

D.I. Berman, A.V. Alfimov, Z.A. Zhigulskaya, A.N. Leirikh

Overwintering and Cold-Hardiness of **Ants** in the Northeast of Asia



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RUSSIAN ACADEMY OF SCIENCES
Far Eastern Branch
INSTITUTE OF BIOLOGICAL PROBLEMS OF THE NORTH

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by

D.I. BERMAN, A.V. ALFIMOV,
Z.A. ZHIGULSKAYA & A.N. LEIRIKH

Edited by

Robert Angus



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TRANSLATOR'S PREFACE

The book *Overwintering and Cold-Hardiness of Ants in the Northeast of Asia* by D. I. Berman, A. V. Alfimov, Z. A. Zhigulskaya and A. N. Leirikh is an English translation of a monograph of the same name published in Russian in 2007 by the Moscow publisher KMK Scientific Press. The Russian version was edited by the well-known Russian myrmecologist Professor Gennady M. Dlussky of Moscow University, and this English version was edited by the British entomologist Robert B. Angus, who has been in Russia several times and happens to have some personal experience of the extreme conditions of northeastern Asian climate discussed in this book. Arkady V. Alfimov, one of the authors, checked the entire English version of the text and consulted the translator and the English editor on special terms and other issues that had to be clarified.

The scope of the book is rather broad: it includes general and local aspects of the study area's peculiar climate, characteristics of the ant species living in the area (including their nest structure, overwintering stages, and geographical and spatial distribution), and the results of numerous experiments that revealed the parameters of cold-hardiness in thousands individual ants from dozens of nests. Preparing a monograph of this scope was possible thanks to the different fields in which the four authors are specialised: D. I. Berman, Chief of the Biocoenology Laboratory at the Institute of Biological Problems of the North in Magadan, is an ecologist and biogeographer, A. V. Alfimov is a microclimatologist, Z. A. Zhigulskaya a myrmecologist, and A. N. Leirikh is a physiologist earlier educated in physics.

In the literature available (both in Russian and in English), there are but a few large-scale studies of insect overwintering and cold-hardiness, and this book is probably the first one where the cold-hardiness of all the species from a particular taxonomic group living in an area with long and severe winters is studied in detail, based on large amounts of material collected in the field and experimented upon in the laboratory. This is one thing that is unique about the book, but there are at least two more unique things about it: the choice of the taxon, and the study area. Ants are the only social insects capable of long-term surviving in the extreme winter cold of the Northeast of Asia. The study area itself is also unique: being not far from, and only slightly warmer in winter than the very coldest area of the Northern Hemisphere, the so-called Pole of Cold in northeastern Yakutia, it is also often affected by strong winter winds (rare in northeastern Yakutia), redepositing the snow and

creating in the soil, where ants are overwintering, conditions sometimes even more severe than under the snow cover in northeastern Yakutia. What makes the overwintering of ants in much of northern Asia, including the Northeast, an especially hard endeavour is the continuous permafrost, which makes it impossible for ants to build the wintering chambers of their nests as deep as they can in other regions.

Permafrost and harsh winter cold of the area make it ideal for studying the overwintering and cold-hardiness of animals, but these same conditions make the process of the study extremely difficult and labour-consuming. It is all the more difficult because the area is sparsely populated; settlements are few and separated by huge distances, roads rare and often barely (if at all) passable, many localities can be reached only by helicopter. The Kolyma region is infamous for housing in Stalin's time the cruellest forced-labour camps, where many thousands of innocent people died of cold and starvation. Years of hard fieldwork in the severe climate of that region stand behind this detailed study. To have a laboratory for working all the year round in the mountains of the Upper Kolyma, D. I. Berman and his colleagues from the Institute of Biological Problems of the North had to build in the mountains of the Upper Kolyma the Aborigin Field Station, 500 km from the city Magadan on the coast of the Sea of Okhotsk. This station enabled much of the work that made this book possible to be carried out.

