5 The Effect of Snow Cover on Small Animals

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5.1 Introduction

Snow cover affects the lives of all animals in contact with it. The physical, chemical, and microbiological characteristics discussed in the previous chapters may influence to varying degrees the ability of animals to survive in snow-covered environments. Larger animals exposed to conditions above snow must adapt their behaviour, feeding habits, and morphology accordingly, while smaller animals may be below, within, or sometimes on snow cover. The thermal properties of snow cover allow organisms to survive in the relatively benign microenvironment of the subnivean (under the snow) space (Mani, 1962). The distribution of areas with snow cover are discussed with respect to animal habitats, and the physical properties and details of the subnivean and intranivean (within snow) microhabitats are described. Snow cover affects fauna where 15 to 25 cm of snow cover persists for at least 2 to 8 weeks per year. Animals may survive in the subnivean or intranivean spaces (Pruitt, 1978) of the tundra, taiga, deciduous, and mixed woods of the arctic, boreal, and temperate regions, respectively. Most of these areas with snow cover are at higher latitudes and/or altitudes, especially where there is a strong continental climate. Enough precipitation is needed to produce the requisite snow cover to provide insulation for animal survival against extreme temperatures (Mani, 1968; Aitchison, 1978a).

Keränen's (1920) classic synopsis on snow, which discusses in detail the effect of meteorology on the physical characteristics of snow, was followed by Geiger's (1965) extensive meteorological work on microclimates, which describes the subnivean space well. The snow cover is an ecotone between two different environments: (1) the dry, very cold, windy, and changeable atmospheric air and (2) the humid, relatively warm, and stable air of the space underneath (Coulianos and Johnels, 1962; Pruitt, 1970; Aitchison, 1978a).

Pruitt (1970) defined the crucial thickness of snow cover as the "hiemal threshold" (HT), i.e., that snow cover thickness at which the subnivean environment is insulated from diel fluctuations of the ambient air temperature. Snow density and grain characteristics affect its effective thermal conductivity and insulative capacity (Pomeroy and Brun, Chapter 2; Pruitt, 1970). Thicknesses greater than 20 cm are not believed to increase the insulating capacity of the snow cover significantly (Coulianos and Johnels, 1962; Geiger, 1965; Pruitt, 1970). In southern Finland the HT is 15 to 20 cm (Ylimäki, 1962), whereas in colder, northern Finland it is 25 to 30 cm (Keränen, 1920).

The thermal regime of the subnivean microenvironment makes it a favourable habitat for many small animals. Once the HT has been established, the temperature regime, not the overall snow cover thickness, affects animal activity (Novikov, 1940). The subnivean space is a thermally stable place in which the soil surface temperature remains near 0°C, while the ambient air temperature fluctuates (Strübing, 1958; Geiger, 1965; Pruitt, 1970; Aitchison, 1974). Generally the subnivean temperature varies between 0°C and −10°C, depending on snow cover thickness and density (Keränen, 1920; Coulianos and Johnels, 1962; Geiger, 1965; Aitchison, 1974, 1978a, 1984a; Pruitt, 1978). However, in the hard tundra snow conditions, it may drop to less than −20°C (Barrow, Alaska) (MacLean, 1975) or −25°C (Devon Island) (Fuller et al., 1975). Bushy vegetation and/or thick litter under snow cover further insulate the soil surface from fluctuations of ambient air temperature (MacKinney, 1929; Walker, Billings, and de Molenaar, Chapter 6).

The intranivean environment occurs within the snow cover, where temperatures are cooler than those of the subnivean space but generally warmer than the ambient air temperature (Geiger, 1965; Pruitt, 1970; Aitchison, 1974; Andreev and Krechmar, 1976; Korhonen, 1980; Leinaas, 1981a). At an extreme subnivean temperature of −18°C with at least 20 cm of snow, the intranivean temperature was about −26°C, while the ambient air temperature was −48°C in Siberia (Andreev and Krechmar, 1976); however, in the snow cover of a warm, maritime climate, the intranivean temperature may not be so different from either the subnivean or ambient air temperature (Leinaas, 1981a).

Light penetration into the snow cover (Pomeroy and Brun, Chapter 2) can affect the subnivean fauna (via biological clocks and photoperiod or "Zeitgeber") (Evernden and Fuller, 1972; Richardson and Salisbury, 1977). The physical characteristics of snow influence the degree of light penetration. For example, in northern Alberta in January, light did not penetrate 25 cm of fluffy, low density snow cover; however, as the snow cover metamorphosed and became denser in March, light penetrated to 36 cm (Evernden and Fuller, 1972).

Gas concentrations under snow cover can vary appreciably in both space and time (Tranter and Jones, Chapter 3). There is no strong correlation between the subnivean temperature and the concentration of CO_2. Gas concentrations can be quite steady over much of the winter period in relatively shallow cold snow cover (0.03 percent in Alaska; 0.02 percent in Manitoba), with a spring maximum of subnivean CO_2 concentration (over 0.05 percent in Alaska [Kelley, Weaver, and Smith, 1968], or 0.08 percent in Manitoba taiga [Penny and Pruitt, 1984]). By late winter, the CO_2 concentration can rise under ice layers within the snow cover. This is partly due to accumulated biological respiration from animals (Bashenina, 1956; Kelley et al., 1968; Batzli et al., 1980; Korhonen, 1980a; Penny and Pruitt, 1984), and partly due to soil microbial activity at −8°C or less (Tranter and Jones, Chapter 3). Mammals respond to increased CO_2 by avoiding areas where concentrations are high. When small mammal population densities are high, ventilation shafts, or snow chimneys, release the gas from under the snow (Batzli et al., 1980). Bashenina (1956) and Penny and Pruitt (1984) found more CO_2 accumulated in low-lying areas.

The nitrogenous excretory products from invertebrates under, within, and on the snow cover are dissolved in spring meltwater (Tranter and Jones, Chapter 3). Generally the metabolic activity of winter-active invertebrates is poorly known (Zinkler, 1966; Steigen, 1975a, 1975b).

5.2 Invertebrates

5.2.1 Nival and Aeolian Fauna

Nival fauna, the permanent residents of snow regions (Edwards, 1972), includes oligochaetes, snails, centipedes, mites (especially oribatids), spiders (especially linyphiids and erigonids), phalangids, pseudoscorpions, snow scorpionflies, springtails, bristletails, and butterflies (Bäbler, 1910; Kaisila, 1952; Janetschek, 1955; Swan, 1961; Mani, 1962, 1968; Edwards, 1972, 1987; Masutti, 1978; Ashmole et al., 1983; Thaler, 1988, 1989, 1992; Janetschek, 1995; Meyer and Thaler, 1995), all commonly seen up to 5,150 m (Swan, 1961) (Table 5.1). Generally the nival fauna is cold stenothermic (cold loving), small, and melanistic, with predatory or scavenging food habits (Edwards, 1987). The nival foragers include flies, springtails, carabid and staphylinid beetles, phalangids, grylloblattids, and ice worms (Mann, Edwards, and Gara, 1980; Ashmole et al., 1983). Even at 6,667 m in the Himalayas, the jumping spider *Euophrys omnisuperstes* was active (Swan, 1961; Wanless, 1975) (Table 5.1). Many of these invertebrates, other than springtails, are predatory (Bäbler, 1910; Edwards, 1987). The true nival fauna contains high-altitude species adapted to permanent habitats and with no adaptations for long-distance migration; 130 species have been collected in the Cairngorms in Scotland (Ashmole et al., 1983). Animal life

Table 5.1. *Endemic nival fauna from various countries and the altitudes at which the specimens were collected.*

Species	Country	Altitude (m)	Reference
Acari			
Pergamasus franzi	Austria	2,600	Janetschek (1993)
Bdella iconica	Austria	2,600	Janetschek (1993)
Araneae			
Euophrys omnisuperstes	Nepal	6,700	Janetschek (1990), Wanless (1975)
Diplocephalus rostratus	Austria	3,100+	Thaler (1988)
Erigone tirolensis	Austria	3,100	Thaler (1988)
Hilaira montigera	Austria	3,100	Thaler (1988)
Lepthyphantes armatus	Austria	3,100	Thaler (1988)
Lepthyphantes baebleri	Austria	3,100	Thaler (1988)
Xysticus bonneti	Austria	3,100	Thaler (1988)
Collembola			
*Hypogastrura himalayana**	Nepal	5,500	Janetschek (1990)
*Tomocerus nepalicus**	Nepal	5,600	Janetschek (1990), Mani (1968)
Isotoma mazda	Nepal	6,000	Janetschek (1990), Mani (1968)
*Isotoma saltans**	Switzerland	4,600	Bäbler (1910)
Isotoma saltans	Austria	2,600	Kopeszki (1988), Janetschek (1993)
*Isotomurus palliceps**	Austria	2,600	Janetschek (1993)
Coleoptera			
Bembidion glaciale	Austria	2,600	Janetschek (1993)
Nebria castanea	Austria	2,600	Janetschek (1993)
Atheta sp.	Nepal	4,875	Mani (1962)
Lepidoptera			
Boloria pales	Austria	2,600	Janetschek (1993)

*On ice and glaciers.

concentrates near the soil surface under stones and in silken chambers (Wanless, 1975; Meyer and Thaler, 1995). In the Italian Alps, winter activity of nival invertebrates was monitored, with typical winter species of springtails, stoneflies, flies, and snow scorpionflies on snow; winter activity was also seen in wasps, some butterflies, and beetles (Masutti, 1978).

