Physiological adaptations in Coleoptera on Spitsbergen

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Metabolic rates and Q_{10} values were determined for three species of Spitsbergen Coleoptera, *Amara quenseli*, *Simplocaria metallica* and *Rhynchaenus flagellum*. The beetles had metabolic rates which were elevated compared to values of Coleoptera from other regions. This is interpreted as an adaptation to the prevailing low temperatures and short activity period on Spitsbergen.

A. quenseli had rates of water loss comparable to values of beetles in temperate and tropical xeric habitats, indicating that the habitat of the beetles on Spitsbergen at least occasionally is xeric.

Determination of cold-hardiness parameters such as supercooling point and haemolymph melting point of *A. quenseli* beetles revealed that the beetles had values corresponding to those of active insects in the temperate and tropical region. They had no thermal hysteresis factors. Thus, during summer they show no physiological adaptations to cold.

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The Spitsbergen area is characterized by long winters and short summers. The season for biological reproduction is generally from medio June to ultimo August. The air temperature during this period rarely exceeds 10°C.

These extreme climatic features are likely to require physiological adaptations. Such adaptations have been demonstrated through numerous studies on terrestrial mammals and birds (Krog et al. 1976; Grammeltvedt & Steen 1978; Ringberg 1979). The physiological adaptations in terrestrial invertebrates have been given only little attention by investigators. Aunaas et al. (1983) investigated several species of insects and arachnids from Spitsbergen, and found that the Spitsbergen arthropods have metabolic rates higher than those of animals from other regions. However, in spite of the prevailing low summer temperatures, the animals displayed few adaptations to cold.

The purpose of the present study was to investigate possible metabolic adaptations in different species of beetles on Spitsbergen. Physiological parameters associated with cold-hardiness were also studied.

Materials and methods

The investigations were carried out on beetles collected in the Kongsfjorden area of Spitsbergen from the end of July to early August 1985.

Four specimens of *Amara quenseli* (Carabidae) and one specimen of *Simplocaria metallica* (Byrrhidae) were found under stones beneath the rookery at Ossian Sars mountain. A total of 11 specimens of *Rhynchaenus flagellum* (Curculionidae) was found in vegetation of *Salix polaris* on Gerd-øyane and beneath stones at Ossian Sars mountain. The animals were kept in small glass tubes at 5–7°C, and used in the experiments during the following six days. The experiments were carried out in the laboratory facilities at the research station of the Norwegian Polar Institute in Ny Ålesund.

The oxygen consumption of the *A. quenseli* beetles was measured with Engelmann constant pressure respirometers as described by Aunaas et al. (1983). The oxygen consumption of the other species, which were considerably smaller than the *A. quenseli* beetles, was measured in micro respirometers developed and described by Husby (1982) (Fig. 1). One animal was used in each respirometer.

The weight of the beetles was measured on a Mettler analytical balance, which was exact on level ±0.1 mg. Due to the low weight of the *R. flagellum* beetles, nine specimens were weighed together and their average weight used. Visually, the beetles seemed to be of the same size.

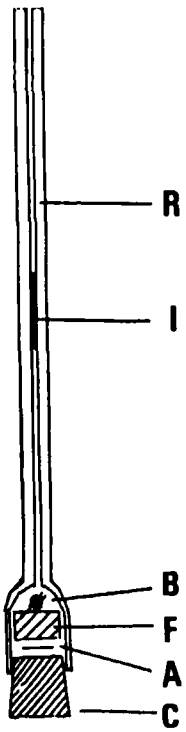

Fig. 1. Micro respirometer used to measure oxygen consumption of the smallest beetles. R: Glass capillary. I: Indicator fluid. B: Beetle. F: Piece of foam rubber. A: Filter paper moistened with a 10% solution of KOH for absorption of CO_2. C: Rubber stopper. To stabilize the temperature, the respirometers were immersed in a water bath. The rate of oxygen consumption of the beetles was indicated by the rate at which the indicator fluid moved down the capillary.