The Russian version of the book was warmly received by myrmecologists and ecologists. It was reviewed by the myrmecologist Elena Fedoseeva, Zoological Museum of Moscow State University, in the leading journal on zoology published by the Russian Academy of Sciences, *Zoologicheskii Zhurnal*. Her review highlighted the novelty of the results and the huge amount of work required from the authors (and those who assisted them) to obtain these results. The reviewer also noted that the mass of scientific information currently accumulated in ecology leaves many problems unsolved because of the extreme specialization of researchers and lack of cooperation between them. The complex nature of the ecological problems discussed in the book required the collaboration of specialists in different fields, and the book shows how productive such collaborations can be.

The publication of this monograph in English will make it accessible to many more readers. The English language has long established itself as the international language of communication and of science, a place occupied until a few hundred years ago by Latin. Scientific results obtained in Russia are, unfortunately, underrepresented in English-language scientific literature. The Iron Curtain, which divided political systems, hindered not only the travelling of people, but also the spreading of scientific knowledge and ideas. Publishing in English was viewed with suspicion and rarely encouraged in the Soviet Union. Another big obstacle was inadequate knowledge of English, which was usually far from fluent even among members of the Soviet academia. Some achievements of Soviet science remained known largely only to Soviet scientists and their colleagues from other socialist countries and not to the whole international scientific community. Fortunately, the situation seems to

be changing for the better. Russian scientists publish their works in English more and more often. For instance, a few years ago (in 2007) another monograph discussing ants, Zhanna Reznikova's study on animal intelligence (*Animal Intelligence: From Individual to Social Cognition*) was published by Cambridge University Press. The publication of the English version of *Overwintering and Cold-Hardiness of Ants in the Northeast of Asia* is another step forward in making the work of Russian scientists known to their colleagues worldwide.

Making the content of this book known outside Russia is all the more important since the results presented in the book could not be obtained in any other country, simply because in no other country winters are as severe. Large areas of Canada and USA's Alaska also have very cold winters, but the winter temperatures of the parts of northeastern Asia with most strongly continental climate are still unmatched by any other place on Earth, with the exception of the Southern Hemisphere's (and the planet's) Pole of Cold in Antarctica—but no ants are native to Antarctica.

The results obtained by D. I. Berman and his team are diverse in nature and will be of interest not only to myrmecologists, but also to ecologists and ecological physiologists, as well as climatologists. The following aspects of ant overwintering and cold-hardiness are elucidated in the book: the bionomics of ant overwintering (including the habitat distribution, nest structure and overwintering stages of each species found in the area); the microclimate and temperature conditions of the overwintering of each species; and the physiological parameters related to cold-hardiness, measured in samples of each species (including supercooling points, freezing points, long-term tolerable temperatures, and levels of cryoprotectant substances in the haemolymph). The study of all these aspects required many years of Herculean labours. Sitting in a warm room in Moscow, where I write this preface, with moderately cold weather outside (only around -15°C , rather cold for Moscow in January, but quite warm compared to the Upper Kolyma, where about -35°C is the average for January, and -50°C is not uncommon), it is hard to imagine the conditions in which fieldwork had to be done in the environs of the Aborigin Station. As if cutting heavy cubes containing ant nests from the frozen ground covered with snow and bringing them to the station was not enough, the authors and their helpers had to put these nests with the ants they contained into a cold laboratory room, to protect the ants from heat shock, which could spoil the results of subsequent experiments. It was in this cold room, at temperatures as low as -10 to -15°C , that individual ants had to be extracted from the nests and sorted out for experiments.