The aeolian fauna, passively deposited on alpine snow fields by updrafts of wind from lower elevations, provides a food source for the resident nival arthropods, birds, and mammals (Mann et al., 1980). Numbers are highest in July, and the specimens mainly consist of dipterans (flies), homopterans (true bugs), coleopterans (beetles), and hymneopterans (wasps), all of which are characterised by dispersal flights (Kaisila, 1952; Edwards, 1972, 1987; Ashmole et al., 1983; Heiniger, 1989; Edwards and Sugg, 1993). The diversity of this fauna decreases with increasing latitude, and when there is little dust and/or vegetation on the snow, there are also few arthropods (Meyer and Thaler, 1995).

Activity by invertebrates at low temperatures may be maintained by following a thermal gradient that is within their preferred temperature range. It has been suggested that they have little competition for food (Viramo, 1983), that the snow surface simplifies mate location (Leinaas, 1981a), and that they have fewer predators (Hågvar and Østbye, 1973; Jonsson and Sandlund, 1975; Leinaas, 1981a; Aitchison, 1984a).

5.2.2 Subnivean, Intranivean, and Supranivean Fauna

During winter many invertebrates inhabit the stable microenvironment of the subnivean space. The subnivean fauna include oligochaetes, molluscs, centipedes, pseudoscorpions, phalangids, spiders, mites, springtails, beetles, flies, wasps, and other insects (Holmquist, 1926; Palmén, 1948; Mezhzherin, 1958; Mani, 1962; Polenec, 1962; Näsmark, 1964; Huhta, 1965; Kawakami, 1966; Kühnelt, 1969; Oswald and Minty, 1970; Berman et al., 1973; Willard, 1973; Thaler and Steiner, 1975; Granström, 1977; Olynyk and Freitag, 1977; Aitchison, 1978a, 1978b, 1979a, 1979b, 1979c, 1979d, 1979e, 1979f, 1983, 1984a, 1984b, 1984c, 1987, 1989; Flatz, 1979; Puntscher, 1979; Flatz and Thaler, 1980; Leinaas, 1981a; Green, 1982; Merriam, Wegner, and Caldwell, 1983; Viramo, 1983; Schmidt and Lockwood, 1992).

Small arthropods move about in their protected microenvironment in the temperature range of 0°C to −10°C (Näsmark, 1964; Aitchison, 1974, 1978a; Schmidt and Lockwood, 1992). Most of these invertebrates are not active below −5°C (Huhta, 1965; Aitchison, 1979b, 1979c, 1979d, 1979e, 1979f; Leinaas, 1981a; Merriam et al., 1983), with the exception of mites, spiders, springtails, and some wasps (Aitchison, 1978a, 1979a, 1979c, 1979d).

The major winter-active groups to be discussed are the mites, spiders, springtails, beetles, flies, and wasps. Probably long before the subnivean fauna was discovered, insects and spiders were noticed on snow. At the Arctic Circle in the former Soviet Union (FSU), Novikov (1940) observed active insects and spiders on snow at −1°C and concluded that their activity on snow depended on the temperature regime of the subnivean space and not on the thickness of the snow cover. Many have noticed this supranivean invertebrate activity (Chapman, 1954; Wolska, 1957; Buchar, 1968; Østbye, 1966; Hågvar, 1971, 1973; Huhta and Viramo, 1979; Koponen, 1983).

Mites (order Acari) are ubiquitous small arachnids, which live predominantly on the soil surface and within the soil. They have even been collected at 5,000 m in the Himalayas (Mani, 1962), on the sub-Antarctic islands (Dalenius and Wilson, 1958), and in the Antarctic (Sømme, 1993), often at subzero temperatures (Dalenius and Wilson, 1958; Sømme, 1993). They move into the humus as temperatures cool in autumn. A number have low thermal preferences (Wallwork, 1970). On the Canadian prairies, Willard (1973) and Aitchison (1979c) found increases in subnivean numbers in February and March. This is a time of increased snow density and metamorphosis, which allows greater light penetration (Geiger, 1965; Evernden and Fuller, 1972), and possibly a response to increased intensity of incident solar radiation from 19 to 55 W/m^2 (Budyko, 1963). Kevan (1962) also noted that mites were active under snow. Likewise, in Australia and Finland subnivean pitfall traps collected many mites (Green, 1982; Viramo, 1983). Although the ecology of the family Rhagidiidae is virtually unknown (Zacharda, 1980), this family is one of the most abundant subnivean, winter-active acarine groups in North America. Up to 4,800 m in the Himalayas rhagidiids have been collected from the upper tree line and at the foot of a glacial moraine (Zacharda and Daniel, 1987). The families Eupodidae and Parasitidae are also common winter-active groups (Aitchison, 1979c; Schmidt and Lockwood, 1992). Table 5.2 shows examples of nival fauna from different parts of the world.

Spiders (order Araneae) are quite active in the subnivean space, down to −8° C (Aitchison, 1978a). Their activity at subzero temperatures in the subnivean microclimate has been documented in Europe (Mezhzherin, 1958; Näsmark, 1964; Huhta, 1965; Granström, 1977; Schaefer, 1977a; Flatz, 1979; Puntscher, 1979; Flatz and Thaler, 1980) and in North America (Holmquist, 1926; Olynyk and Freitag, 1977; Aitchison, 1978a, 1984b; Merriam et al., 1983; Schmidt and Lockwood, 1992). In south central Canada five families (Linyphiidae, Erigonidae, Lycosidae, Clubionidae, and Thomisidae) are winter active, especially the small erigonid spiders, such as *Ceraticelus* spp., comprising 34.6 percent of the catch and being active down to −8° C (Aitchison, 1978a, 1984b). Immature *Agroeca* and *Pardosa* and adult linyphiids maintained activity during winter months (Holmquist, 1926; Wolska, 1957; Almquist, 1969; Huhta, 1971; Hågvar, 1973; Thaler and Steiner, 1975; Aitchison, 1978a).

Spiders are often encountered on snow surfaces (Levander, 1913; Chapman, 1954; Mani, 1962; Thaler and Steiner, 1975; Huhta and Viramo, 1979; Koponen, 1983, 1989; Fox and Stroud, 1986; Janetschek, 1993). Figure 5.1 shows *Bolyphantes index* in its

Table 5.2. *Arachnids associated with snow cover in different countries, location in the snow cover and temperature range of activity.*

Species	Country	Location*	Temperature (°C)	Reference
Acari				
Rhagidia sp.	Nepal	SP?	>–10	Mani (1962)
Rhagidia sp	Canada	SB	>–10	Aitchison (1979c)
Bdella sp.	Nepal	SP?	>–10	Mani (1962)
Bdella sp	Canada	SB	>–10	Aitchison (1979c)
Parasitus sp.	Nepal	SP?	> 10	Mani (1962)
Parasitus sp.	Canada	SB	>–10	Aitchison (1979c)
Parasitus sp.	USA	SB	>–5	Schmidt and Lockwood (1992)
Eupodes sp.	USA	SB	>–5	Schmidt and Lockwood (1992)
Evadorhagidia sp.	USA	SB	>–5	Schmidt and Lockwood (1992)
Araneae				
Ceraticelus spp.	Canada	SB	>–8	Aitchison (1978a, 1984b)
Agroeca spp.	Canada	SB	>–6.8	Aitchison (1978a)
Pardosa spp.	Canada	SB	>–6.2	Aitchison (1978a)
Lepthyphantes cristatus†	Czechoslovakia	SP	0	Buchar (1968)
Centromerus incilium†	Norway	SP	0	Hågvar (1973)
Bolyphantes index†	Norway	SP	>–5	Østbye (1966)
Bolyphantes index	Finland	SP	0	Huhta and Viramo (1979), Koponen (1983, 1989)
Macrargus rufus	Finland	SP	+2 to –2	Huhta and Viramo (1979), Koponen (1983, 1989)
Tmeticus affinis	Finland	SP	+2 to 2	Huhta and Viramo (1979), Koponen (1983, 1989)
Helophora insignis	USA	SB	–4 to –5	Schmidt and Lockwood (1992)
Gnaphosa intermedia	Finland	SP	0	Koponen (1983, 1989)
Pseudoscorpionida				
Neobisium spp.	Spain, Germany	SP	–1 to –3	Schwaller (1980)
Microbisium spp.	Canada	SB	>–4	Aitchison (1979f)
Phalangida				
Undetermined species	Finland	SP	>–1.5	Levander (1913), Viramo (1983)

*SB – subnivean; SP – supranivean.

†Webs over snow depressions.

