

Temperature adaptations of Siberian *Pterostichus* species (Coleoptera: Carabidae)

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Abstract. Thermopreferenda and supercooling points of the following Siberian species of Carabidae were examined: *Pterostichus vermiculosus*, *P. montanus*, *P. brevicornis*, *P. kaninensis*, *P. dilutipes*, *P. subaeneus* (= *wagneri*), *P. ehneri*, *P. magus* and *P. drescheri*.

Thermopreferenda of the different species were invariable over their area of distribution and correlated with their distribution within natural zones and altitudinal belts. Species examined had no seasonal changes of thermopreferenda. Instar specific thermopreferenda were observed.

The species examined demonstrated slight seasonal dynamics in supercooling points (SCP). All individuals were freeze intolerant. Age variations in SCPs were observed. Larvae demonstrated lower supercooling temperatures than adults, but there were no differences in SCPs between the sexes. The seasonal and age dynamics of the supercooling point temperature were similar for all species of *Pterostichus*.

INTRODUCTION

There is a strong correlation between temperature and the structure of the natural community and especially Arctic and Subarctic flora and fauna (Chernov, 1985, 1989). This dependence is reflected in latitude zonality, linked to the temperature gradient. Species distributions are correlated with subzonal landscapes in tundra (Chernov, 1978). In previous investigations of invertebrate adaptations to the Subarctic and Arctic environment much attention has been paid to the reaction of organisms to temperature (MacLean, 1975; Danks, 1978; Zachariassen, 1985; Block, 1990).

In the study of animal adaptations to the environment it is often useful to study the influence of one ecological factor on an organism. This is not easy in the field, but in the laboratory it is possible to establish conditions that limit the influence of physical and biological factors.

The aim of this study was to understand the reaction of organisms to temperature using two methods: determination of individual thermopreferenda and supercooling points. In this way, the relationship between temperature preference and freezing avoidance/tolerance could be examined.

MATERIAL AND METHODS

Study sites

This study was conducted in Subarctic and Arctic Russia in seven field seasons during 1985–95 at various locations in Siberia: the Polar Urals (67°N, 65°E), the Tyumen' area: Nadym (66°N, 72°E), three areas of the Taimyr Peninsula: Vorontsovo (72°N, 83°E), Karaul (70°N, 83°E) and Potapovo (69°N, 86°E), Goroshikha (66°N, 87°E), Mirnoe (62°N, 89°E), Ust'-Pit (59°N, 94°E), Predivinsk (57°N, 93°E)

and the Sayan Mountains (52°N, 92°E). Live beetles were collected for experimental study in different habitats and at different altitudes on mountains.

In the Polar Urals and Sayan Mountains, material was collected along an altitude profile from the mountain lichen tundra to the tundra of the river valley. In the Krasnoyarsk area and the Taimyr Peninsula, localities were along the east bank of the Enisei river, separated by 200–500 kilometers.

All sites were characterised by a strongly continental climate.

Animal material

Species of carabids investigated belonged to the genus *Pterostichus*. They were *P. vermiculosus* Ménétries, *P. montanus* Motschulsky, *P. brevicornis* Kirby, *P. kaninensis* Poppius, *P. dilutipes* Motschulsky, *P. subaeneus* Chaudoir, *P. ehneri* Poppius, *P. magus* Mannerheim and *P. drescheri* Fisher-Waldheim.

Adults and juvenile beetles were collected in the field using pitfall traps, hand sorting or sifting of soil and litter. They were kept in the laboratory at 4–6°C.

Experiments on thermopreferenda and SCPs were conducted either in a field laboratory or in the Moscow laboratory. At the field station live material was kept for 2–3 days and in Moscow for 2–3 weeks before the experimentation.

Laboratory procedures

THERMOPREFERENDA. Experiments on temperature preference were made using an original thermal gradient apparatus made of plaster with concentric experimental canals (Tikhomirov & Tikhomirova, 1972; Rossolimo & Rybalov, 1979). The size of the apparatus was 70 × 40 × 7 cm with the canals' diameter of 0.5–2.0 cm. Different body sizes were examined in canals of corresponding diameter. Temperatures ranged from 6–30°C. Relative humidity of the air equalled 100%, the humidity normally observed for the air within the soil. This is the natural humidity for all soil-dwelling terrestrial invertebrates. All the *Pterostichus* species were predators and during the experiment individuals were placed in separate canals. At the beginning of the experiment the beetles were placed in the 16–18°C zone and left to explore for 60–90 minutes. The temperature was recorded for the zone where the animal stopped and rested. The beetle was then disturbed and forced to reselect its preferred temperature once more. The average number of individuals examined for each species was 20, giving 150–200 observations of temperature preferenda.

