. The measurements started at noon (legal summer time \approx 10 a.m. solar time) after a 2-hour period of temperature stabilisation and were run for 24 hours without opening the vials. This led to a regular decrease of the oxygen partial pressure that could be calculated and taken into account. These measurements were performed with 10 individuals in May, 18 in June, 8 in August and 10 in September.

Influence of annual cycle. SMR was measured monthly at 5, 10 and 15 °C on the same six male and five female adults kept under semi-natural conditions.

The *respiratory quotient*, RQ, is the ratio between the number of produced CO₂ moles and consumed O₂ moles:

$$RQ = CO_2 / O_2$$

In order to assess the RQ, SMR was measured at 15 °C in 10 male and 10 female adults kept under summer conditions. The measurements were first performed for two hours with KOH; this was then removed and the measurements were performed again for two hours without KOH.

3. Gravimetry

Adults caught in October 1991 and kept under laboratory conditions (winter conditions for 10 weeks and summer conditions thereafter) until August 1992 (some of them had laid some eggs in the meantime) were first starved for one week. They were then put individually in vials with a saturated water vapour atmosphere and weighed weekly until their death. Four temperatures were experimented: 4, 10, 15 and 25 °C with 11, 10, 11 and 9 individuals, respectively.

Results

Influence of stage and temperature

SMR (ρ) increased with temperature in the range 5–25 °C in all the stages (Table 1 and Fig. 1), but this increase was clearly exponential only in the range 5–15 °C, resulting in linear regressions of $\ln(\rho)$ as functions of temperature (Table 2). First-instar larvae and adults were the most sensitive to changes in temperature ($Q_{10} = 3.0$) whereas pupae were the least ($Q_{10} = 2.1$) (Table 2). Beyond 15 °C, available data for third-instar larvae and adults showed decreasing Q_{10} s (Table 3). The SMR of third-instar larvae and male and female adults were very similar. Although figure 1 suggests that males regularly consumed more oxygen than females, the difference became significant only at 25 °C ($t = 2.3$, $df = 22$, $p < 0.05$).

We were unable to detect egg respiration, which suggests that it was below 1 $\mu\text{l O}_2 \text{ h}^{-1}$ per egg (sensitivity threshold of the respirometer) and hence their $\text{SMR} < 0.14 \mu\text{l O}_2 \text{ mg}^{-1} \text{ h}^{-1}$, even at 15°C. Of course some eggs could have been pooled in a respirometric vial but they were never available simultaneously in large enough numbers.

Table 1. SMR ($\mu\text{l O}_2 \text{ h}^{-1} \text{ FM mg}^{-1}$) for the various developmental stages of *A. ater* at various temperatures (mean \pm standard deviation; n: number of individuals)

Temp (°C)	L ₁	L ₂	L ₃	Pupae	Adult males	Adult females
5	0.160 \pm 0.014 (n = 8)	0.136 \pm 0.016 (n = 12)	0.069 \pm 0.016 (n = 22)	0.035 \pm 0.005 (n = 3)	0.061 \pm 0.014 (n = 12)	0.056 \pm 0.011 (n = 12)
10	0.256 \pm 0.018 (n = 8)	0.198 \pm 0.017 (n = 12)	0.098 \pm 0.037 (n = 22)	0.057 \pm 0.011 (n = 3)	0.105 \pm 0.023 (n = 12)	0.095 \pm 0.036 (n = 12)
	0.487 \pm 0.07 (n = 8)	0.360 \pm 0.056 (n = 12)	0.184 \pm 0.037 (n = 22)	0.075 \pm 0.013 (n = 3)	0.179 \pm 0.016 (n = 12)	0.167 \pm 0.019 (n = 12)
20			0.214 \pm 0.053 (n = 8)		0.275 \pm 0.076 (n = 12)	0.249 \pm 0.065 (n = 12)
25					0.332 \pm 0.024 (n = 12)	0.294 \pm 0.05 (n = 12)

Table 2. Relationships between SMR (ρ , in $\mu\text{l O}_2 \text{ h}^{-1} \text{ FM mg}^{-1}$) and temperature (T, in °C) from 5 to 15 °C for the various stages of *A. ater*

Stage	n	Equation	r ²	Q ¹⁰
First instar larvae		$\ln \rho = 0.110 T - 2.44$	0.927	
Second instar larvae		$\ln \rho = 0.096 T - 2.55$	0.865	
Third instar larvae		$\ln \rho = 0.097 T - 3.25$	0.514	
Pupae		$\ln \rho = 0.076 T - 3.71$	0.805	
Adult male		$\ln \rho = 0.109 T - 3.37$	0.846	
Adult female		$\ln \rho = 0.110 T - 3.48$	0.726	

Table 3. Q_{10} for the various stages of *A. ater* and temperature ranges

Temperature range	L ₁	L ₂	L ₃	Pupae	Adult males	Adult females
5–10	2.18	1.71	2.02	2.65		
10–15	4.26	4.09	3.53	1.73		
15–20			1.35			
20–25						