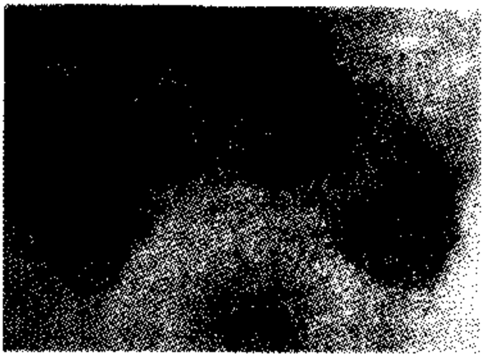


Figure 5.1. A pair of *Bolyphantes index* in a web constructed over a fox footprint in snow (Hågvar, 1973).

web over a fox footprint in the snow cover. The families Linyphiidae, Erigonidae, Thomisidae, Gnaphosidae, Lycosidae, and Salticidae frequent the snow surface as well as the subnivean space (Buchar, 1968; Mani, 1968; Hågvar, 1973; Thaler and Steiner, 1975; Aitchison, 1978a, 1984c; Huhta and Viramo, 1979). Subnivean trapping produced a richer fauna, as some species never migrate to the snow surface (Koponen, 1989). Table 5.1 provides some details about winter-active spiders.

Other arachnids on the snow surface include pseudoscorpions (Schwaller, 1980) and phalangids (harvestmen) (Levander, 1913; Viramo, 1983). The former also are active in the subnivean space (Aitchison, 1979f) (Table 5.1).

Springtails (order Collembola) are a major group of winter-active insects that are active in the subnivean space at temperatures down to −7.8°C (Kevan, 1962; Aitchison, 1979a) (see also Table 5.3). Activity peaks were seen in late winter (February and March), as with the mites (Wallwork, 1970; Willard, 1973), perhaps because of greater light penetration through the denser snow cover (Geiger, 1965; Evernden and Fuller, 1972). The family Isotomidae is dominant in the Arctic, with cold-hardy *Isotoma viridis* active on snow (Agrell, 1941; Chapman, 1954). This is also a common winter-active, subnivean species in continental North America (Aitchison, 1979a; Schmidt and Lockwood, 1992), along with other species of *Isotoma*. Isotomids were also collected in subnivean pitfall traps in the Australian Alps (Green, 1982).

Collembolans are commonly seen on snow at about 0°C (Table 5.2) and are abundant at high altitude, with some species even living on permanent snow and ice at 6,000 m in the Himalayas (Mani, 1962, 1968). In the European mountains *Isotoma saltans* (see Figure 5.2) is associated with glacier ice and is often called "Gletscherfloh," or glacier flea (Strübing, 1958). Especially abundant on melting snow (Chapman, 1954),

Table 5.3. *Collembolans associated with snow cover in different countries, location in the snow cover, and temperature range of activity.*

Species	Country	Location*	Temperature (°C)	Reference
Dicyrtomina rufescens	Japan	SP	eats at –1	Uchida and Fujita (1968)
Hypogastrura socialis	USA	SP	eats at 0	MacNamara (1924)
Hypogastrura socialis	Finland	SP	0	BK & BK (1980)†
Hypogastrura socialis	Norway	SP	migrates at 0	Hågvar (1995)
Hypogastrura spp.	Nepal	SP	0	Mani (1962)
Hypogastrura spp.	Norway	SP	0	Østbye (1966)
Hypogastrura spp.	Finland	SP	0	Levander (1913), Koponen (1983)
Hypogastrura spp.	Germany	SP	0	Strübing (1958)
Entomobrya nivalis	Finland	SP	0	BK & BK (1980)†
Entomobrya spp.	USA	SB	0	Holmquist (1926)
Tomocerus flavescens	USA	SB	0	Holmquist (1926)
Tomocerus flavescens	Finland	SP	0	BK & BK (1980)†
Tomocerus flavescens	Canada	SB	eats at 2	Aitchison (1983)
Tomocerus spp.	USA	SP	eats at 0	Knight (1976)
Lepidocyrtus cyaneus	Canada	SB	eats at –2	Aitchison (1983)
Lepidocyrtus lignorum	Finland	SP	0	BK & BK (1980)†
Orchesella bifasciata	Finland	SP	0	BK & BK (1980)
Orchesella ainslei	Canada	SB	eats at –2	Aitchison (1983)
Isotoma alpa	USA	SB	>–4	Schmidt and Lockwood (1992)
Isotoma gelida	USA	SB	>–4	Schmidt and Lockwood (1992)
Isotoma hiemalis	Finland	SP	0	BK & BK (1980)†
Isotoma hiemalis	Switzerland	SP	>–3	Zettel (1984)
Isotoma olivacea	Poland	SP	+5 to –5	Wolska (1957)
Isotoma saltans	Poland	SP	0 to –4	Wolska (1957), Wojtusiak (1951)
Isotoma saltans	Germany	SP	+5 to –5	Strübing (1958)
Isotoma viridis	Sweden	SP	>–8	Agrell (1941)
Isotoma viridis	Canada	SB	eats at –2	Aitchison (1983)
Isotoma viridis	USA	SB	>–4	Schmidt and Lockwood (1992)

*SB – subnivean; SP – supranivean.

†BK & BK, Brummer-Korvenkontio and Brummer-Korvenkontio.

Figure 5.2. Collembolans *Isotoma saltans* on snow (Schaller, Vienna).

collembolan aggregations produce sooty, red, or gold snow, depending upon the colour of the aggregating species (Strübing, 1958; Mani, 1962). In Norway, *Hypogastrura socialis* masses on snow in mild conditions, possibly to migrate to snow-free patches for early reproduction. This species can travel 200 to 300 m/day; or 2 to 3 km in 10 days of fair weather, by steadily jumping in a certain direction (Hågvar, 1995). In mild conditions entomobryids and isotomids are on snow cover, moving into it to avoid freezing soil or flooding (Brummer-Korvenkontio and Brummer-Korvenkontio, 1980; Leinaas, 1983).

Solar radiation and temperature conditions affect collembolan activity on the snow cover; the former can raise the body temperature of *Isotoma violacea* several degrees Celsius (Fox and Stroud, 1986). Nival collembolans have many pigment granules in their epidermal cells as protection against strong solar radiation (Eisenbeis and Meyer, 1986; Kopeszki, 1988). The activity of some of these animals has been documented down to −6°C (Levander, 1913; Tahvonen, 1942; Chapman, 1954) and to −9.8°C (Tahvonen, 1942). The snow surface activity by *Isotoma hiemalis* is limited by temperature (down to −3°C) and changing barometric pressure, causing the species to aggregate in depressions with warmer microclimates (Zettel, 1984). In the maritime climate of southern Norway springtails can be found throughout the snow cover, which has a minor temperature gradient of only a degree or so (Leinaas, 1981a, 1983). Ice layers within the snow can prohibit migration to the surface by springtails, which constantly move up and down in the snow cover (Zettel, 1984; Kopeszki, 1988).

Some beetles (order Coleoptera) are active at temperatures near 0°C (Holmquist, 1926; Chapman, 1954; Renken, 1956; Wolska, 1957; Näsmark, 1964; Aitchison, 1979b). The winter-active families include Staphylinidae, Carabidae, and Cantharidae, especially the small species of *Atheta*, *Bembidion*, and *Philonthus* (Chapman, 1954; Heydemann, 1956; Renken, 1956; Näsmark, 1964; Wallwork, 1970; Aitchison, 1979b; Viramo, 1983; Schmidt and Lockwood, 1992). Active cantharid larvae, often associated with winter, have been called "Schneewürme" (Renken, 1956) and prefer cool temperatures (Wolska, 1957). Heydemann (1956) found that below −4°C beetles ceased moving. In Finland, Palmén (1948) noted survival of staphylinids and carabids below snow from 0° to −5.5°C. In the subnivean microclimate carabids stay active, with some inactivity of adults in midwinter (Holmquist, 1926; Flatz and Thaler, 1980; Green, 1982).

The beetles may also be active on the snow surface, especially the carabids and staphylinids, which often prefer low temperatures (Tahvonen, 1942; Chapman, 1954; Wolska, 1957; Viramo, 1983). Likewise, the nival coleopterans, consisting of 45 percent carabids and 17 percent staphylinids, are mostly small and peculiar to the nival zone above 4,000 m but not to the taiga zone (Mani, 1962). In the Himalayas, *Bembidion* was the most important carabid genus (over 25 species from the nival zone), and *Atheta* was the dominant staphylinid genus (Mani, 1962). The same genera are active in the subnivean space in Canada (Aitchison, 1979b) (Table 5.1).

A number of flies (order Diptera), especially the tipulid genus *Chionea*, are associated with snow in the arctic and alpine regions – e.g., the families Anthomyidae, Chironomidae, Simuliidae, Stratiomyidae, Tipulidae, Trichoceridae, Mycetophilidae, Phoridae, Sciaridae, and Sphaeroceridae (Holmquist, 1926; Tahvonen, 1942; Wojtusiak, 1951; Chapman, 1954; Renken, 1956; Mani, 1962; Dahl, 1969; Hågvar, 1971; Hågvar and Østbye, 1973; Jonsson and Sandlund, 1975; Aitchison, 1979d). Unidentified, red cecidomyiid larvae crawled around on the snow surface at about 0°C on windless days (Aitchison unpublished data). Hågvar (1971) recorded a supercooling point of −7.5°C in *Chionea araneoides*. *Chionea lutescens* has been frequently collected on snow (Novikov, 1940; Tahvonen, 1942; Mani, 1962; Hågvar, 1971, 1976; Mendl, Müller, and Viramo, 1977; Koponen, 1983), even at −10°C (Brummer-Korvenkontio and Brummer-Korvenkontio, 1980), and in subnivean pitfall traps (Broen and Mohrig, 1964; Itämies and Lindgren, 1985) (Table 5.4). Species of the family Chironomidae of the genus *Diamesa* have been encountered walking on the snow surface and occasionally flying about at around −1°C on windless, cloudy days (Hågvar and Østbye, 1973; Jonsson and Sandlund, 1975). Chironomids have a thermal preference between 0° and −2°C (Hågvar and Østbye, 1973).