SUPERCOOLING POINTS. Determinations of individual SCPs were made using a microrefrigerator with a cooling rate of 1°C min⁻¹. The SCP was recognised by the chromel-kapel thermocouple and registered as an exotherm on a chart recorder KSP-2. The average number of individuals examined for each species was 40.

Student's t-test was used in the SCP's data analysis. Analysis of Variance (F) was used for testing the influence of factors on thermopreferenda.

RESULTS

Species distribution

Investigations on the distribution of Carabidae species in Siberia revealed that the majority of species belong to one of two ecological groups (Kryzhanovsky, 1983). One group contains the boreal species distributed mostly in taiga and in birch forest belts on the mountain slopes. These include *P. montanus*, *P. dilutipes*, *P. magus*. The other group includes species distributed in the tundra and Arctic-alpine zones. These are *Pterostichus brevicornis*, *P. vermiculosus*, *P. kaninensis*. These species were collected in moss-lichen tundra, moss-shrub tundra and tundra lowlands (Table 1).

Thermopreferenda

The thermal preferendum of *P. brevicornis* was examined for individuals collected at the Polar Urals and Taimyr Peninsula. The species is widespread, giving the possibility of comparisons between regions. *P. brevicornis* populations did not differ in their thermal preferenda. Individuals from the Polar Urals preferred 9–22°C in July and 11–21°C in

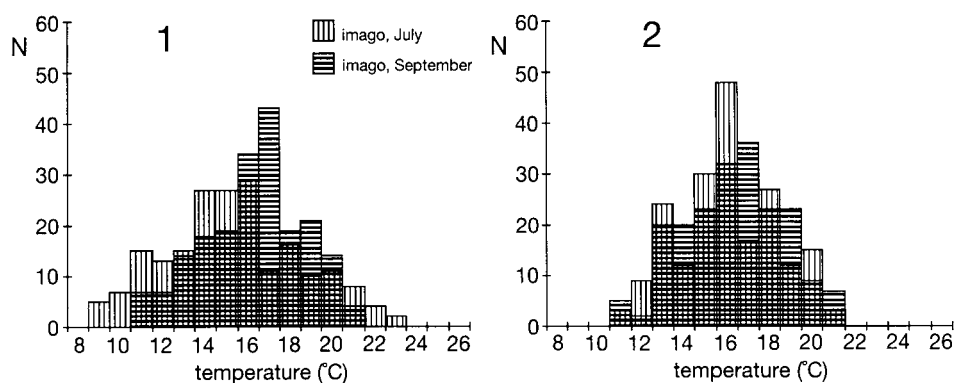
September (Figs 1–10). Equivalent figures for the Taimyr Peninsula (Karaul) were both 11–21°C. Individuals were collected in different localities along the mountain slopes.

TABLE 1. Species distribution of Carabidae in the regions investigated.

Species	Geographical regions									
	1	2	3	4	5	6	7	8	9	10
<i>P. brevicornis</i>	+	+	+	+	+	+	+			
<i>P. vermiculosus</i>	+	+	+	+	+					
<i>P. kaninensis</i>	+									
<i>P. montanus</i>	+		+	+	+	+	+		+	
<i>P. dilutipes</i>	+	+			+	+	+	+	+	
<i>P. magus</i>							+	+	+	+
<i>P. drescheri</i>					+		+	+	+	+
<i>P. ehnborgi</i>						+	+	+	+	
<i>P. subaeneus</i>										+

1 – Polar Urals; 2 – Nadym (Tyumen' area); 3 – Vorontsovo (Taimyr Peninsula); 4 – Karaul (Taimyr Peninsula); 5 – Potapovo (Taimyr Peninsula); 6 – Goroshikha; 7 – Mirnoye; 8 – Ust-Pit; 9 – Predivinsk; 10 – Sayan Mts.