These hard labours allowed the authors to obtain really interesting results. The ants found in the study area belong to four genera (*Myrmica*, *Leptothorax*, *Camponotus* and *Formica*). Species of these genera differ in their strategies of adaptation to overwintering at low temperatures. *Leptothorax* and *Camponotus* display extremely low values of supercooling point. (Unlike some other overwintering invertebrates, but like all vertebrates, ants are unable to survive freezing, i.e. formation of ice crystals in cells and bodily fluids; to protect themselves from freezing under sub-zero

temperatures, they have to stay in the supercooled state, cooled but not frozen; supercooling point is the temperature below which the supercooled state is no longer possible). Species of the genus *Myrmica* and one of the several species of *Formica* (*F. gagatoides*) have higher supercooling points, but their supercooled state is more stable, compared to that of *Leptothorax* and *Camponotus*, and can be maintained longer; these species build their nests in localities with a rather deep permafrost table, where wintering chambers can be positioned far from the surface and the temperatures in them are not so low and more stable than closer to the surface. The other species of the genus *Formica* are the least cold-hardy; they build their nests only in habitats with winter conditions as favourable as possible; fluctuations of winter weather probably repeatedly wiped out populations of these species over large areas, resulting in long-term changes in their geographical ranges. This diversity of adaptation strategies is surprising, but it was convincingly shown by experiments with large sample of ants of each species.

Although the conditions of the Northeast of Asia require effective adaptations to overwintering at very low temperatures, it is probably rather lack of summer heat than excess of winter cold that causes the depletion of the ant fauna towards the north and the disappearance of them farther, on the tundra. Short summers with relatively low temperatures do not allow ants of most species to complete their life cycle in one year and overwinter as adults. Only a few species are capable of prolonging the life cycle to more than one year and overwintering for the first time as larvae.

The monograph contains plenty of information on the cold-hardiness and overwintering of ants, but the subject is still far from closed, and several further research objectives are outlined in the book. One of them is the study of cold-hardiness in ants that overwinter at even lower temperatures than those in the Kolyma region, for instance in northeastern Yakutia (the Pole of Cold), Transbaikalia and the Upper Amur valley, where the snow cover is often very thin and fails to insulate the upper layers of the soil from the cold winter air. Time and further experiments will show whether the adaptive strategies of ants at the very limit of their potential cold-hardiness are different from those found in the extreme conditions of the Kolyma region. The monograph sets an example and provides a firm foundation for further studies of overwintering and cold-hardiness, not only in ants, but also in other invertebrates living in areas with extremely cold winters.

PYOTR PETROV

PREFACE OF THE EDITOR OF THE RUSSIAN EDITION

More than half the area of Russia and large portions of North America (Alaska, Canada) are covered with permafrost. These territories are inhabited by thousands of invertebrate species, but the actual overwintering conditions, physiological mechanisms, and behavioural features enabling them to withstand low temperatures are known only in a few of them.

Studies of cold-tolerance in animals of Russia were started at the end of the 19th century by P. I. Bakhmetyev, who showed that surviving in a state of anabiosis is only possible if tissue fluids remain supercooled. In the 1930s, N. I. Kalabukhov published the brilliant book *Animal Dormancy*, which inspired new studies of the hibernation of animals in their natural environments. In the Soviet Union, these studies were especially intense in the 1950s–1970s, resulting in the monographs *Fundamentals of Insect Cold-Tolerance* by R. S. Ushatinskaya (1957) and *Essays in Cryobiology* by L. K. Lozina-Lozinsky (1972). Since the 1960s, cold-tolerance has been the subject of detailed studies in Canada, Japan and Scandinavia. In contrast, in the Soviet Union such studies virtually ceased from the mid-1980s and were continued only by a small group of scientists headed by D. I. Berman, Chief of the Biocoenology Laboratory at the Institute of Biological Problems of the North, Far Eastern Branch, Russian Academy of Sciences. Following the interesting publications of these researchers over many years, we have finally prepared a monograph summarizing their work on the biology of ants under extreme northern conditions.

It should be emphasized that so far most of the publications have only discussed the issues of animal overwintering in the temperate climatic zone, whereas the peculiar features of cold-hardiness in the invertebrates of the vast areas with very cold winters are clearly in need of more studies. As for the works carried out in Antarctica and Svalbard, they include detailed results of research on the physical and chemical mechanisms of cold-tolerance in only a few species, whereas the ecology of overwintering animals remains almost entirely unknown.