Table 5.4. *Other insects and oligocheates associated with snow cover in different countries, location in the snow cover, and temperature range of activity.*

Species	Country	Location*	Temperature (°C)	Reference
Diptera				
Chionea araneiodes	Norway	SP	0 to –4	Sømme and Østbye (1969)
Chionea lutescens	Poland	SP	>–5	Wolska (1957)
Chionea lutescens	Germany	SP	>–4	Strübing (1958)
Chionea lutescens	Finland	SP	–2.3	Tahvonen (1942)
Chionea lutescens	Finland	SB	>–10	Itämies and Lindgren (1985)
Chionea spp.	Finland	SP	>–2.3	Tahvonen (1942)
Chionea sp.	Poland	SP	>–5.6	Wojtusiak (1951)
Chionea sp.	USA	SP	>–5.6	Chapman (1954)
Chionea sp.	FSU	SP	>–6	Novikov (1940)
Chionea sp.	Norway	SP	>–6	Hågvar (1971)
Chionea sp.	Nepal	SP	>–8	Mani (1962)
Exechia sp.	Sweden	SB	0	Plassman (1975)
Mycetophila sp.	Sweden	SB	0	Plassman (1975)
Mycetophila sp.	Canada	SB	>–4	Aitchison (1979d)
Suilla longipennis	Canada	SB	>–4	Aitchison (1979d)
Megaselia spp.	Canada	SB	>–4	Aitchison (1979d)
Bradysia spp.	Canada	SB	>–4	Aitchison (1979d)
Leptocera spp.	Canada	SB	>–4	Aitchison (1979d)
Diamesa spp.	Nepal	SP	0 to –7.2	Kohsima (1984)
Diamesa spp.	Nepal	SP	–16	Kohsima (1984)
Musidora lutea	Finland	SP	–6	Tahvonen (1942)
Mecoptera				
Boreus spp.	Finland	SP	–1	Tahvonen (1942), Viramo (1983)
Boreus spp.	Germany	SP	–1	Strübing (1958)
Boreus spp.	Norway	SP	–5.5	Fjellberg and Greve (1968)
Oligochaeta				
Lumbricids and enchytraeids	FSU	SB		Berman et al. (1973)
Lumbricids	Canada	SB	>+2	Aitchison (1979e)

*SB – subnivean; SP – supranivean.

In the subnivean space, flies of the families Anthomyidae, Mycetophilidae, Phoridae, Sciaridae, and Sphaeroceridae (species of *Suilla*, *Mycetophila*, *Megaselia*, and *Bradysia*) are winter-active (Holmquist, 1926; Broen and Mohrig, 1964; Plassman, 1975; Aitchison, 1979d; Merriam et al., 1983; Viramo, 1983). All are cold resistant (Renken, 1956), and some are active to −5°C (Dahl, 1969). In southern Canada this order ceased subnivean movement below −3.5°C (Aitchison, 1979d) (Table 5.4).

The winter-active wasps (order Hymenoptera) include the families Ceraphronidae, Diapriidae, and Scelionidae, which cease movement at −5.5°C (Aitchison, 1979d). Winter-active genera include *Ceraphron*, *Dendrocerus*, *Belyta*, *Scelio*, and *Trimorus* spp. (Aitchison, 1979d). Of other insects, one group that is commonly winter-active, even under the snow cover, is the true bug family Cicadellidae (leafhoppers) (order Homoptera) (Holmquist, 1926; Aitchison, 1978b; Green, 1982; Viramo, 1983), whose nymphs are active at subnivean temperatures of −1.5°C to −4.5°C (Aitchison, 1978b).

Another well-known winter insect is the snow scorpionfly *Boreus* spp. (order Mecoptera), whose cold-resistant adults were observed jumping on snow (Tahvonen, 1942; Strübing, 1958; Fjellberg and Greve, 1968; Viramo, 1983) (Table 5.4). On the snow cover these dark insects absorb solar radiation to increase their body temperature on sunny days as much as 4°C above the ambient air temperature. When the air temperature drops below −3°C, the insects retreat to the warmer subnivean space (Shorthouse, 1979; Courtin, Shorthouse, and West, 1984). The thermal preferendum of this genus is between 0° and −1°C (Wojtusiak, 1951; Fjellberg and Greve, 1968).

Figure 5.3 and its commentary delightfully depict the snow fauna commonly seen in boreal situations in Canada. In this fantasy by Flahey, different species of collembolans act as sled dogs, with *Chionea* and *Boreus* acting as "mushers," while mites cheer them on in their race.

The rock crawlers of the genus *Grylloblatta* (order Grylloblattodea) are flightless carnivores and scavengers from mountains and are associated with snow and low temperatures down to −6°C (Chapman, 1954; Strübing, 1958; Pritchard and Scholefield, 1978; Edwards, 1987). These insects are darkly coloured and readily absorb the sun's rays on the snow surface (Pritchard and Scholefield, 1978).

Within glaciers, *Mesenchytraeus solifugus* or "ice worms" of the Oligochaete family Enchytraeidae survive year round at approximately 0°C in polar and temperate regions, appearing on the snow surface at dusk and burrowing into ice by day (Janetschek, 1955; Goodman, 1971).

I would like to thank the following, for without their unwitting participation this card would not have been possible. Not all the insects are drawn to scale, but are depicted as accurately as possible with the aid of stereo and compound microscopes. They are listed under Common name, Scientific name, Family name, Order under which they are classified and location where all were collected.

Je tiens à remercier les participants (volontaires ou non) suivants sans lesquels la réalisation de cette carte aurait été impossible. Les insectes ainsi que l'équipement entomologique n'ont pas tous été dessinés à l'échelle mais ont été représentés avec autant de précision que possible à l'aide du microscope et à la loupe binoculaire. Ils ont été décrits d'après leur nom commun, leur nom scientifique, leur nom de famille et le lieu de récolte de la majorité des échantillons.

1 Winter stone fly, Taeniopteryx nivalis, Nemouridae, Plecoptera, Orleans Island, Quebec.
2 Winter snow fly, Chionea alexandriana, Tipulidae, Diptera, Gatineau Park, Quebec.
3 Springtail, Isotoma viridis, Isotomidae, Collembola, Belleville, Ontario.
4 Leodid beetle, Agyrtes longulus, Agyrtidae, Coleoptera, Salmon Arm, B.C.
5 Winter tick, Dermacentor albipictus, Ixodidae, Acari, Fort Smith, N.W.T.
6 Dog flea, Ctenocephalides canis, Ctenocephalidae, Siphonaptera, Vancouver, B.C.
7 Springtail, Tomocerus flavescens, Tomoceridae, Collembola, Ottawa, Ontario.
8 Springtail, Hypogastrura nivicola, Poduridae, Collembola, Arnprior, Ontario.
9 Predatory mite, Pergamasus crassipes, Parasitidae, Acari, St John's, Newfoundland.
10 Snow scorpionfly, Boreus nivoriundus, Boreidae, Mecoptera, Ithaca, N.Y.

In the winter of 1925, on the frozen north-west shore of Alaska's Norton Sound, the inhabitants of Nome were smitten by a diphtheria epidemic. Because the closest community was 1200 miles away in the gold-rush town of Iditarod, the problem of obtaining life saving serum was almost insurmountable. The formidable terrain and high Arctic winds allowed only one possibility, that of sending the serum by a relay of dog sled teams. To commemorate those heroic mushers and dogs who saved the people of Nome, the Iditarod dog sled race is held annually, with over 20 checkpoints along the route.

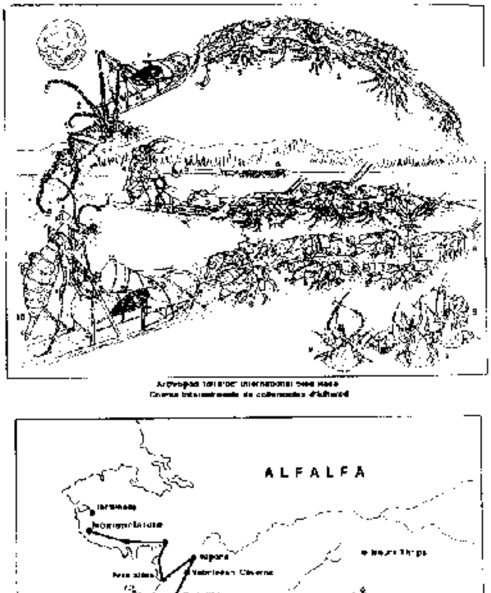
The "Arthropod Iditarod" sled race is also held annually over quite a different route (see map). It commemorates the transportation of the antidote Atropine from the colony of Anchorius (one hundred million inhabitants per cubic metre) to rescue the small arthropod community of Nomenclature. In 1956, an intoxicated entomologist, of no fixed address, inadvertently sprayed the local insect population with an experimental organophosphate, causing outbreaks of involuntary stridulation, systemic agoraphobia, and permanent diapause.