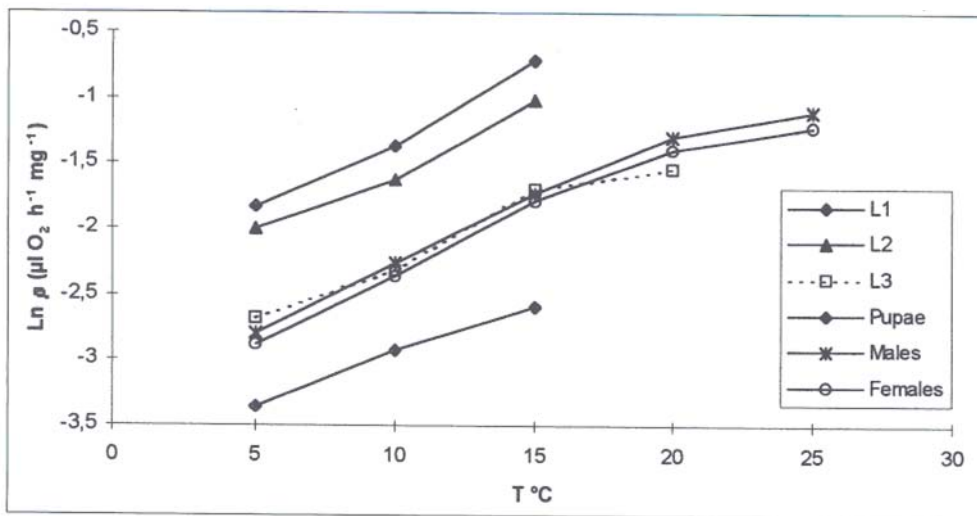


Fig. 1. Semi-log relationships between SMR ($\mu\text{l O}_2 \text{ h}^{-1} \text{ FM mg}^{-1}$) and temperature in the various developmental stages of *A. ater*. Standard deviations (see table 1) are not shown for the sake of clarity

Influence of stage and body mass

All the active stages showed the classical relationship of decreasing SMR with increasing body mass (Table 4, Fig. 2). Pupae had a lower SMR than expected from their body mass (Fig. 3). Individual respiration increased regularly during the beetle life-span except in the pupal stage (Fig. 4).

Influence of daily cycle

No significant difference was found between males and females; therefore all the results were pooled. The four experimental series (May, June, August and September) exhibited the same pattern: a main peak of metabolic rate around 8 p.m. (solar time) (but in September this peak occurred at 11 p.m.), a main minimum around 3 a.m., a secondary peak around 10 a.m. and a secondary minimum around 4 p.m. Thus the four series were combined into a single curve (Fig. 5).

Influence of digestion

The day after being fed ad libitum, the respiration rate of adults was about doubled when compared with SMR. It then decreased until it reached standard metabolism four days later (Fig. 6). Respiration accumulated over the four days including digestion amounted to $5660 \mu\text{l O}_2$, to be compared with standard metabolism over the same period ($3540 \mu\text{l O}_2$). Thus, the digestion of a full meal accounted for a 60% extra respiration.

Table 4. Relationship between SMR ($\mu\text{l O}_2 \text{ h}^{-1} \text{ FM mg}^{-1}$) and body mass (M, in FM mg) for all the active stages of *A. ater* at three temperatures

Temp (°C)	n	Equation	r ²	Q ¹⁰
5	66	$\text{Ln } \rho = -0.338 \text{ Ln } M - 0.428$	0.793	< 0.0001
10	66	$\text{Ln } \rho = -0.285 \text{ Ln } M - 0.354$	0.626	< 0.0001
15	108	$\text{Ln } \rho = -0.330 \text{ Ln } M + 0.005$	0.779	< 0.0001

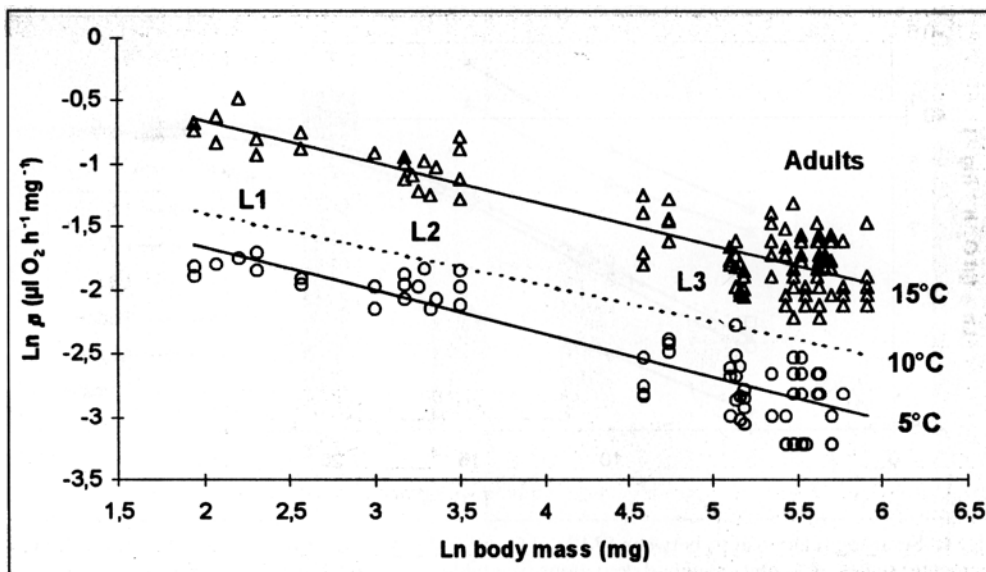


Fig. 2. Relationships between SMR ($\mu\text{l O}_2 \text{ h}^{-1} \text{ FM mg}^{-1}$) and body mass (FM mg) in the various developmental stages of *A. ater* at 5°C (open triangles) and 15°C (open circles); detailed data at 10°C are not plotted for the sake of clarity