P. vermiculosus is distributed mostly in tundra, in subarctic and alpine localities. The thermopreferendum of adults in July and September was 14–19°C and 15–19°C respectively. Second instar larvae in September chose a wide temperature zone (12–23°C), the majority of individuals chose 17–22°C. Third instar larvae preferred 14–24°C in September (majority 18–22°C). The age dynamics of thermopreferenda was observed ($P < 0.05$). Individuals of *P. kaninensis* an arcto-boreal species collected in shrub tundra had an adult thermopreferendum of 13–20°C in both July and September. Individuals of *P. montanus*, a widespread species in tundra, northern taiga and birch forests on mountain slopes showed, in July, thermopreferenda of 14–24°C (majority 19°C) and in September 17–24°C.



Figs 1–2. Thermopreferenda of *Pterostichus brevicornis*. 1 – the Polar Urals; 2 – Taimyr Peninsula, Karaul.

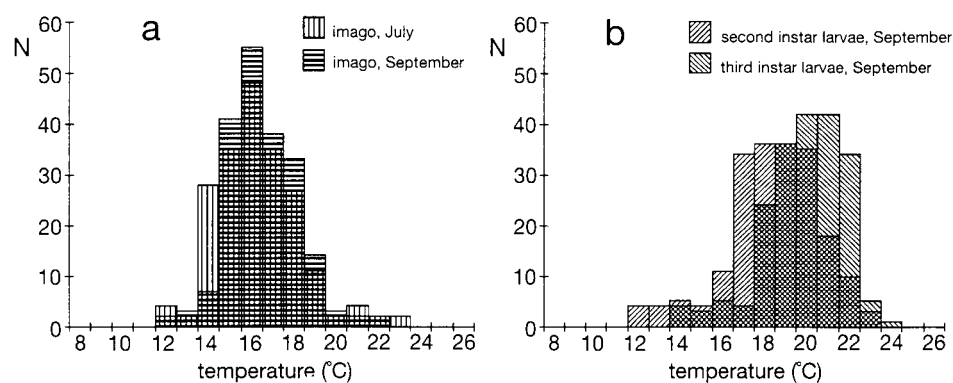


Fig. 3. Thermopreferenda of *Pterostichus vermiculosus*.

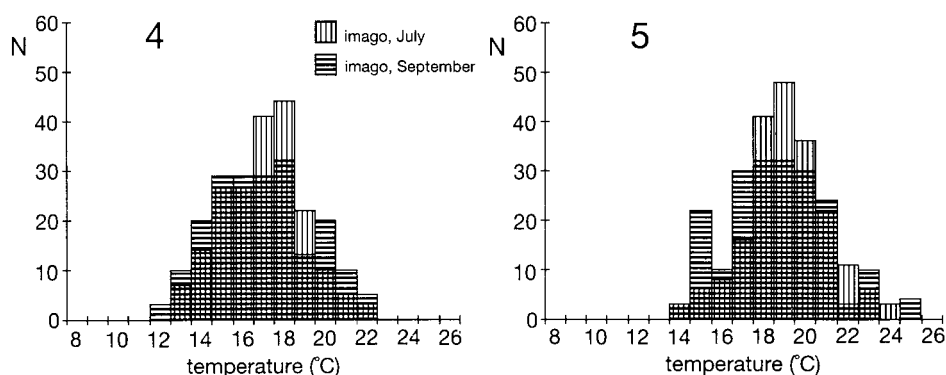
Thermopreferenda of adult *P. dilutipes*, another widespread species, were similar in July and September (16–23°C). Thermopreferenda of adult *P. magus*, *P. drescheri*, *P. ehnbnergi*, all wide, spread boreal species, were 15–22°C, 14–24°C, 13–24°C in September respectively. *P. subaeneus*, an alpine species, collected in the Sayan Mountains from its hibernacula displayed a wide thermal preferendum in September (10–26°C).

Supercooling points

The supercooling points (SCPs) of the species examined were similar (–4.0 to 5.8°C) with no difference between the sexes ($P > 0.01$). All adults and juveniles examined were freezing intolerant and died at temperatures close to their SCP. SCPs of individuals from different geographic areas were similar in all species ($P > 0.05$) (Table 2). *P. brevicornis* from the Polar Urals demonstrated a SCP of –5.8°C in July, in September –4.9°C. For the population from Khibini –5.6°C and –5.0°C accordingly (Rossolimo, 1989), from Karaul and Potapovo in September –4.8°C and –4.6°C accordingly. There were, however, small differences in July and September, SCPs being slightly higher in autumn than summer ($P > 0.05$) (Table 3). The SCP was lower in juveniles than in adults ($P < 0.01$) (Table 3).