As in the rescue attempt, most sled teams are comprised principally of winter snow fleas and exhibit the multidirectional and unpredictable movements over the snow typical of their breed. Despite the efforts of their mushers, checkpoints are rarely found. Constantly harassed by roving bands of predaceous mites, the race often takes many months to complete.

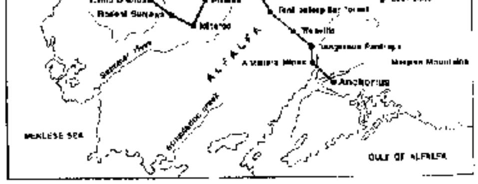
À l'hiver de 1925, au large de la côte glacée nord-ouest de Norton Sound en Alaska, les habitants de Nome étaient pris d'une épidémie de diphtérie. La communauté la plus rapprochée, étant à 1200 milles de la ville Iditarod, ville connaissant la ruée vers l'or, posait un obstacle infranchissable: comment se procurer d'un sérum qui leur sauverait la vie? Ce terrain redoutable, joint aux vents élevés arctiques, ne permettaient qu'une possibilité. Il faudrait donc expédier le sérum par un relais de traîneaux tirés par des chiens. Afin de commémorer ces chauffeurs de traîneaux et ces chiens héroïques qui ont sauvé la vie aux habitants de Nome, la course de traîneaux tirés par chiens de Iditarod est devenue internationale et a lieu annuellement avec plus de vingt points de contrôle placés au long de la route.

La course de traîneaux "Arthropode Iditarod" a lieu annuellement sur une route très différente (Voir carte). Celle-ci commémore la transportation de l'antidote Atropine de la colonie Anchorius, (population: de cent millions habitants par mètre carré) afin de sauver la petite communauté d'arthropodes à Nomenclature. En 1956, un entomologiste ivre, sans domicile connu, pulvérise la population d'insectes locale avec un organophosphate, provoquant chez ces derniers des manifestations de stridulation involontaires et d'agoraphobie systématique.

Contenant principalement des puces d'hiver, la plupart des traîneaux tirés par chiens manifestent des mouvements sur la neige totalement multidirectionnels et irrationnels. En dépit des efforts des chauffeurs, les points de contrôle sont rarement trouvés. Harcelés incessamment par des bandes errantes de mites prédatrices, la course requiert souvent plusieurs mois pour compléter.



Arthropod Iditarod International Sled Race
Course internationale de collemboles d'Iditarod



Anticipated route of Arthropod sled race

Information regarding cards and posters in this series can be obtained by writing to the artist; Barry Flahey, P.O. Box 296, Manotick, Ontario, Canada K4M 1A2.

Figure 5.3. Fantasy card of winter-active invertebrates by Barry Flahey, with a description of the race involved.

5.2.3 Physiological and Morphological Mechanisms

There are several physiological mechanisms by which invertebrates can tolerate the low temperatures of winter: cold-hardiness and thermal hysteresis (the difference between the melting and freezing points of the haemolymph). Factors determining cold-hardiness are the ability 1) to resist freezing, 2) to supercool (avoiding freezing below the freezing point of haemolymph by introducing "antifreeze" agents), and 3) to survive long exposures to low temperatures (Asahina, 1966; Leinaas, 1983; Sømme, 1989). Invertebrates fall into two groups: the freezing-resistant group, which tolerates intracellular freezing of body tissues (e.g., insect larvae and pupae), and the freezing-sensitive group, which avoids intracellular freezing but tolerates extracellular freezing by means of lowering the freezing point and supercooling points of the haemolymph and/or the accumulation of low molecular weight, cryoprotective polyhydric alcohols such as glycerol (Salt, 1961; Asahina, 1966; Storey, 1984; Sømme, 1989; Lee, 1991). Inactive invertebrates in diapause tolerate low temperatures by supercooling (accumulating cryoprotective compounds that lower freezing and supercooling points) and by dehydration, both of which increase haemolymph viscosity (MacLean, 1975; Husby and Zachariassen, 1980; Sømme, 1989). The supercooling point is also affected by the amount of food in the gut and the presence of moisture (Sømme, 1989). In *Entomobrya nivalis* cold-hardiness is influenced by temperature and photoperiod (Zettel and Allmen, 1982). Invertebrates are capable of muscular and metabolic activity when supercooled (MacLean, 1975). Winter-active invertebrates do not appear to supercool; it seems that thermal-hysteresis proteins permit them to move (Duman, 1979; Husby and Zachariassen, 1980).

Another physiological adaptation found in this fauna is that of anaerobiosis. There are times when insects become completely encased in ice, resulting in periods of oxygen deficiency. For example, in Norwegian mountains the carabid beetle *Pelophila borealis* can live without oxygen for 6 months; arctic and polar mites, dipterans, and springtails also can undergo anaerobiosis (MacLean, 1975; Sømme, 1993).

Feeding may be deleterious for winter-active invertebrates that ingest food particles containing dust that act as potential ice nucleators (Salt, 1953, 1961). For many insects at the start of winter, cessation of feeding and emptying the gut of ice crystal nucleators enhances their ability to supercool; with resumption of feeding in the spring, the insects lose the capability to supercool (Ohymama and Asahina, 1972; Østbye and Sømme, 1972; Sømme, 1989). The carabid beetle *Pterostichus brevicornis* changed its diet in autumn from insects to dry wood and then ceased feeding in early winter at about −4°C (Kaufmann, 1971).

In south central Canada winter-active, subnivean invertebrates were all frost sensitive, with freezing points of haemolymph between −7°C and −8°C (Aitchison and Hegdegar, 1982). These animals were prohibited in their movements, as they did not have cryoprotective compounds in their haemolymph (Husby and Zachariassen, 1980). It appears that they use thermal hysteresis. Most winter-active collembolan specimens, however, do have empty guts below 0°C (Leinaas, 1981a; Aitchison, 1983).

Most of these cold-active invertebrates exhibit a low temperature preference, often associated with a low supercooling point. The winter-active spider *Bolyphantes index* preferred 4.1°C, maintained normal activity down to −5°C, and had a chill-coma temperature of −9.3°C and a supercooling point of −15.3°C (Hågvar, 1973). The preferred temperatures are above the chill-coma values. Likewise, the springtail *I. hiemalis*, which preferred −2.5°C and above, was active down to −6°C, experienced chill-coma at −8°C, and had a supercooling point of −15°C (Zettel, 1984). *Chionea* collected on snow between 0°C and −6°C had a supercooling temperature of −7.5°C (Sømme and Østbye, 1969). Mani (1962) noted pronounced cold stenothermy in nival insects, around 0°C, often with normal development, growth, and metamorphosis between −1.5°C and 1.7°C. The mites and springtails are the arthropods most tolerant of cold (Mani, 1962; Sømme, 1993).

Some springtails undergo a unique morphological change from summer to winter, which reverses in the spring, called cyclomorphosis (Fjellberg, 1976, 1978a; Leinaas, 1981b; Zettel, 1984). In late autumn during a moult (ecdysis) to the winter morph, the locomotory furcula and tibiotarsae change from the simple summer form to a more complex winter form, which is enlarged and has more setae (see Figures 5.4 and 5.5). Zettel (1984) noted that only those specimens of *I. hiemalis* that undergo cyclomorphosis (morph *I. h. hiemalis*) move to the snow surface, while those

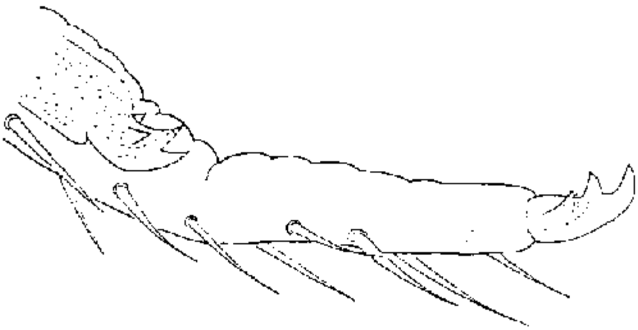


Figure 5.4. Furca (dens and mucro) of a specimen of the collembolan *Isotoma hiemalis* in ecdysis showing transformation from the *mucronata* form to the *hiemalis* form (from Fjellberg, 1976).

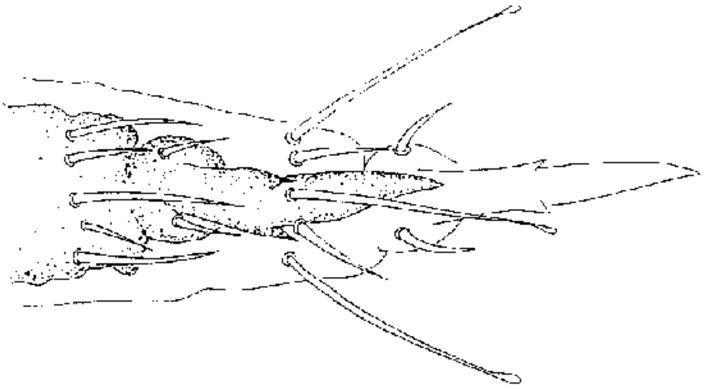


Figure 5.5. Collembolan *Isotoma nivea*: tibiotarsus II of a specimen in ecdysis, showing transformation from the *Vertagopus* form (clavated spur hairs) to the normal form (dotted) (from Fjellberg, 1978a).

that do not change (morph *I. h. mucronata*) stay in the subnivean space. Fjellberg (1978a) observed an even more pronounced change, a taxonomic artefact: an autumn specimen of an unknown species of springtail *Vertagopus* appeared very similar to *Isotoma nivea* with different tibiotarsal spur hairs. In spring, specimens of this "species" were found in ecdysis, changing from *Vertagopus* to *I. nivea* (Fjellberg, 1978a)! In Manitoba, winter specimens of *Isotoma manitoba* and *Isotoma blufusata* underwent cyclomorphosis (Fjellberg, 1978b).