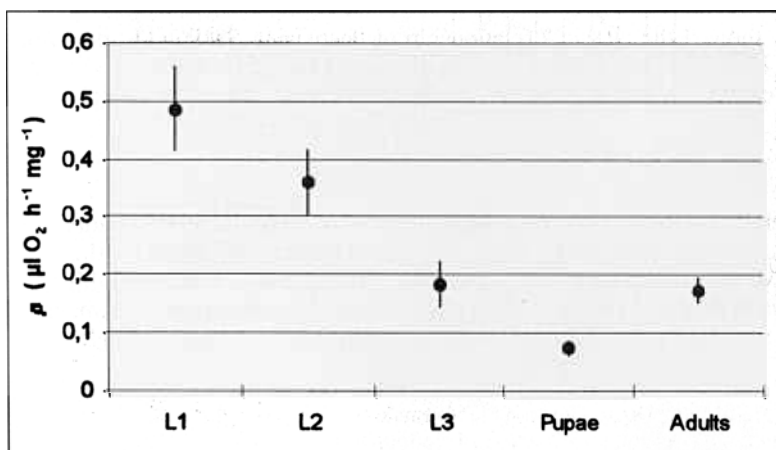


Fig. 3. SMR ($\mu\text{l O}_2 \text{ h}^{-1} \text{ FM mg}^{-1}$) of the various developmental stages of *A. ater* at 15°C (mean \pm standard deviation)

AMR and BMR

The respiration rate when the beetles were forced to run was two to three times higher than SMR and three to six times higher than the basal metabolism of anaesthetised individuals, whose Q_{10} was 2.2 (Fig. 7). Once again we found that males regularly consumed more oxygen than females, but the difference was not significant; all the data were thus pooled.

Influence of acclimation to temperature

In the event of metabolic acclimation, SMR was expected to be higher for individuals kept at lower temperatures. In all cases but one, no metabolic acclimation was found (Fig. 8). SMR at 15°C, however, was found to be higher for adults kept at 15°C than for those kept at lower

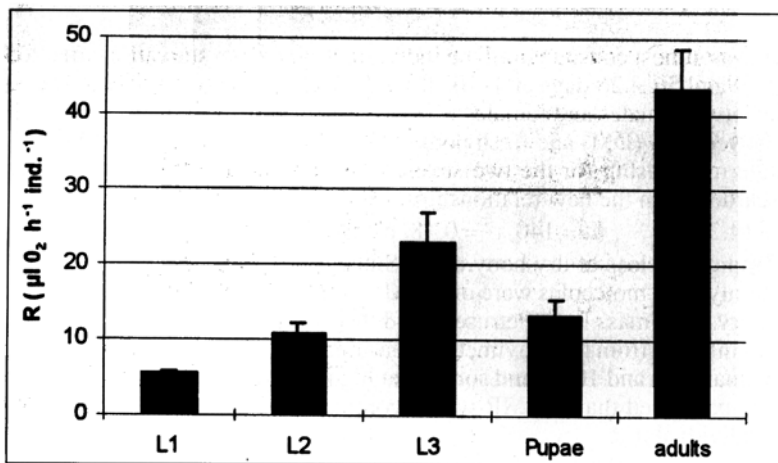


Fig. 4. Individual hourly respiration of the various developmental stages of *A. ater* at 15°C (mean \pm standard deviation)

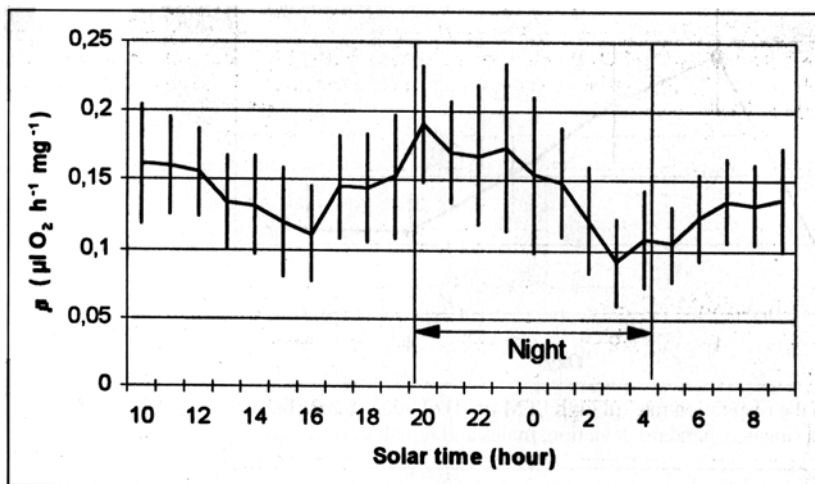


Fig. 5. Circadian cycle of metabolic rate ($\mu\text{l O}_2 \text{ h}^{-1} \text{ FM mg}^{-1}$) of adult *A. ater* (mean \pm standard deviation, four experimental series and males and females combined). Hours are mentioned in solar time; night length is an average of the four series

temperatures (ANOVA, 2 and 71 df, $p = 0.008$), which was unexpected. The difference was induced by males only (there was no difference in females).

Influence of annual cycle

At any of the reference temperatures, a clear tendency emerged: SMR was higher during summer and lower during the period of hibernation (Fig. 9). Variations in SMR actually paralleled those of monthly average temperature ($r^2 = 0.86, 0.71$ and 0.86 at $5, 10$ and 15°C , respectively). Once again we found that males regularly consumed more oxygen than females, but the difference was not significant; all the data were thus pooled.