The values of oxygen consumption were calculated at STPD by multiplying the observed values by the factor

$$\frac{(P_{atm} - P_{H_2O}) \cdot 273\ K}{T_A \cdot 760\ mm\ Hg}$$

where P_{atm} is the local barometric pressure, P_{H_2O} the vapour pressure and T_A the temperature at which the oxygen consumption was measured. The values of barometric pressure were taken from records at the meteorological station in Ny Ålesund.

Rates of transpiratory water loss and adaptations to cold were investigated only on *A. quenseli* beetles, in that the other species were too small to allow exact weighing and sampling of body fluid.

In order to measure the rate of transpiratory water loss, *A. quenseli* beetles were kept at 20°C inside a desiccator, where the relative air humidity was kept close to zero by means of silica gel. A temperature of 20°C was used in order to allow comparison with water loss data obtained at this temperature for insects from other climatic regions. The beetles were weighed at known intervals, and the rate of weight loss was taken as a measure of the rate of water loss. In order to make this an exact measure, the beetles were kept without food for 5 days prior to the experiments. During this period they were kept at a high relative humidity to prevent excessive dehydration prior to the experiment.

The supercooling points of the carabids were determined by cooling one at a time while kept in intimate contact with a thin thermocouple probe connected to a Fluge digital thermometer. The freezing of the insects was indicated by a sudden rise in temperature, due to the release of heat of fusion of freezing water. The lowest temperature recorded prior to the rise in temperature was taken as the supercooling point. To ensure slow cooling, the tube containing the animal was placed inside a thermos, which was transferred to a deep freezer. The temperature was recorded manually every 30 seconds.

Samples of body fluid were obtained and the melting point and presence of thermal hysteresis factors (THF) investigated on a Clifton nanolitre osmometer as described by Aunaas et al. (1983).

Results

The values of oxygen consumption of the respective beetles are given in Table 1 and plotted against the temperature in Fig. 2. As the temperature increases, there is a marked increase in the rates of oxygen consumption, and as shown in Table 2, the Q_{10} values of the three species range between 2.1 and 3.2.

In order to study the temperature dependence of the metabolic processes in greater detail, the data are plotted in an Arrhenius plot (Fig. 3). The Arrhenius plot is based on the Arrhenius equation

$$M = a \cdot e^{-\mu/(R \cdot T)}$$

where M is the metabolic rate (measured as oxygen consumption), a is a constant, μ is the activation energy, R is the universal gas constant and T is the absolute temperature in K. The Arrhenius equation can be expressed as $\ln M = \ln a - (\mu/R)(1/T)$, where ln M and 1/T are used directly

Table 1. Values of body weight and metabolic rates* at different temperatures of three species of Coleopterans from Spitsbergen.

Body weight (g)	Temperature (°C)						
	4.2		9.2		12.6	21.5	
Amara quenseli:							
0.0156	3.04		3.85		5.03	10.6	
0.0153	3.99		5.70		9.35	15.8	
0.0150	3.77		4.47		7.78	13.9	
0.0160	4.06		3.90		4.95	10.4	
	0		7.1		12.4	21.0	
Simplocaria metallica:							
0.00285	2.06		5.43		11.5	22.4	
	0	7.1	8.8	12.4	14.4	19.9	21.0
Rhynchaenus flagellum:							
0.00051	3.6	23.0	—	24.3	—	—	47.5
0.00051	2.5	—	9.8	—	19.6	34.2	—
0.00051	5.5	—	11.7	—	18.7	46.0	—
0.00051	1.3	—	13.8	—	4.7	23.3	—

* Metabolic rates are given as mm^3 O_2/min · g body weight.