5.2.4 Food Webs

The aeolian fauna, deposited onto snow fields from wind updrafts from lower elevations, contain wind-borne pollen grains, microorganisms, and arthropod fallout, an important nutrient source ("manna") in montane systems for resident nival arthropods, birds, and mammals (Swan, 1961; Mann et al., 1980; Edwards, 1987). On the snow surface food chains are short with few specific interactions. Most other snow insects are scavengers or carnivores that could feed on animals such as springtails. In Chapter 4 Hoham and Duval discuss a microbial food web that may serve as a basis for the higher invertebrate component of a nival food web. Snow communities have many carnivorous and predatory members.

Certainly many of these animals do feed at temperatures near 0°C – e.g., springtails (MacNamara, 1924; Mani, 1962; Uchida and Fujita, 1968; Edwards, 1972; Eisenbeis and Meyer, 1986). Cold room experiments with winter-collected specimens fed on fungal hyphae at 2°C and −2°C (Aitchison, 1983) corroborate this. These collembolans may well form the basis of a subnivean and/or nival food chain (Mani, 1962; Aitchison, 1984b). The herbivorous chironomid fly *Diamesa* feeds on algae in a high Nepalese glacier (Kohshima, 1984). When food is scarce, the nocturnal nival fauna is active for longer periods. Generally the small invertebrates are active by day and the larger ones are active by night, thus avoiding predation (Mann et al., 1980). Fox and Stroud (1986) found a strong correlation between the numbers of spiders and their collembolan prey on the snow surface. There are very few beetles in this habitat (Thaler, 1989; Janetschek, 1990, 1993). Common prey of spiders, springtails (Huhta, 1965) were fed upon by winter-active spiders in laboratory experiments (Aitchison, 1984a). Other possible predators include grylloblattids, which feed at low temperatures (Mann et al., 1980), carabid beetles, and mites (Mani, 1962).

The arachnids are detritivous (mites) or predatory (mites and spiders). Mites in large numbers (e.g., genus *Rhagidia*) wander on the snow surface and usually are associated with springtails (Mani, 1962), on which they probably prey (see Tables 5.1 and 5.2). Winter-active spiders, such as *Lepthyphantes cristatus*, feed at −2°C on surface active springtails and small flies (Polenec, 1962; Buchar, 1968; Hågvar, 1973; Schaefer, 1976, 1977a; Aitchison, 1984b, 1989) (Table 5.1). Fox and Stroud (1986) found a strong correlation between spider numbers and their collembolan prey, while Aitchison (1989) presented data on winter-active collembolans and spiders, implicating a possible subnivean food chain.

Springtails are capable of feeding at temperatures near 0°C, eating blue-green algae from tree trunks (Uchida and Fujita, 1968), red snow algae (Kopeszki, 1988), coniferous pollen on the snow surface (MacNamara, 1924), organic debris (Knight, 1976), kryokonite (fine micaceous particles with algae, protozoans, rotifers, tardigrades, pollen grains, and detritus) (Eisenbeis and Meyer, 1986; Schaller, 1992), and fungal hyphae (Aitchison, 1983) (Table 5.2). Snow algae in the snow cover (Hoham and Duval, Chapter 4) could provide a good food source for intranivean collembolans. At subzero temperatures the lack of feeding avoids the problem of ingesting dust particles into the gut, which may act as ice nucleators causing freezing and subsequent death (Salt, 1953; Joosse and Testerink, 1977). Subnivean onychiurids had no gut contents (Aitchison, 1983), and *Onychiurus subtenuis* under snow consumed little, but once freed of the snow cover fed voraciously (Whittaker, 1981).

Other winter-active invertebrates also feed on a variety of substances. With a carnivorous summer diet, the carabid *Pterostichus brevicornis* fed on rotten wood down to −4°C during winter. This dietary change from insects to dry wood possibly avoids inoculation of the gut with ice nucleators (Kaufmann, 1971). Nepalese *Diamesa* species may feed down to −7.2°C on blue-green algae (Kohshima, 1984) (Table 5.4). Winter-active wasps are parasitic and possibly in search of hosts (usually dipteran). The insects of the genus *Grylloblatta* are voracious at 4°C (Strübing, 1958) and forage on snow fields (Mann et al., 1980), where they feed on species of *Chionea* (in Alberta) (Pritchard and Scholefield, 1978). Ice worms eat cryobiont snow algae and have a low rate of respiration (Goodman, 1971; Mann et al., 1980) (Table 5.4).

5.2.5 Life Cycles and Development

Although they may be active and feed between −2°C and −4°C (Aitchison, 1983, 1984b), most invertebrates do not develop or reproduce at subzero temperatures (Leinaas, 1981a; Aitchison, 1984b, 1984c; Schmidt and Lockwood, 1992). No winter development in collembolans has been noted (Leinaas, 1981a, 1983; Aitchison, 1984c), with the exception of *Isotoma saltans*, which develops between 0°C and 2°C (Strübing, 1958). The population densities of winter-active invertebrates are poorly known (Hågvar, 1971, 1973; Hågvar and Østbye, 1973; Aitchison, 1979a, 1979b, 1979c, 1979d).

At cool winter temperatures, there was no growth in spiders and their life cycles were prolonged (Huhta, 1965; Almquist, 1969; Schaefer, 1976, 1977a, 1977b; Aitchison, 1984c), as they are at high altitudes (Schmoller, 1970). Those that mate on the snow surface during winter frequently do so in webs over depressions (Buchar, 1968; Hågvar, 1973) – e.g., *Bolyphantes index* (see Figure 5.1). Other species, like the linyphiid *Centromerus bicolor*, also reproduce in winter (Schaefer, 1976, 1977a, 1977b; Flatz and Thaler, 1980). Winter-active species, such as *Centromerus sylvaticus*, have high winter mortality compared with species not active during winter (Schaefer, 1977b).

The females of the dipteran *Chionea araneiodes* have fully developed eggs in January and lay eggs at 0°C in winter (Hågvar, 1976). The genus *Diamesa* is active on the snow surface at around 0°C, sometimes *in copula*, and its aquatic larvae develop only at temperatures less than 5°C (Hågvar and Østbye, 1973; Jonsson and Sandlund, 1975).

Densities of supranivean *Boreus* spp. are high in January and February (Fjellberg and Greve, 1968). In late winter on sunny days with ambient air temperatures at about 0°C, copulating adults are often on the snow surface (Wojtusiak, 1951; Chapman, 1954; Shorthouse, 1979) (Table 5.3).

5.3 Vertebrates

5.3.1 Subnivean Vertebrates

Vertebrates are also active under, in, and on the snow cover. Most subnivean animals are small mammals weighing less than 250 g (Pruitt, 1984), such as the microtines and insectivores, together with their predators, mustelid weasels. Before the hiemal threshold is established, shrews and the microtine *Clethrionomys* are active on the snow surface; after its establishment, they go underneath (Soper, 1944; Pruitt, 1972). Under insulative, thick snow cover and with an adequate food supply, the brown lemming, *Lemmus sibericus*, at Barrow, Alaska, can reproduce in winter months (Batzli et al., 1980). On Hokkaido, the northern island of Japan, Kawakami (1966) observed the Alpine Salamander *Hynobius retardatus* as extremely active down to −8°C between December and March under snow. These animals were found under 1 m of snow in burrows 50 cm deep. In early spring they briskly ran up onto the snow cover to ponds and laid eggs between 0°C and −4°C (Kawakami, 1966).

Of the small mammals, the more omnivorous cricetid rodents tend to be hibernators or in torpor (a more southerly phenomena), exhibiting little winter activity (e.g., torpid *Peromyscus* in aggregations with food caches) (Howard, 1951), while the herbivorous microtine rodents are active in the subnivean space in more northerly climes (Bergeron, 1972). Only in the subnivean space can these small mammals survive the thermal rigours of winter, with large, insulated nests in the softer pukak (Zonov, 1982; Pruitt, 1984). Many voles store a food cache up to 3 kg, so that they do not need to forage widely (pikas can store up to 20 kg); the cache size depends on the biotope (Zonov, 1982).

The region of snow cover and its density affect how the animals respond to snow. In steppes or prairies with thin snow cover, the nests are smaller (Zonov, 1982). Voles avoid areas where the snow density exceeds 150 kg m^{-3} (Spencer, 1984). Also snowmobile tracks become barriers to small mammals because of a collapsed subnivean space, and the animals cross over them rather than burrow through the dense snow (up to 400 kg m^{-3}) (Schmid, 1971).