Respiratory quotient

The respiratory quotient, RQ, was 0.715 ± 0.046 (mean (standard deviation), suggesting that mainly lipid molecules were oxidised. Once again we found that males regularly consumed more oxygen than females, but the difference was not significant.

Gravimetry

The loss of fresh mass was almost constant until the individuals died from starvation after 265 ± 33 , 157 ± 25 , 99 ± 29 and 56 ± 26 days at 4, 10, 15 and 25°C, respectively. There was no significant difference between males and females.

The relationship between dry (DM) and fresh body mass (FM) (Chaabane et al 1997) was recalculated as a single relationship for the two sexes (four individuals weighing less than 175 mg FM were discarded from the new relationship) :

$$DM = 0.325 FM + 14.24 \quad (n = 140, r^2 = 0.48, p < 0.001)$$

This enabled us to compute the loss of dry body mass. Since it was assumed from the respiratory quotient that mainly lipid molecules were oxidised, we used a respiration equivalent of 2.04 ml O₂ per mg of dry body mass loss (Petruszewicz & Macfadyen 1970).

The respiration rates inferred from the gravimetric measurements were fairly close to those of anaesthetised individuals at 5 and 10 °C and somewhat higher at 15°C (Fig. 10). The curve obtained by gravimetry paralleled that of SMR with a comparable Q₁₀ of 3.1 (Q₁₀ was only 2.2 for anaesthetised individuals).

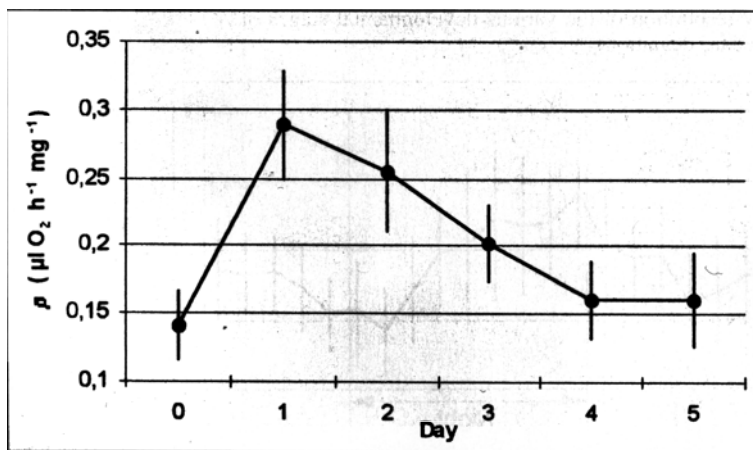


Fig. 6. Changes in the respiration rate ($\mu\text{l O}_2 \text{ h}^{-1} \text{ FM mg}^{-1}$) of adult *A. ater* before and after a full meal (mean \pm standard deviation, males and females combined)

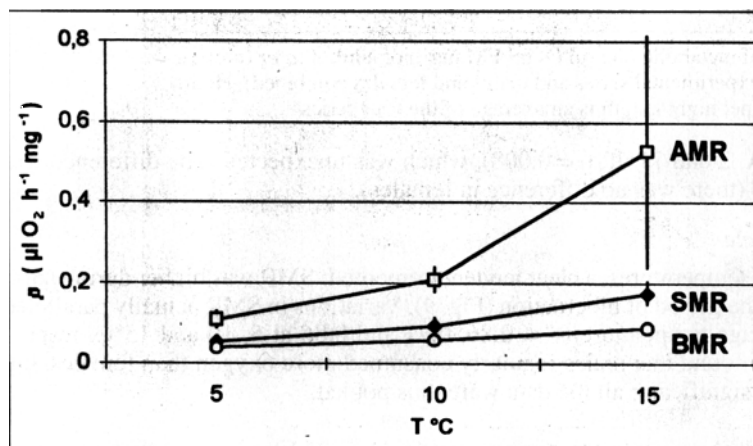


Fig. 7. Respiration rate ($\mu\text{l O}_2 \text{ h}^{-1} \text{ FM mg}^{-1}$) of adult *A. ater* at rest (SMR), running (AMR) and anaesthetised (BMR) at 5, 10 and 15 °C (mean \pm standard deviation, males and females combined)

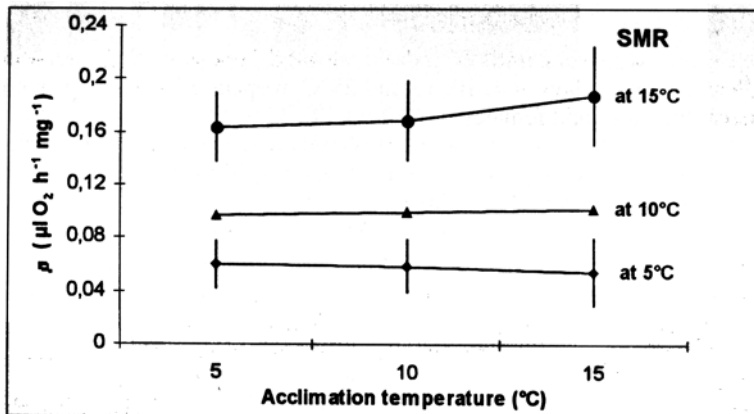


Fig. 8. SMR ($\mu\text{l O}_2 \text{ h}^{-1} \text{ FM mg}^{-1}$) of adult *A. ater* after being acclimated at 5, 10 or 15 $^{\circ}\text{C}$ (mean \pm standard deviation, males and females combined, standard deviations not shown at 10 $^{\circ}\text{C}$ for the sake of clarity)