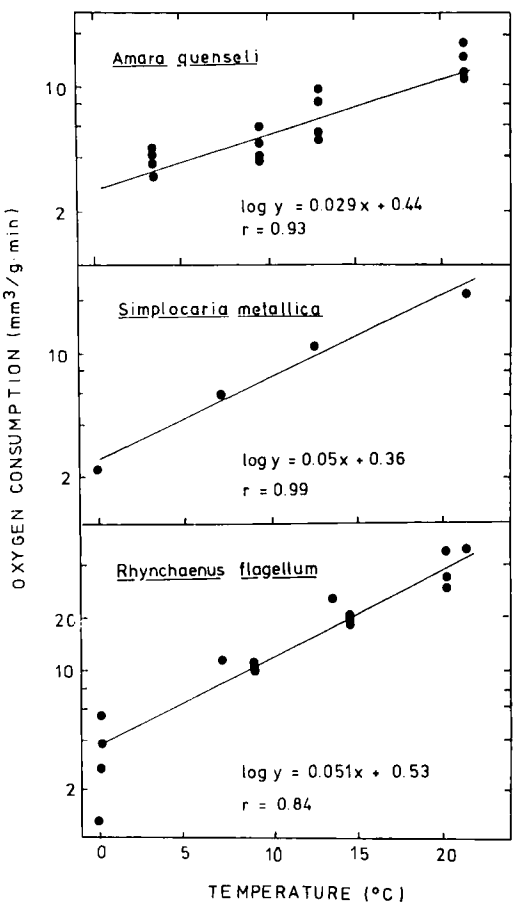

Fig. 2. Rates of oxygen consumption of three species of beetles from Spitsbergen, plotted as a function of temperature. Scale on ordinate is logarithmic.

in the plot as they are linearly related variables. ln a and $-\mu/R$ represent the ordinate interception point and the slope of the line, respectively, and can be determined by calculating the linear regression line of ln M and 1/T. The activation energy μ is calculated by multiplying the slope of the line by the negative value of the universal gas constant (1.98 cal/mol·K). The estimated values of activation energy are given in Table 2.

The data in Table 2 reveal that the activation energy of the metabolic process of the beetles ranges from 12.0 to 18.5 kcal/mol.

The rate of water loss as determined for two *A. quenseli* beetles is shown in Table 3. The data show that the *A. quenseli* beetles have an average rate of water loss of 0.82 per cent of the body weight per hour.

The experiments revealed that the *A. quenseli* beetles had supercooling points of -7.3 ± 0.1°C, while the melting point of their haemolymph was

Table 2. Estimated values of Q_{10} and activation energy of Coleopterans from Spitsbergen. Correlation coefficients of the regression lines in the Arrhenius plots in Fig. 3 are shown in column r, and the number of beetles measured are listed in column n.

Species	Q_{10}	Activation energy (kcal/mol)	r	n
Amara quenseli	2.1	16.0	−0.93	4
Simplocaria metallica	3.1	12.0	−0.99	1
Rhynchaenus flagellum	3.2	18.5	−0.84	4

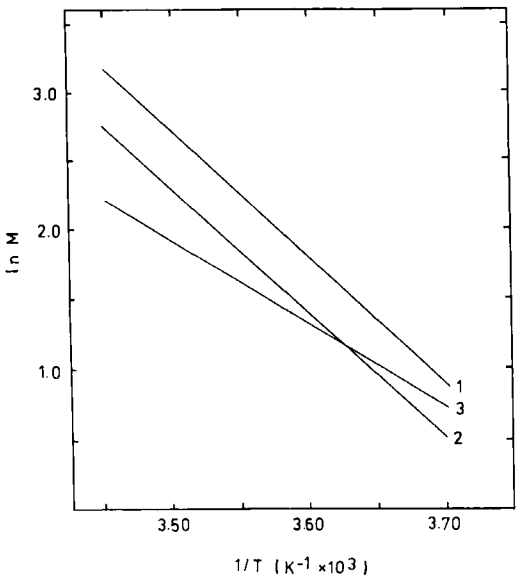

Fig. 3. Arrhenius plot of metabolic data of three species of beetles from Spitsbergen: 1. *Rhynchaenus flagellum*, 2. *Simplocaria metallica*, 3. *Amara quenseli*. For further information see text.

-0.85 ± 0.01°C. Investigations of thermal hysteresis gave hysteresis freezing points equal to the respective melting points, implying that THFs were not present in the body fluid of the *A. quenseli* beetles.

Discussion

The present data allow comparisons to be made between respiratory rates of Coleoptera from Spitsbergen and corresponding rates of Coleoptera from other regions. Of particular interest are comparisons between values of Spitsbergen animals and animals from temperate alpine areas, in that the same species are frequently distributed in both high arctic regions and in temperate regions. Since even tropical alpine areas may offer low temperatures, data from beetles in such biotopes have also been included.