One way voles reduce heat and moisture loss is by huddling in communal nests (West, 1977; Madison, 1984; Wolff, 1984). During winter months there is a reduction of intraspecific aggression, which allows huddling (West, 1977), especially in the genera *Microtus* and *Clethrionomys*. This mechanism is also good for predator avoidance and defense, and foraging is easier (Madison, 1984). Taiga voles consume about 90 percent of their food from winter caches, foraging one at a time for the remainder. Warmer nest temperatures, with about seven individuals per nest, decrease food requirements (Wolff, 1984). Also, those areas with vole aggregations have significantly thicker moss layers and thus more insulation (West, 1977).

Insectivores have high metabolic rates and therefore must feed almost constantly to survive (Seton, 1909; Aitchison, 1987). Shrews also favour varied habitats with litter, deep humus, or snow cover as protection (Yudin, 1964; Ackefors, 1964; Pernetta, 1976). Some behavioural adaptations in the shrews during winter are construction of nests, reduced activity, and hoarding of food (Crowcroft, 1957; Dehnel, 1961; Churchfield, 1982b; Zonov, 1982). Winter foraging trips are short (about 3 min for *Sorex araneus*), with long stays in the nest and subsequent reduction of energy needs (Churchfield, 1982b; Merritt, 1986). For example, the short-tailed shrew *Blarina brevicauda* and other large shrews build elaborate winter nests (Crowcroft, 1957; Dehnel, 1961; Churchfield, 1982a). The nests and relative inactivity further reduce the metabolic rate and food requirements (Churchfield, 1982a; Aitchison, 1987).

The shrews also respond to the presence of snow cover in their microenvironment. Before the HT is established (snow cover less than 20 cm), *Sorex* and *Microsorex* are active on or near the snow surface and around logs, sometimes producing slight ridges near the surface (Seton, 1909). Once the HT is established, the animals remain in the subnivean space (Pruitt, 1970). In early spring, as the thermal character of the snow cover changes, *Sorex cinereus* may go onto the snow, at times dying of starvation or exposure when it cannot find a ventilation shaft by which to return to the subnivean space (Seton, 1909) (see Figure 5.6). In the FSU, the northern limit of shrew distribution is the −30°C mean January isotherm (Yudin, 1964), and those found in the coldest areas are the smallest *Sorex* species – e.g., *Sorex minutissimus* (mean weight about 4 g) (Mezhzherin, 1964).

Another group of vertebrates using the intranivean environment of the snow cover is birds. In extreme ambient air temperatures, small and larger gallinaceous birds will take refuge within the snow (Novikov, 1972; Korhonen, 1980b). Grouse will burrow into the

Figure 5.6. Shrew *Sorex araneus* on snow at Kilpisjärvi, Lapland, in northern Finland (A. Kaikusalo).

top 10 cm or so of the snow cover, a thermoneutral environment which usually does not drop below −11°C (Korhonen, 1980b); more snow mass means more insulation (Novikov, 1972). Smaller birds, such as sparrows, shelter under snow to survive within holes, subnivean tunnels, and even in subnivean vole nests (Novikov, 1972).

5.3.2 Physiological and Morphological Mechanisms

Small mammals also have some physiological constraints at low temperatures. The minute size of soricine shrews (less than 10 g) approaches the critical mass for maintaining endothermy during winter when much energy is lost as heat, putting the animal at risk and in need of accelerating its metabolic rate (Mezhzherin, 1964; McNab, 1983). In autumn as temperatures fall below the thermoneutral zone, relative food requirements and metabolic rates increase. Some of the specific physiological factors affecting the animal's activity during winter include inactivation of the thyroid (Hyvärinen, 1969), pituitary, adrenals, and parathyroid as well as changes in salivary glands and in brown adipose tissue, which is converted to heat (Rudge, 1968; Pucek, 1970; Hyvärinen, 1984), and all of which reduce metabolism and activity (Aitchison, 1987). In *Sorex araneus* almost all the endocrine system is inactivated during winter (Hyvärinen, 1984). There are great changes in body weight, more in Finnish specimens than in Polish ones (Hyvärinen, 1984). Also the larger shrew, *B. brevicauda* (about 20 g), has an increased thermogenic capacity during winter months at a constant subnivean temperature by means of nonshivering thermogenesis; physiologically this occurs through metabolism of brown adipose tissue (Merritt, 1986).

There are also some morphological adaptations to winter peculiar to the soricine shrews, all of which are called Dehnel's phenomenon. These include reduced body weight (up to about 35 percent) and shortened body length (Mezhzherin, 1964; Hyvärinen, 1969; Pucek, 1970; Merritt, 1986), with reductions in brain volume and weights of the kidneys, liver, and spleen but not the heart (Pucek, 1970). Skeletal changes also occur, with reduced intervertebral discs and decreased skull height (Mezhzherin, 1964; Hyvärinen, 1969; Pucek, 1970). The reduced size increases the hair density, giving greater insulation per unit surface area (Mezhzherin, 1964). Dehnel's phenomenon, which is more marked at northern latitudes than at southern ones, aids in minimising the total energy expenditure of the animal (Mezhzherin, 1964; Hanski, 1984), as does the reduced winter activity (Churchfield, 1982a). This shrinkage in the skull also might be a result of aging and changes in shrew population dynamics (Pruitt, 1954).

Another morphological adaptation occurs in the lemming genus *Dicrostonyx*. This animal has enlarged winter claws (see Figures 5.7 and 5.8) (Formosov, 1946) with which

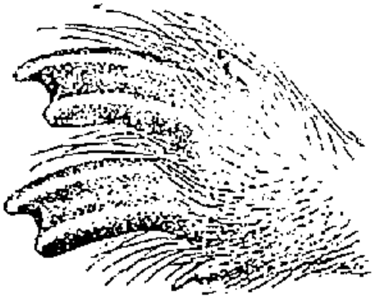


Figure 5.7. Front paw of a collared lemming, *Dicrostonyx*, with winter claws (Yamal Peninsula) (from Formosov, 1946).

it can dig; this genus made tunnels through the softer layers (20 kN m^{-2}) of the hard tundra snow of Alaska (Pruitt, 1984). The large winter claws on the forefeet (middle two claws) are highly modified for a fossorial life in snow and are present during the winter only. Lemmings of the genus *Lemmus* do not have these winter claws and stay in snow, which is much less hard and dense (Sutton and Hamilton, 1932).

5.3.3 Subnivean Food Webs

The Alpine salamander in Japan feeds on earthworms, isopods, snails, and slugs found under the snow cover (Kawakami, 1966).

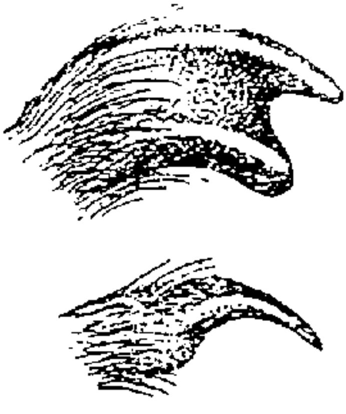


Figure 5.8. Winter and summer claws of the third digit of a *Dicrostonyx* specimen from the Yamal Peninsula (Formosov, 1946).

In the Arctic at Devon Island (75°N), winter nests of the collared lemming *Dicrostonyx groenlandica* are found in areas of the deepest snow accumulation. These animals ate *Dryas*, *Saxifraga*, and *Pedicularis* in autumn and were prey of *Mustela erminea* (Fuller et al., 1975). In taiga, grey and wood voles feed under the snow. Areas with no subnivean caches have extremely active voles; for example, root voles have no caches and forage 60 to 120 m under snow to green grass (Zonov, 1982). In alpine tundra, northern pocket gophers (*Thomomys talpoides*) have 90 percent of their activity under moderately thick alpine snow cover, consuming up to 80 percent of the available vegetation (Walker, Billings, and de Molenaar, Chapter 6).

The insectivores, especially shrews of the genera *Sorex* and *Blarina*, forage continuously in the subnivean space, eating whatever they encounter and can subdue, including voles and other shrews (Crowcroft, 1957; Dehnel, 1961; Yudin, 1962; Churchfield, 1982a). In Sweden a direct correlation between the diversity of winter-active subnivean invertebrates taken in pitfall traps (Näsmark, 1964) and the diversity of stomach contents of shrews was found (Ackefors, 1964). The soricine shrews mainly feed on common winter-active invertebrates (mites, spiders, springtails, and beetles) during winter months (Mezhzherin, 1958, 1964; Ackefors, 1964; Pernetta, 1976; Aitchison, 1984a). They eat most invertebrate prey and, when available, other food such as coniferous seeds (Yudin, 1962; Zonov, 1982). Larger predators take larger prey, and smaller ones take smaller prey (Buckner, 1964). The winter shrews can be very small (mean weight 2.6 g for a winter *Sorex cinereus*) (Aitchison, 1987). The winter-active invertebrates are mainly small (1 to 5 mm) (Aitchison, 1984a) and more energy-rich than larger ones (Hanski, 1984). In a subnivean food chain, shrews are probably the major predators e.g., *Sorex* in the northern hemisphere (Aitchison, 1984a, 1987) and the small marsupial insectivore *Antechinus* in Australia (Green, 1982). Some species of larger shrews, such as *Blarina brevicauda*, hoard food (e.g., beechnuts, earthworms [up to 40 percent], insects [up to 95.5 percent], snails [up to 1.8 percent], plant material [up to 25.3 percent], and small mammals [up to 60.5 percent]) (Crowcroft, 1957; Dehnel, 1961; Churchfield, 1982a; Aitchison, 1987). Shull (1907) reported *B. brevicauda* hoarding and cacheing snails immobilised by the shrew's toxic salivary venom (Shull, 1907; Merritt, 1986). Table 5.5 compares winter diets of *Sorex minutus* in snow-free Ireland (Grainger and Fairley, 1978) and in snow-covered Siberia where the more common winter-active groups were prey – e.g., spiders, 47.6 percent; beetle adults, 58.5 percent (Yudin, 1962).