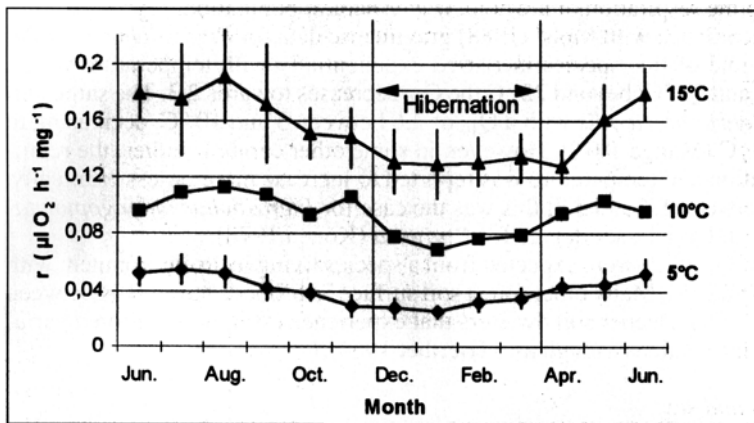


Fig. 9. SMR ($\mu\text{l O}_2 \text{ h}^{-1} \text{ FM mg}^{-1}$) of adult *A. ater* under standard conditions at 5, 10 and 15 $^{\circ}\text{C}$ over a full annual cycle (mean \pm standard deviation, males and females combined, standard deviations not shown at 10 $^{\circ}\text{C}$ for the sake of clarity)

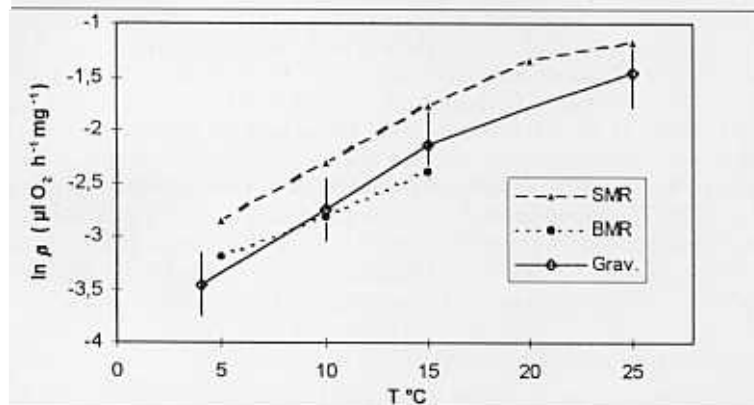


Fig. 10. Semi-log relationships between respiration rates ($\mu\text{l O}_2 \text{ h}^{-1} \text{ FM mg}^{-1}$) and temperature: comparison between SMR, BMR (anaesthetised individuals) and respiration rate derived from gravimetry of starved *A. ater* adults (males and females combined, mean \pm standard deviation)

Discussion

Influence of temperature

Most of our measurements were performed at 5, 10, 15 (and 20) °C which is in the range of temperature experienced by *A. ater* during its nocturnal activity at the soil surface in the beechwood at Lembeek. The activity of adult *A. ater* occurs from early April to late October and seems only limited by a lower threshold temperature of 7 °C (weekly average) (Loreau 1983a). The preferred temperature of *A. ater* ranges between 9.7 and 20.6 °C (Van Heerd 1950). The weekly average temperature never exceeded 19°C at the soil surface in our semi natural rearing, with peaks of no more than 24 °C in the afternoon, but at that moment, the beetles were hidden in deeper layers where the temperature was probably lower.

In our work, SMR (metabolism of resting individuals with an empty stomach) increased exponentially with temperature between 5 and 15 °C (with Q_{10} between 2.1 and 3.0 depending on the stage) and tended to increase less than exponentially at higher temperatures. Therefore the semi-log descriptive relationships (Table 2) can be used with confidence as predictive tools in the range 5–15 °C and with an increasing overestimation between 15 and 20 °C (the error reaches 12 % in excess at 20 °C). They were used in a previous paper (Chaabane et al 1996) for calculating the respiration of a whole *A. ater* natural population.

Our results are in accordance with Mols' (1988) gravimetric data for *Pterostichus coerulescens*. The respiration rate of this species increased exponentially with temperature with a Q_{10} of 3.0 between 12 and 22 °C; beyond 22 °C the Q_{10} decreases towards 2.3. The same tendency was found for *Nebria brevicollis* with a Q_{10} of 2.6 between 5 and 10 °C, decreasing to 1.9 between 15 and 20 °C (Manga 1972). However, in some other carabid studies, the relationship between respiration and temperature was reported to increase more or less erratically, with Q_{10} 's fluctuating between 1.1 and 5.8; this was the case for *Pterostichus oblongopunctatus* (Weidemann 1972) and to a lesser degree for *P. nigrita* (Könen 1978).

Rather high values of Q_{10} (> 2) were expected from a species living in an environment with damped temperature variations. Many other forest soil surface arthropods have Q_{10} s between 2.2 and 3.6 (Altmüller 1979). Deeper soil dwellers that experience even more buffered variations of temperature exhibit values as high as 5 (Berthet 1964).