These circumstances highlight the current importance of the present monograph, summing up 30 years of studies on the ecology and physiology of ants under extreme northern conditions, virtually at the northern boundaries of their geographical distribution. It is noteworthy that the book is written by a group including two zoologists (D. I. Berman, Z. A. Zhigulskaya), a microclimatologist (A. V. Alfimov) and an ecological physiologist (A. N. Leirikh). At this time of nar-

row expertise, such a complex and high-quality work could only be produced by a well-coordinated group of researchers, this book being another evidence of this. Such an approach has allowed the authors to appreciate the entire range of strategies—not only physical chemical and physiological, but also ecological, ethological and others—of adaptation to spending the entire life cycle or some of its stages at low temperatures of the environment. The authors correctly emphasize that within this approach the most promising objective is the study of widely distributed species under extreme conditions, where the adaptive potential of the organism is especially strikingly revealed. In the northern continental areas, animal species of diverse origins and with different ecological and physiological potentials coexist due to the vast range of microclimatic conditions.

The study was carried out mostly at the Aborigen Field Station in the upper reaches of Kolyma River and some other places in the Magadan Region, Russian Far East. The winter climatic parameters of this area are close to those of the "Pole of Cold" in northeastern Yakutia, where even in the uniquely "warm" habitats winter temperatures never exceed -9°C , whereas background temperatures in near-surface layers of the soil in winter usually drop as low as -45 to -50°C in snowless areas (which is close to the lowest air temperatures) and as low as -20 to -25°C in areas covered with thick snow.

The choice of the study object is not arbitrary either: ants are perfect models for studying many phenomena, including cold-hardiness in natural environments. Cold-hardiness is usually studied in the laboratory, by collecting individual invertebrates in autumn and observing their overwintering under conditions the experimenter believes to be as close to natural as possible. The overwintering of ants, however, can be studied in their natural environments. The authors marked ant nests with long stakes in autumn and in winter cut out frozen monoliths containing the nests, brought them into a cold laboratory room and distributed small portions of ants in weighing bottles, subsequently using them for experiments as required. Certainly, this technique demanded considerable efforts on the part of the researchers possible only through great enthusiasm and teamwork. But their labours seem to have been fully rewarded by the results obtained. This monograph is virtually the first work in the world providing a comprehensive picture of the life of ants under extreme northern conditions.

Like most works of this kind, the monograph begins with descriptions of the landscapes and climates of the study area. There is, however, an important distinction. Zoologists normally limit themselves to data from reference books and other literary sources, whereas this work provides much original data on the microclimate of particular localities, helpful for better understanding the conditions under which ants live in particular habitats. Now we know for certain what the thermal regime is in the "ecologically active layer" (i.e. the soil and the inhabited upper part of the underlying grounds) near the Pole of Cold. It should be emphasized that although permafrost is extremely widespread in the forest zones of Eurasia and North Amer-

ica, there are no special studies on the living conditions of the soil-dwelling animals of such areas. The data of the authors on conditions occurring in different types of permafrost ("dry" and icy) are of special interest in themselves, because they can be used for analysing the distribution of any organisms inhabiting the permafrost areas not only in the subarctic Northeast Asia, but also across much of Siberia and North America.

As a myrmecologist, above all I expected getting from this book new data on ants, and my expectations were fulfilled. The monograph contains unique data on the bionomics of particular species in subarctic climate at the northern boundaries of their ranges. All that was known to science on this subject was the bionomics of ant species in Scandinavia, at latitudes close to those studied by these authors (60–70° N), but with immeasurably warmer climate, and thus, in a way, less interesting. This study provides information on the geographical distribution, habitat allocation, nest-building characteristics and seasonal dynamics of ants inhabiting northeastern Siberia. Of special interest are the data on the structure of ant nests, based on materials the collection of which required the both physically laborious and simultaneously accurate work of excavating the nests both in summer and in winter.