Comparative studies of this kind are complicated by the fact that the metabolic rate is strongly affected by factors like body size (Schmidt-Nielsen 1972) and phylogeny (Zachariassen et al. 1987). For this reason such comparisons should preferably be undertaken between species of about the same body weight and of the same family. Thus, the respirometry data of the carabid species from Spitsbergen are being compared with those of carabids from the Finse area on Hardangervidda high mountain plateau in southern Norway, and with data of subantarctic carabids from South Georgia. Data of the Spitsbergen curculionids are compared with corresponding data of curculionids from Finse, Mount Kenya and the Andes Mountains in Venezuela. Unfortunately, no literature data are available for byrrhid beetles, and thus, comparisons between byrrhids from different regions could not be made.

Fig. 4 shows the metabolic activities of carabid beetles from different regions. The figure shows that at all temperatures the *Amara quenseli* beetles from Spitsbergen have oxygen consumption rates which are considerably higher than those of carabids from the other areas. Fig. 4 also shows that a correspondingly marked difference exists between the metabolic rates of the Spitsbergen curculionids and the curculionids from the temperate and tropical regions. All carabids in Fig. 4 have about the same body weight (Zachariassen unpublished results), implying that the values are suitable for direct comparisons. However, the Spitsbergen curculionids have body weights which are considerably lower than those of the other curculionids represented in Fig. 4, but the difference in body weight can explain only a minor part of the elevated metabolic rate of the curculionids from Spitsbergen (Zachariassen unpublished results).

Comparisons of the data in Figs. 2 and 4 show that even the byrrhid beetles from Spitsbergen have oxygen consumption values above those of the temperate alpine carabids and the temperate and tropical curculionids, indicating that even these beetles have oxygen consumption rates above those of beetles from other regions.

The present results are in agreement with the

Table 3. Body weights (mg) of two *Amara quenseli* beetles kept for different periods of time in a dry atmosphere at 20°C. The corresponding percentages of weight loss (related to initial weight) are given in parentheses, and the average rate of weight loss (± S.D.) is given under b.

Beetle no.	Time (hours) 0	8.5	18.2	b (%/hour)
1	15.2	14.4 (5.3)	13.6 (10.5)	0.82 ± 0.33
2	17.3	15.6 (9.8)	14.0 (19.1)	

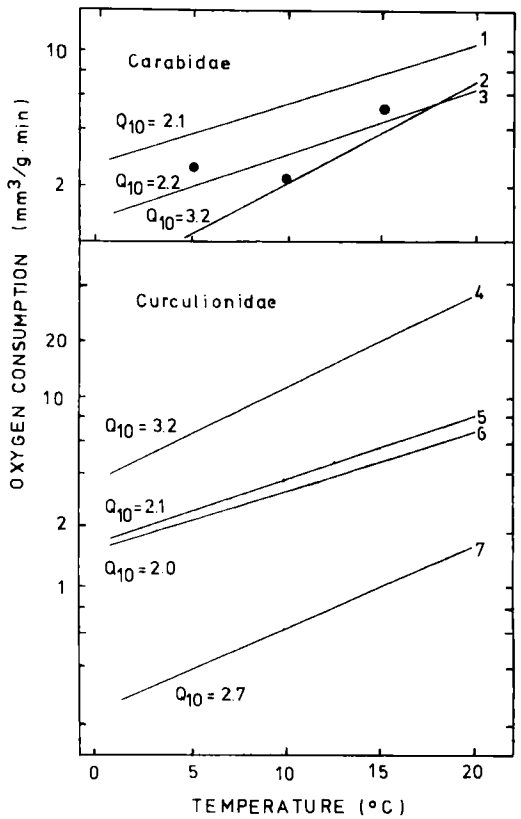

Fig. 4. Linear regression lines of values of oxygen consumption as a function of temperature of beetles from Spitsbergen and other regions. Ordinate scale is logarithmic. 1. *Amara quenseli* from Spitsbergen (present study), 2. *Pelophila borealis* from Finse, Norway (Conradi-Larsen & Sømme 1973), 3. *Amara alpina* from Finse, Norway (Hågvar & Østbye 1974), 4. *Rhynchaenus flagellum* from Spitsbergen (present study), 5. *Stricto-seneciobius ebininus* from Mount Kenya, East Africa (Zachariassen unpublished), 6. *Otiorrhynchus dubius* from Finse high mountain plateau, Norway (Hågvar & Østbye 1974), 7. *Curculionidae indet.* from Piedras Blancas, the Andes Mountains, Venezuela (Zachariassen unpublished). Black circles represent values from *Merizodus soledadinus* carabid beetles from South Georgia (Block 1981).