Influence of body mass and sex

SMR was high in young larvae and decreased afterwards, following the classical relationship between body mass and metabolism as in *Nebria brevicollis* (Manga 1972). This work shows that a single relationship works for all the active stages (pupae and probably also eggs have a lower than expected SMR).

In most respirometric studies on carabid beetles there was no significant difference between males and females; no sexual influence was mentioned for *Pterostichus nigrita* and *P. oblongopunctatus* (Könen 1978), for *Harpalus pubescens* (Kabacik & Steygwillo 1971) and for *P. coerulescens* (Mols 1988). However, Manga (1972) found that the respiration rate of males was higher than that of females during the breeding season in *Nebria brevicollis*. In this work we regularly measured higher SMR in males than in females. Although the difference was significant only once at 25 °C, the repeated slight differences suggest that they could become significant if more measurements were performed. However, this should not necessarily be linked with sex. Males are significantly lighter than females; therefore the relationship between SMR and body mass could explain the difference between males and females.

Influence of daily cycle and oxygen partial pressure

No periodicity in respiration was observed during the circadian cycle in *Nebria brevicollis* (Manga 1972). In this work the observed cycle was clear-cut, with a metabolic rate varying between 0.09 and 0.19 $\mu\text{l O}_2 \text{ mg}^{-1} \text{ h}^{-1}$, a proportional variation that is almost as high as that between SMR and AMR. The observed periodicity is roughly in accordance with the fact that *A. ater* is a nocturnal species with its activity cycle peaking during the first four or five hours

of the night (Thiele & Weber 1968). However, this species has no known diurnal activity that might account for the secondary respiration peak around 10 a.m.

No information is available on the influence of partial oxygen pressure on the respiration of carabid beetles. In this study this parameter can be taken into account and its influence estimated from the circadian cycle measurements.

In figure 11 it can be seen that there was a decreasing trend in the metabolic rate over a daily cycle: it was 23 % lower at 10 a.m. on the second day than at 10 a.m. on the first day. Since the vials were left closed during the 24-hour experiments, a decrease of oxygen partial pressure must have occurred. For an average adult of 260 mg, the partial pressure of oxygen calculated hour by hour must have decreased from 209 to 185 hPa (a partial pressure of saturating water vapour of 17 hPa at 15°C was taken into account in the calculation), a 11.5 % decrease (Fig. 11). It is likely that the decrease in the metabolic rate was due to this decrease in oxygen partial pressure, although we have not experimentally tested this hypothesis. Assuming that the metabolic rate is related linearly to oxygen partial pressure (i.e. *A. ater* is considered as a „conformer“), we rectified the data and plotted the expected metabolic rate as if oxygen partial pressure had remained constant at 209 hPa (Fig. 11).

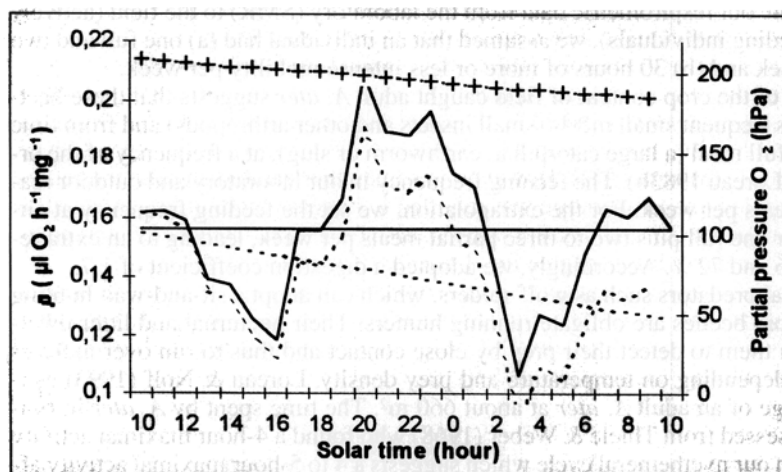


Fig. 11. Original (dotted curve) and rectified (solid curve) circadian cycles of metabolic rate ($\mu\text{l O}_2 \text{ h}^{-1} \text{ FM mg}^{-1}$) in adult *A. ater* (hours are mentioned in solar time). Rectification consisted in making horizontal the linear trend (solid straight line) that was initially decreasing (dotted straight line). The top line (+++++) shows the decrease in partial oxygen pressure

Influence of annual cycle

Obvious differences were found in the respiration rates of prediapausing (June–July) and reproductive (September) adult *Nebria brevicollis* at 15 °C, with ratios of 1.55 and 1.84 for females and males, respectively (Manga, 1972). But *Nebria brevicollis* is a rather short-lived species; no data have been gathered before for a long-lived species such as *A. ater*. In our study, the ratios between summer and winter SMR were of the same order of magnitude : 1.69, 1.40 and 1.37 at 5, 10 and 15 °C, respectively.

Influence of digestion

Short-term starvation does not influence respiration in carabid beetles; as with many other predators, they can withstand long periods without food (Mols 1988). On the other hand it is known that the metabolic costs of digestion are important (Brafield & Llewellyn 1982), even though a significant part of the extra respiration might be due to an increased metabolism of the gut microflora rather than of the host (Kiffer & Benest 1981).

In this work we found that the respiration rate was increased by a factor of 2 the day after a meal and digestion of a full meal accounted for a 60 % extra respiration. These results agree roughly with Ernsting & Isaaks (1987, 1988), who reported a 30 % increase in the respiration rate of *Notiophilus biguttatus* during its digestion. Koehler (1976) claimed that the respiration rate of *Pterostichus oblongopunctatus* was multiplied by four to six after a meal, which seems unrealistically high (although this increase was not integrated over the whole digestion process).