TABLE 2. Supercooling points (°C) of *Pterostichus* species from different geographic areas (mean $\pm$ ISE).

	Khibini Mts	Polar Urals	Karaul	Potapovo	Nadym
<i>P. brevicornis</i>					
July	–5.6 $\pm$ 0.2	–5.8 $\pm$ 0.1	–	–	–
September	–5.0 $\pm$ 0.1	–4.9 $\pm$ 0.2	–4.8 $\pm$ 0.1	–4.6 $\pm$ 0.3	–
<i>P. vermiculosus</i>					
July	–	–4.6 $\pm$ 0.2	–	–	–5.0 $\pm$ 0.3
September	–	–4.0 $\pm$ 0.2	–4.3 $\pm$ 0.3	–4.5 $\pm$ 0.1	–
<i>P. montanus</i>					
September	–	–5.2 $\pm$ 0.1	–	–4.9 $\pm$ 0.3	–
<i>P. dilutipes</i>					
July	–	–5.3 $\pm$ 0.1	–	–	–5.0 $\pm$ 0.2

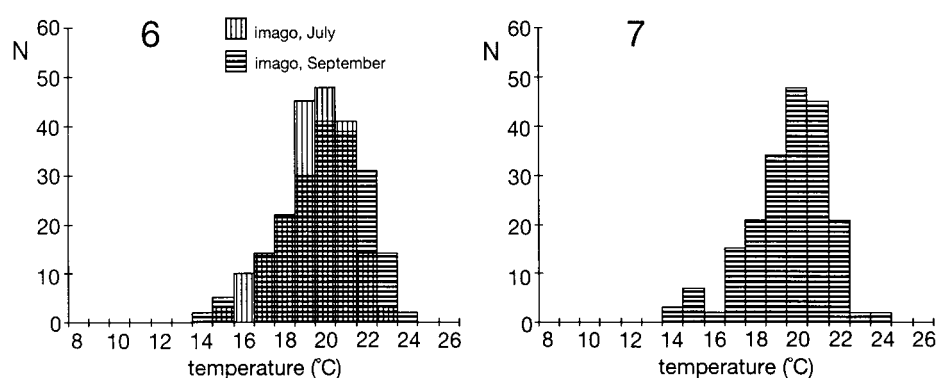


Figs 4–5. Thermopreferenda of *Pterostichus* species. 4 – *P. kaninensis*; 5 – *P. montanus*.

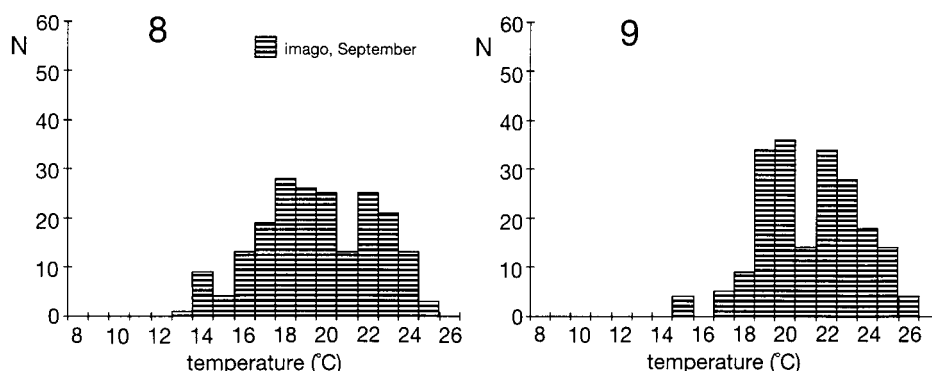
Some overwintered adults of *P. brevicornis* and *P. vermiculosus* from the Polar Urals and the Taimyr Peninsula remaining alive in March had similar SCPs to prewinter individuals. Adults of *P. subaeneus* in the post-molt condition were collected in the Sayan Mts in September in hibernation. Thus, some *Pterostichus* species overwinter as adults.

TABLE 3. Supercooling points (°C) of *Pterostichus* species according to time of year (mean $\pm$ ISE).