results obtained by Aunaas et al. (1983), who also found that staphylinid beetles and collembolans from Spitsbergen have metabolic rates higher than those of insects from other regions. Thus, the results obtained so far strongly suggest that the insects on Spitsbergen differ from insects from other climatic regions in having markedly elevated metabolic rates.

The Q_{10} values of beetles from Spitsbergen and other areas are shown in Table 2 and Fig. 4. The data show that the curculionid and byrrhid beetles from Spitsbergen have relatively high values of Q_{10}, being within the same range as those of alpine and sub-antarctic beetles. The *A. quenseli* beetles from Spitsbergen, however, have a Q_{10} value which is low compared to that of the other carabids. Thus, with respect to this parameter the Spitsbergen beetles display no clear adaptation, and it looks as if the only metabolic adaptation which is common to the insects on Spitsbergen is the elevation of the metabolic rate at all temperatures.

It is tempting to speculate upon the biological importance of this pattern of adaptation. Due to the comparatively low intensity of solar radiation, the ground temperatures on Spitsbergen do not become as high as those in alpine areas in tropical and temperate regions. Thus, insects on Spitsbergen have to complete their development at lower temperatures than insects in the other regions, and it is therefore likely to be advantageous to the Spitsbergen insects to increase their metabolic rate at low temperatures. The short season during which the development has to be completed will probably also contribute to favour a high metabolic rate at low temperatures.

Assuming that it is important to the animals to secure a high metabolic rate at low temperatures, the Q_{10} values are likely to be reduced, at least in the low temperature range.

The relatively low summer temperatures on Spitsbergen may have caused insects to maintain a certain degree of cold-hardiness during summer. Several studies have shown that insects in temperate and tropical high mountain areas are able to tolerate low temperatures even in summer (van der Laak 1982; Sømme & Zachariassen 1981). The cold-hardiness may have been obtained either through an ability to tolerate freezing of the body fluid or through the ability to remain supercooled even when cooled to low subzero temperatures. The first mentioned form of cold-hardiness is based on the production of potent ice nucleating agents in the extracellular body fluid (Zachariassen & Hammel 1976; van der Laak 1982), whereas the latter involves the removal of all ice nucleating agents and the production of thermal hysteresis antifreeze proteins in the body fluid (Zachariassen 1985).

The present results reveal that the *A. quenseli* beetles have none of the features characteristic of cold-hardy insects. The beetles had supercooling points typical of active summer beetles in warmer climates (Zachariassen 1980), and they were not

tolerant to freezing. The lack of thermal hysteresis between the melting point and the freezing point of their body fluid indicates that the beetles do not have proteinaceous antifreeze agents in their body fluid (Duman et al. 1982). Thus, the low temperatures prevalent during the summer at Spitsbergen have not caused the beetles to develop any of the protective mechanisms characteristic of cold-hardy insects.

The values shown in Table 3 reveal that the *A. quenseli* beetles have rates of water loss comparable to those of temperate and tropical dry habitat beetles of the same body weight (Andersen et al. 1986). This is in agreement with the information provided by Lindroth (1945), who described *A. quenseli* as a xerophilic species, preferring dry moraine and sandy habitats, and which has a distribution extending up to the alpine region. The habitat of the species on Spitsbergen was a steep slope with sterile stones and rocks. Although the climate on Spitsbergen is generally not xeric, the microhabitat of *A. quenseli* may be so. Water is probably quickly drained from the ground, and there are no creeks or ponds in the area. Occasionally the microhabitat may be exposed to long-lasting solar radiation, which is likely to make it very dry. Such conditions are not likely to occur very frequently on Spitsbergen, but an animal population will tend to adapt to the most extreme environmental conditions its members experience.

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