Activity metabolic rate

Grüm (1980) showed that the activity metabolic rate (AMR) of *Pterostichus niger* and four *Carabus* species was three to five times higher than their SMR. This is consistent with our results: the respiration rate of running individuals was three times higher than that of resting individuals (and up to six times higher than that of anaesthetised ones).

Extrapolation to field conditions

In order to extrapolate our respirometric data from the laboratory (SMR) to the field (actively prey seeking and feeding individuals), we assumed that an individual had (a) one full and two partial meals per week and (b) 30 hours of more or less intense mobility per week.

The examination of the crop content of field caught adult *A. ater* suggests that these beetles have more or less frequent small meals (small insects and other arthropods) and from time to time by chance a full meal (a large caterpillar, earthworm or slug), at a frequency of the order of once a week (Loreau 1983b). The feeding frequency in our laboratory and outdoor rearing was two full meals per week. For the extrapolation, we set the feeding frequency at either two full meals or one full plus two to three partial meals per week, leading to an extra respiration between 66 and 72 %. Accordingly, we adopted a digestion coefficient of 1.7.

Contrary to diurnal predators such as wolf spiders, which can adopt a sit-and-wait hunting strategy, forest carabid beetles are obligate running hunters. Their nocturnal and litter-dwelling habits constrain them to detect their prey by close contact and thus to run over more or less long distances depending on temperature and prey density. Loreau & Nolf (1993) estimated the home range of an adult *A. ater* at about 660 m². The time spent by *A. ater* in running activity was assessed from Thiele & Weber (1968) who found a 4-hour maximal activity after sunset and from our nycthemeral cycle which suggests a 4 to 5-hour maximal activity after sunset. For the extrapolation, we fixed a duration of 30 hours of mobility per week, that is, five hours per night for six days and one day without running activity (following the full meal). During this time, the respiration rate is multiplied by three, which leads to an extra respiration of 36 %. Accordingly, we adopted a mobility coefficient of 1.36.

Multiplying the digestion coefficient by the running coefficient provides a general activity coefficient of 2.3 to be used in the extrapolation to field conditions during the active part of the annual cycle, from April to November.

Error analysis

This study exemplifies the complexity of respiration and thus the difficulty in extrapolating laboratory measurements to field populations or even to a general energy budget in the laboratory. In this section, we attempt to quantify the errors that would be made if only simplified measurements had been taken into account. By 'simplified measurements' we mean that only the influences of temperature and body mass are taken into account, as is often the case in laboratory studies, but not other parameters such as digestion, mobility, daily and annual cycles, and oxygen partial pressure.

The influence of *digestion* has already been discussed: neglecting this parameter would probably result in an *underestimation* of respiration of about 70 %.

The influence of *mobility* has also been discussed: neglecting this parameter would probably result in an *underestimation* of about 36 %.

Daily cycle: since most of the measurements are generally taken between 9:00 a.m. and 5:00 p.m. (legal summer time, that is between 7 a.m. and 3 p.m. solar time), which is a consequence of the human circadian rhythm, both the main peak and the main minimum of *A. ater* respiration would be missed. By chance, however, they would balance each other if one extrapolates the day-time measurements to the whole daily cycle, and the resulting error in this case is a *negligible underestimation* (< 3 %).

Acclimation: *A. ater* exhibits no sensitivity to temperature acclimation. Therefore this parameter can be neglected with no detectable *error*.

Annual cycle (acclimatisation effect): *A. ater* is a species that is active from April to November with a maximum from June to September. If respirometric measurements were performed only at peak activity in *June – September*, the extrapolation to the whole year would result in an *overestimation* of 16 %, negligible errors would result from measurements performed in May, October or November, and an underestimation of about 9 % would result from measurements made in April.

Oxygen partial pressure: since the Gilson respirometer was used between two and four hours after closing the vials, the average oxygen partial pressure during measurements was probably reduced at 205 hPa (instead of 209 hPa). This could have reduced the beetles' respiration. Adult *A. ater*, however, hunt their prey at the soil surface or in the litter layer, where oxygen partial pressure may be closer to that of the respirometer than that of the open atmosphere, and resting adults as well as larvae (whether active or at rest) are found in deeper litter layers or shallow mineral soil where oxygen partial pressure could be even lower depending on temperature and rainfall. Therefore the *error* is probably *negligible*.

Carbon dioxide partial pressure: since the Gilson respirometer works with virtually no carbon dioxide in the respirometric vials, whereas it can reach concentrations as high as 2 or 3 % in the soil, depending on temperature and rainfall, it seems reasonable to admit that the measured respiration can be an *unknown overestimation* of the actual field respiration.

Water vapour is an important parameter for most forest carabids and a deficit of humidity could increase the beetles' respiration (Barton-Browne 1964) leading to an unknown overestimation of the actual field respiration; its influence, however, *can be neglected* in this study since the piece of wet paper in the respirometric vials must have maintained water vapour near saturation.

Finally, once temperature, body mass and life stage have been accounted for, the most important known sources of error in the assessment of *A. ater* respiration are the underestimations linked with digestion and mobility, which together require SMR to be multiplied by a factor 2.3 during the whole period of activity; secondly comes the change induced by the annual cycle. Our respiration estimates with all the required correction factors were used to establish complete energy budgets (Chaabane et al. 1996) both for the full life span of an individual (two years) and for a natural population. These budgets showed the quantitative importance of respiration in both cases (respectively 74 and 72 % of total energy processed), and they were balanced, suggesting that the main factors affecting respiration were successfully taken into account.