The chapter *Ant Cold-Hardiness and Its Determining Physiological and Biochemical Factors* makes the entire study especially valuable. It provides the first quantitative data on the cold-hardiness of ten species of ants from four genera (*Myrmica*, *Leptothorax*, *Camponotus* and *Formica*) most abundant in the study area. The physiological mechanisms behind this hardiness are shown.

Thus, the book presents an integral picture: the regional geographical distribution, habitat allocation, nest organization, overwintering family composition, thermal conditions in nests, reactions to low temperatures (supercooling points, freezing points, lowest tolerable temperatures) and seasonal changes of cryoprotectant concentrations were studied in one taxonomic group in one really cold area. This picture is valuable by itself, even without any conclusions. The generalizations made by the authors are, however, both important and interesting. The authors have convincingly shown the multidimensionality of adaptive strategies of survival in the extreme north. In some species the ability to exist in such an environment is determined mainly by their strong physiological cold-hardiness, and in some their lack of physiological capacities is compensated by choice of appropriate habitats with specific microclimate or by peculiar structure of nests. The conclusion that each of the studied species has its own specific adaptive strategy is somewhat unexpected, but is convincing. The authors believe that this fact makes it rather unlikely that a general strategy of adaptation to cold (including its physiological/biochemical and behavioural aspects) will ever be revealed, at least in ants. It would be extremely interesting and important to test this pessimistic conclusion with other animal taxa (no such data are available in the literature at present).

The analysis in this book explains the causes of ant fauna depletion at the northern boundaries of ranges and shows the diversity of these causes. Only a small

proportion of the species in the Northeast of Asia are free from the pressure of low winter temperatures, and in these species the northern limits of distribution are determined by summer conditions. The monograph shows, however, that even in the extreme north biotic relations still play an important part in the genesis of fauna.

A great merit of this book is its detailed description of the methods of field and laboratory work, which can be used in the future by other researchers. One of the accomplishments of the authors is, undoubtedly, the development of techniques for estimating the parameters of cold-hardiness in individuals overwintering in their natural environments. These techniques will guard against mistakes in adjusting the conditions for winter maintenance of animals in the laboratory. This is particularly important since the authors have revealed very rapid changes in physiological parameters, including the lower supercooling temperatures, in all the species under changing conditions.

The monograph is certain to appeal not only to myrmecologists (in this respect it is unique in the abundance of facts it provides on the ecology of particular species), but to all biologists interested in the cold-hardiness and survival of animals under the severe conditions of the subarctic climate.

To conclude this brief preface, I would like to note that the Biocoenology Laboratory in Magadan is currently the only research unit in Russia studying the winter ecology of invertebrates. I wish them every success in their future difficult and exciting work and hope that this book will attract new researchers to work in this field.

PROFESSOR GENNADY DLUSSKY

INTRODUCTION

The main feature common to all the climates of Russia is the cold winter. The proportion of areas with positive temperatures in winter is negligible, and permafrost covers almost 60% of the country. In the northern parts of North America—Canada and Alaska—the situation is similar. Thousands of invertebrate animal species winter every year in these areas. The actual conditions of overwintering and mechanisms of cold-resistance are known in only a few dozen of these species. The current knowledge of the phenomenon, unfortunately, fails to match its scale.

Physiological, ecophysiological and ecological studies of this extreme aspect of invertebrate animal life are developing and their scope is becoming broader. At the beginning of the last century studies of how animals withstand low temperatures were focused on anabiosis (works of P. I. Bakhmetyev, P. Yu. Schmidt), and in the middle of the century such studies were largely oriented towards agricultural pest control and cryopreservation of tissues and organs. The most important landmarks in the development of these approaches were the monographs *Fundamentals of Insect Cold-Tolerance* by R. S. Ushatinskaya (1957), *Essays in Cryobiology* by L. K. Lozina-Lozinsky (1972) and *Ecology and Physiology of the Colorado Potato Beetle* by R. S. Ushatinskaya & G. G. Yirkovsky (1976). Cryopreservation became in due course a separate, successfully developing discipline, focused mostly on applied objectives. The cold-hardiness of invertebrates was studied for some time at Leningrad State University, at the University of Tartu, and at the Institute of Animal Evolutionary Morphology and Ecology (Moscow). A conference on cold-tolerance of insects and acarines was held in Tartu in 1971, and the monograph *Cold-Hardiness of Insects* by E. E. Merivee was published in 1978.