Species	July	September	March
<i>P. subaeneus</i> , imago	–	-5.5 ± 0.1	–
<i>P. brevicornis</i> , imago	-5.6 ± 0.1	-4.9 ± 0.2	-5.5 ± 0.2
<i>P. brevicornis</i> , L2	-7.1 ± 0.2	–	–
<i>P. brevicornis</i> , L3	-6.0 ± 0.2	–	–
<i>P. montanus</i> , imago	-5.0 ± 0.3	-5.2 ± 0.2	–
<i>P. montanus</i> , L2	-6.8 ± 0.2	–	–
<i>P. kaninensis</i> , imago	-4.9 ± 0.1	-5.1 ± 0.1	–
<i>P. vermiculosus</i> , imago	-4.6 ± 0.3	-4.0 ± 0.2	-5.0 ± 0.2
<i>P. dilutipes</i> , imago	-5.3 ± 0.1	–	–



Figs 6–7. Thermopreferenda of *Pterostichus* species. 6 – *P. dilutipes*; 7 – *P. magus*.



Figs 8–9. Thermopreferenda of *Pterostichus* species. 8 – *P. drescheri*; 9 – *P. ehnerbergi*.

DISCUSSION

Pterostichus contains many species with different biologies and distributions. However, the thermopreferenda of the species are invariable across the area of their distribution (Rossolimo & Rybalov, 1979, 1994). These data confirm the hypothesis of the temperature requirements of the species for the environment (Tikhomirova, 1973; Kaufman, 1985).

Experiments were conducted on animals kept in laboratory conditions close to those occurring naturally and reflecting their temperature adaptations. Some species are known to change thermopreferendum, e.g. *Pseudoophonus pubescens* (Carabidae), after prolonged temperature acclimation (Likventov, 1960). In natural environments they can, by contrast, find the temperature conditions corresponding to their biological needs and physiological state.

Thermopreferenda are correlated with the distribution of each species. Boreal carabid species (*P. dilutipes*, *P. montanus*, *P. magus*) preferred higher temperatures (16–23°C) than subarctic species (*P. vermiculosus*, *P. brevicornis*) (13–20°C). In arctic and subarctic regions the boreal *Pterostichus* species were distributed only in river valleys and other intrazonal landscapes with a more favourable climate. The wide range of thermopreferenda of *P. brevicornis* appears correlated with its landscape distribution. Bimodal thermopreferenda of *P. drescheri*, *P. ehnerbergi*, *P. subaeneus* demonstrated physiological differences of individuals in the population in autumn when preparing for overwintering.

Arctic and subarctic Coleoptera species have few seasonal changes of thermopreferenda but boreal species usually display seasonal dynamics (Rossolimo, 1989, 1991; Rossolimo & Rybalov, 1994). The species of *Pterostichus* examined had no seasonal change in their thermoprefer-

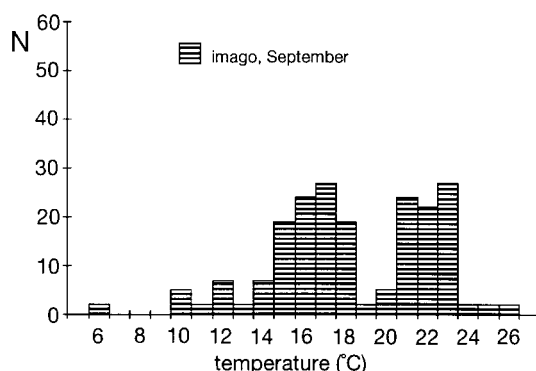


Fig. 10. Thermopreferenda of *Pterostichus subaeneus*.

enda. Instar specific thermopreferenda were observed, suggesting the occupation of different environmental niches by different instars (Arnoldi, 1957).

The SCP's revealed little dependence of species' distributions on the low temperature of their environment. The species examined demonstrated slight seasonal dynamics in SCP, a normal feature in freeze tolerant species (Sømme, 1982). All the individuals of *Pterostichus* species were freeze intolerant. However, *P. brevicornis* showed freeze tolerance in Alaska (Baust & Miller, 1970; Baust & Rojas, 1985). The difference may be attributed to the different experimental cooling and heating rates. However, freeze tolerance occurs in *Curtonotus alpinus* (Carabidae) and *Lathrobium poljarnis* (Staphylinidae) adults when cooled and heated at the same rate (Rossolimo, 1994). Larvae demonstrated lower SCP than adults. There was no SCPs difference between the sexes.

The SCP's and their seasonal and age dynamics were similar for the species of *Pterostichus* studied.

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