References

- Altmüller, R. (1979) Untersuchungen über den Energieumsatz von Dipterenpopulationen im Buchenwald (*Luzulo-Fagetum*). *Pedobiologia* 19, 245–278.
- Berthet, P. (1964) L'activité des Oribatides (Acari, Oribatei) d'une chênaie. *Mémoires de l'Institut Royal des Sciences Naturelles de Belgique* 152, 1–152.
- Barton-Browne, L. B. (1964) Water regulation in insects. *Annual Review of Entomology* 9, 63–72

- Brafield, A. E., Llewellyn, M. J. (1982) Animal energetics. Blackie, Glasgow, London.
- Chaabane, K., Loreau, M., Josens, G. (1996) Individual and population energy budgets of *Abax ater* (Coleoptera, Carabidae). *Annales Zoologici Fennici* 33, 97–108.
- Chaabane, K., Loreau, M., Josens, G. (1997) Growth and egg production in *Abax ater* (Coleoptera, Carabidae). *Pedobiologia* 41, 385–396.
- Ernsting, G., Isaaks, J. A. (1987) Effects of food intake and temperature on energy budget parameters in *Notiophilus biguttatus* (Coleoptera, Carabidae). *Acta Phytopathologica et Entomologica Hungarica* 22, 135–145.
- Ernsting, G., Isaaks, J. A. (1988) Reproduction, metabolic rate and survival in a carabid beetle. *Netherlands Journal of Zoology* 38, 46–60.
- Gilson, W. E. (1963) Differential respirometer of simplified and improved design. *Science* 141, 531–532.
- Grüm, L. (1980) Methods of approximate estimation of energy flow through carabid populations. *Ekologia Polska* 28, 129–149.
- Kabacik, W. D., Steygwill, B. L. (1971) Starvation and the average survival time of Carabidae. *Ekologia Polska* 19, 419–425.
- Kiffer, E., Benest, G. (1981) Microflore du tractus digestif chez *Abax ater* (Coleoptera, Carabidae). *Revue d'Ecologie et de Biologie du Sol* 18, 567–578.
- Koehler, H. (1976) Nahrungsspektrum und Nahrungsumsatz zweier Carabiden des Solling, *Pterostichus oblongopunctatus* (F) und *Pterostichus metallicus* (F). Diplomarbeit Göttingen.
- Könen, J. (1978) Physiologisch-ökologische Untersuchungen zur Steuerung der Gonadenreifung und Fortpflanzungsperiodik von *Pterostichus oblongopunctatus* (F) (Coleoptera, Carabidae) in Abhängigkeit von Temperatur, Fotoperiode und Juvenilhormon. Inaugural-Dissertation der Universität zu Köln.
- Loreau, M. (1983a) Les niches écologiques des Carabides en milieu forestier à Lembeek (Belgique). Unpublished Ph.D. thesis, Université Libre de Bruxelles, 303 pp.
- Loreau, M. (1983b) Le régime alimentaire de *Abax ater* Vill. (Coleoptera, Carabidae). *Acta Oecologica, Oecologia Generalis* 4, 253–263.
- Loreau, M. (1984) Composition et structure de trois peuplements forestiers de Carabides. *Académie royale de Belgique, Bulletin de la Classe des Sciences* 70, 125–160.
- Loreau, M., Nolf, C. L. (1993) Occupation of space by the Carabid beetle *Abax ater*. *Acta Oecologica, Oecologia Generalis* 14, 247–258.
- Manga, N. (1972) Population metabolism of *Nebria brevicollis* (F) (Coleoptera, Carabidae). *Oecologia* 10, 223–242.
- Mill, P. J. (1972) Respiration in the invertebrates. Macmillan St Martin's Press, London. 212 pp.
- Mols, P. J. M. (1988) Simulation of hunger, feeding and egg production in the carabid beetle *Pterostichus coerulescens* (L) (= *Poecilus versicolor* Sturm). *Agricultural University Wageningen Papers*. 88–3, Veenman B V, Wageningen.
- Petrusewicz, K., Macfadyen, A. (1970) Productivity of terrestrial animals. Principles and methods (IBP Handbook Nr. 13) Blackwell, Oxford.
- Phillipson, J. (1963) The use of respiratory data in estimating annual respiratory metabolism, with particular reference to *Leiobunum rodundum* (Latr.) (Phalangiida). *Oikos* 14, 212–223.
- Thiele, H. U. (1968) Zur Methode der Laboratoriumszucht von Carabiden. *Decheniana* 120, 335–341.
- Thiele, H. U., Weber, F. (1968) Tagesrhythmen der Aktivität bei Carabiden. *Oecologia* 1, 315–355.
- Van Heerd, P. F. (1950) The temperature and humidity preferences of certain coleoptera. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen* 53, 347–360.
- Weidemann, G. (1972) Die Stellung epigäischer Raubarthropoden im Ökosystem Buchenwald. *Verhandlungsbericht der Deutschen Zoologischen Gesellschaft* 65, 106–116.
- Wightman, J. A. (1981) Why insect energy budgets do not balance. *Oecologia* 50, 166–169.
- Zinkler, D. (1972) Factors affecting metabolic activities. *Symposium on Soil fauna and decomposition processes, Leuven* 18–20 juillet 1972.