The results of these works largely determined the development of this approach in the following decades. For instance, the connection between cold-tolerance and the presence and profundity of diapause was revealed in some invertebrate taxa (Merivee, 1972; Ushatinskaya, 1980), the existence of nonspecific cold-tolerance related to particular stages of ontogeny and diapause (Merivee, 1978; Ushatinskaya & Ivanchik, 1974; Luik, 1975; Ushatinskaya &

Chesnek, 1974) and differences in cold-tolerance between insect populations from different geographical localities (Pantyukhov, 1956, 1964; Hansen, 1978) were shown. The characteristics of cold-hardiness were described for many invertebrate species (Hansen, 1980a), and the list of species surviving winter in their natural environments in a frozen state was enlarged (Hansen, 1980b). The criteria of cold-hardiness were developed and improved (Merivee, 1978), along with studying facilities (Goryshin, 1966) and methodological techniques (Merivee, 1970; Kuusik, 1971) for acquiring adequate results and interpreting them unambiguously. The most excellent summation of this period of studies was the publication of the book *Hidden Life and Anabiosis* by R. S. Ushatinskaya (1990). Work in this field virtually ceased in the former USSR by the mid-1980s.

Meanwhile, studies of cold-hardiness started developing rapidly in Canada, Japan and Scandinavia since the 1960s. The first international meeting on different aspects of invertebrate cold-hardiness was held in 1982 in Oslo. The same year marked the publication of the first part of a bibliographic checklist on the physiology and biochemistry of low-temperature tolerance in insects and other terrestrial arthropods (Baust et al., 1982), containing over 500 references. In 1986 the second part of the checklist with over 150 references was published (Lee et al., 1986). Finally, in 1991 a group of 39 authors published the monograph *Insects at Low Temperature* edited by R. E. Lee & D. L. Denlinger (1991), which reflected the state of the discipline and became the reference book for all who study cold-hardiness. In this monograph, the basic notions were formulated and the general principles of insect cold-hardiness, as well as the properties and balance of water and the biochemistry of cryoprotectants and specific proteins important for providing tolerance to negative temperatures were discussed. Much attention was paid to the adaptations of particular species, to groups of terrestrial and aquatic Arctic invertebrates, as well as to the practical applications of the knowledge on cold-hardiness to cryopreservation of cells, tissues and entire insect organisms, to pest control, bee overwintering and silkworm breeding.

All these areas were successfully developed over the last 15 years by many researchers, including the unofficial group that authored the above-mentioned monograph. Reviews were regularly published, not only on the key elements of the physiology of cold-hardiness, such as water balance (Danks, 2000; Block, 2002), ice nucleation (Lee & Costanzo, 1998; Zachariassen & Kristiansen, 2000; Lundheim, 2002), inorganic ions (Zachariassen et al., 2004), low-molecular cryoprotectants (Kostal et al., 2001, 2004; Wharton, 2003; Fuller, 2004; Williams et al., 2004) and antifreeze proteins (Davies et al., 2002; Duman et al., 2004), but also on the state of the field in general (Somme, 1995; Denlinger & Lee, 1998; Bale, 2002; Danks, 2004, 2005; Turnock & Fields, 2005). The

biochemistry of cryoprotectants (Muisse & Storey, 1999, 2001), the regulation of metabolic rate (Storey & Storey, 2004) and the mechanisms of cold stress damage and repair (Joanisse & Storey, 1998) were studied. Cold-hardiness featured prominently in programs of the regularly held international workshops on the ecophysiology of invertebrates (for materials of the 2nd, 3rd and 4th workshops see Proceedings..., 1996, 1999, 2002 in *European Journal of Entomology*).