The rodents, especially the microtines, and the insectivores are all potential prey for the small weasels. During winter months in Sweden *Mustela nivalis* consumed 48 percent *Microtus* species, 28 percent other rodents, 19 percent rabbits, and 5 percent shrews (Erlinge, 1975). In North America the small-sized mustelids, such as the

Table 5.5. *Percentage frequency of occurrence of winter food items in the guts of S. minutus (after Grainger and Fairley, 1978; Yudin, 1962).*

Food item	Ireland ($n = 87$)	Siberia ($n = 35$)
Lumbricids	0	5.6
Molluscs	0	19.6
Isopods	69	0
Araneae	21	47.6
Acari	42	5.6
Opilionids	30	0
Collembola	0	11.2
Hemiptera	37	17.0
Carabidae	0	42.0
Staphylinidae	0	19.6
Chrysomelidae	0	14.0
Coleopteran adults	90	58.8
Coleopteran larvae	37	0
Hymenoptera	0	16.8
Diptera	49	16.8
Vegetation	53	0

shorttail weasel *Mustela erminea* and the least weasel *Mustela rixosa* are well adapted to areas with prolonged snow cover and abundant prey species. Some female *M. erminea* can easily pass through vole tunnels (Simms, 1979) or dive down through the snow to the subnivean space to prey on voles (Formosov, 1946). As well, ventilation shafts serve as access for these small predators to the subnivean space (Madison, 1984). The small weasel with its long, slender body and large surface-to-volume ratio can rapidly chill and therefore spends most of the winter in the subnivean space in search of voles. Its forays to the snow surface are short (Formosov, 1946). In stressful winter conditions (temperatures below −40°C) and with 60 to 90 cm of snow cover in Minnesota, *M. erminea* was found to feed on 22 percent (by volume) shrews (Aldous and Manweiler, 1942).

A possible subnivean food chain in the southern boreal forest could easily begin with soil and snow fungi (Aitchison, 1983) and snow algae (Kopeszki, 1988; Hoham and Duval, Chapter 4) as primary producers. The fungivorous and detritivorous springtails are potential consumers of fungi and algae and in turn may be preyed upon by winter-active mites and spiders (Buchar, 1968; Håvgar, 1973; Aitchison, 1984a, 1984b, 1989). Winter-active subnivean spiders in turn are readily consumed by insectivores, such as the ever-hungry shrews (Yudin, 1962; Ackefors, 1964; Pernetta, 1976). Weasels are known to kill shrews but not necessarily to eat them; however, in some areas shrews are consumed (Aldous and Manweiler, 1942; Hamilton, 1933; Simms, 1969; Aitchison, 1987). Also raptors such as the great grey owl *Strix nebulosa* dive into snow cover to retrieve small mammals, including soricine shrews (Nero, 1969; Collins, 1980), taking a possible secondary predator out of the subnivean space. This is summarised in Figure 5.9.

5.4 Recommendations for Future Research

The lack of economic importance of this fauna and the technical difficulties of analysis associated with subnivean and other snow studies have resulted in a natural history approach to this fauna. There is considerable potential in this field for analytical approaches to energetics and trophic and population dynamics. There are a number of unknowns relating to the subnivean, intranivean, and supranivean micro- and mesofauna: for example, many abiotic components could be better studied, such as the effects of temperature, snow density, snow hardness, light penetration, and CO_2 concentration on the flora and fauna. With regard to CO_2, there is a need to understand its sources (bacteria, fungi, plants, invertebrates, and mammals) (Tranter and Jones, Chapter 3). The snow cover itself could be modified by 1) spraying it with water to produce an ice layer; 2) stirring it to produce a denser and harder surface; and 3) covering it with plastic to create an artificial ice layer. Then faunal reactions, both invertebrate and vertebrate, could be monitored.

Although many experiments have been done on mammals, not that many have been done with invertebrates. There is a need for more research, possibly using the methods previously mentioned, to simulate and monitor natural parameters and to correlate them to faunal activity.

Trophic relations within this microenvironment are only partially known. Radiotracers or stable isotopes might elucidate these pathways, especially in the invertebrates. The supposition that faunal movements, both within and onto the snow cover, are triggered by thermal changes needs to be confirmed.

Further studies on life histories of winter-active invertebrate species would determine overwintering stages and possible cyclomorphic-type changes. The taxonomy of many of these groups is poorly known (Aitchison, 1979a, 1979b, 1979c, 1979d; Zacharda, 1980). Any morphological, physiological, and behavioural changes of this fauna that enhance their winter activity and survival might help explain the mechanisms of low temperature tolerance.

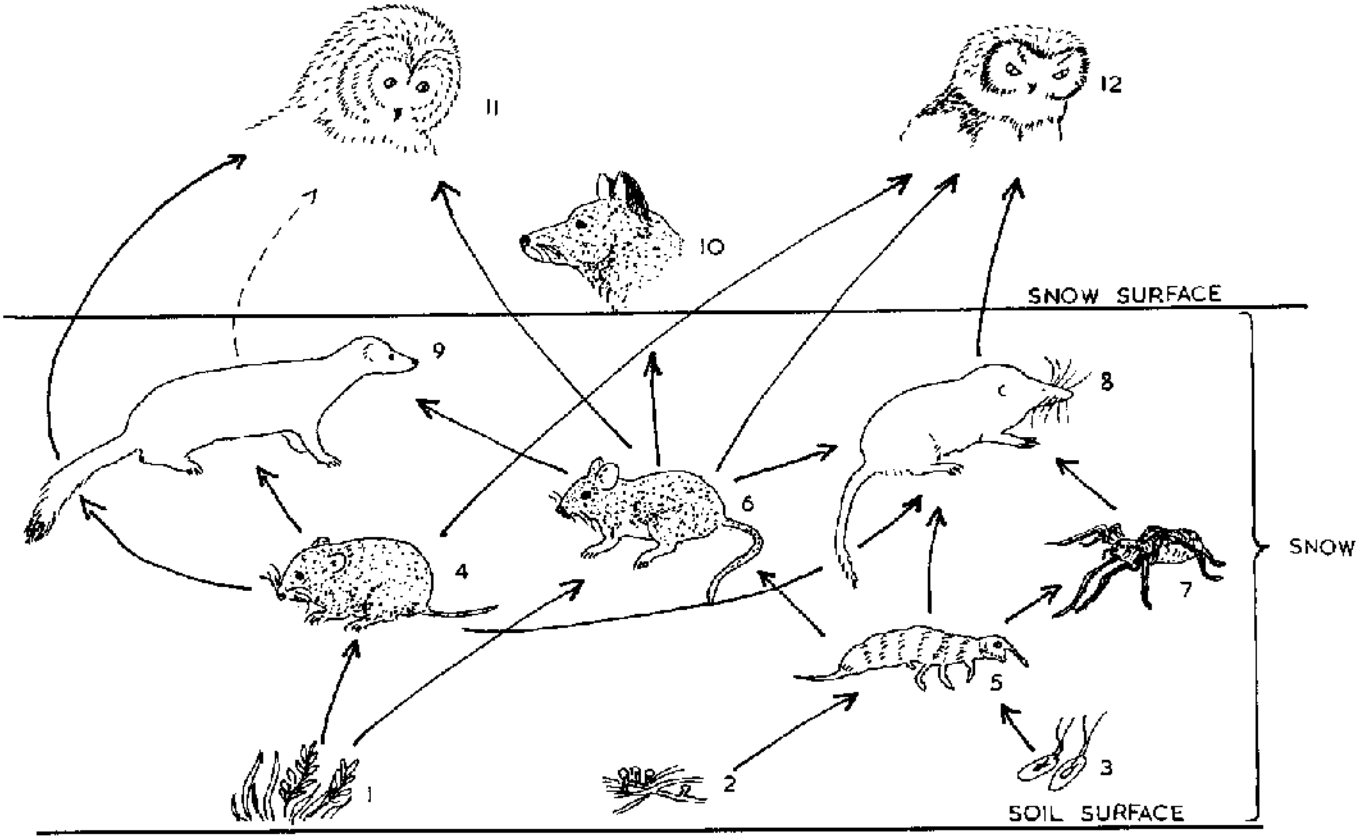


Figure 5.9. Hypothetical winter food web in a boreal region: 1) vegetation, 2) *Cladosporium* fungi, 3) snow algae (*Chloromonas* sp.), 4) red-backed vole *Clethrionomys gapperi*, 5) collembolan *Isotoma* sp., 6) deermouse *Peromyscus maniculatus*, 7) wolf spider *Pardosa* sp., 8) masked shrew *Sorex cinereus*, 9) shorttail weasel *Mustela erminea*, 10) red fox *Vulpes fulva*, 11) great grey owl *Strix nebulosa*, and 12) boreal owl *Aegolius funereus*.

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