Many authors have discussed the possible physical-chemical mechanisms of cell and organism survival both in supercooled and frozen states, using data on membrane condition, free and bound water etc. (Lozina-Lozinsky, 1973; Somme, 1967; Asahina, 1966; Salt, 1957, 1959, 1962, 1966a; Baust & Morrissey, 1975; Ring & Tesar, 1981; Poinot-Balaguer & Barra, 1983; Yi & Lee, 2003; Worland et al., 2004; Ozernyuk, 2000). Works on the cold-hardiness of invertebrates are still mostly inventory-like: temperature parameters of cold-hardiness are measured and mechanisms of cryoprotection are explored.

Unfortunately, ecological aspects of cold-hardiness are nothing like so well elucidated. Barely a few dozen such studies are available. Most of them either treat the adaptations of invertebrates overwintering under conditions with known and easy to measure temperature parameters: in tree trunks or even in the air above the snow surface (Madrid & Stewart, 1981; Ring & Tesar, 1980; 1981; Lee & Zachariassen, 2006), or deal with the "exotic" Antarctic insects (Baust & Lee, 1981; Block, 1981; Worland, 2005; Block & Zettel, 2003; Block & Convey, 1995, 2001). For instance, the gall midge *Eurosta solidaginis*, often overwintering above the snow line in the third instar larval stage, has become a model subject for such studies. Many dozens of works were published on its ecology, physiology and biochemistry (see Danks, 2005; Williams & Lee, 2005; Williams et al., 2004; Fuller, 2004; Irwin & Lee, 2002; Yi & Lee, 2003). A series of papers describes the ecology of the arctic moth larva *Gynaephora groenlandica* (see Danks, 2005; Bennett et al., 1999, 2003). Collembola are the taxon with the most thoroughly known taxonomic composition, set of life forms and diverse aspects of ecology and cold-hardiness (Somme, 1976, 1978, 1981, 1999).

Most works on the cold-hardiness of invertebrates naturally deal with species occurring in areas of the Northern Hemisphere with temperate climates, whereas studies of the peculiarities of invertebrate cold-hardiness in areas with very cold winters, marked by the distribution of permafrost, are virtually missing.

Yet it is under the extreme conditions of regions with continental climates, where microclimatic differentiation is strongly pronounced and seasonal ranges of temperatures are wide, that the adaptive capacities of organisms vividly manifest themselves. Communities and species of animals with different physiological requirements and adaptive strategies exist side by side in small territories of continental areas due to huge microclimatic contrasts. This is often the case,



This monograph attempts to determine how land insects (several abundant species of ants taken as an example) adapt to winter survival in northeastern Russia, the region with the lowest winter temperatures in the Northern Hemisphere. Data on the geographical, landscape and habitat distribution of species, the abundance of nests and families, location and organization of nests and population structure are given. Winter thermal regimes under conditions of extreme continental climate in differently positioned nests are described in detail. The influence of permafrost on the vital functions and wintering conditions of ants is examined. Characteristics of the cold-hardiness of larvae and adults (supercooling points and long-term tolerable temperature), seasonal changes in these parameters and concentrations of substances enabling cold-hardiness are given. The summarizing part of the book contains analysis of the relations between spatial distribution and cold-hardiness in ants in general, as well as of the adaptive strategies of these insects, which are intolerant of tissue freezing, that enable them to exist under extremely harsh climatic conditions.

The book is addressed not only to entomologists working in biological and agricultural research institutes, but also to all ecologists interested in the strategies of animal adaptations to extreme conditions and cold in particular. The book will also be of use to students of biology and of local lore.

"This excellent monograph brings together the results of fundamental, field-based studies on ants in north eastern Asia undertaken over 30 years of research collaboration by a group of researchers in the Magadan Region."

DR WILLIAM BLOCK,
Emeritus Fellow,
British Antarctic Survey,
Cambridge, UK

