THE UNIVERSITY OF MANITOBA

The Activity of Subnivean Invertebrates in Southern Manitoba

by

Caroline Williams Aitchison

A thesis

submitted to the Faculty of Graduate Studies in partial
fulfilment of the requirements for the degree of
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ABSTRACT

Snow cover affects the activity of invertebrates and determines which invertebrates are winter-active. Snow cover varied between 40 and 60 cm in all habitats in the first winter that was slightly colder than average. Subnivean temperatures ranged between 0° and -8°C, depending on the ambient air temperature; dips in the former occurred just after sudden drops of the latter. Snow cover for the second winter was established six weeks later than the previous year due to unusually warm weather; snow thickness varied between 30 and 50 cm. Subnivean temperatures ranged between 0° and -10.5°C. Snow density also affected the subnivean temperature.

Catch consisted predominantly of Acarina, Araneae, Collembola and Staphylinidae in both winters. Numerous invertebrates were active immediately prior to the establishment of permanent snow cover. When adequate insulation from snow was available (20+ cm thickness of snow), subnivean temperatures stabilised at about -3° to -4°C, and hardy invertebrates continued their activity. Species diversity, and usually numbers of specimens also, decreased in the autumn, were low in winter, and increased gradually in late spring to reach a vernal maximum.

Exceptions to low numbers in midwinter were the orders Acarina and Collembola which included many immatures in February and March when subnivean temperatures were as low

as -9°C.

The activity of Araneae was positively correlated with subnivean temperature during the first winter, but was negatively correlated in the second winter. Both adults and immatures in most families overwintered. Forty-nine species were active throughout the year, with the exception of eleven species which occurred only in summer and autumn. Hence, no "winter species" were present, only winter-active ones. Many species of spiders were taken the second winter. Six of the 49 species had holarctic distributions.

Coleopterans, mainly staphylinids, were extremely abundant in October and November, but ceased activity in winter, spring and much of the summer.

Snow cover and soil surface temperatures below 0°C caused cessation of activity of Oligochaeta, Gastropoda, Pseudoscorpionida, Opiliones, and many orders of Insecta. Carabidae, some dipterans and hymenopterans were active down to -4°C.

Cold-hardiness of the spider families Clubionidae and Lycosidae and insect families Mycetophilidae and Staphylinidae was revealed by their activity at -7°C or lower in the laboratory.

Three provincial distribution records were established (Neanura muscorum Templeton, Stenamma diecki Emery, and Lamyctes sp.), a national record for Isotoma subequealis Folsom-fennica Reuter group, and a continental one for Entomobrya sp. near sibirica-quinquelineata group. Also four new species and one new genus were taken.

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Chapter I

INTRODUCTION

In North America, little is known concerning activity of invertebrates on or under snow. Information about snow properties is more abundant, and literature on how snow properties affect mammals, particularly small ones, is constantly increasing in volume. Some of that literature may be applied to invertebrates. This research project was undertaken to ascertain just how snow affects the activity of invertebrates in southern Manitoba, and what invertebrates are winter-active.

I. OBJECTIVES

The objectives of this research project were: (1) to determine the properties of snow that affect the temperature under snow cover in southern Manitoba, (2) to determine the groups of invertebrates that are active in winter, (3) to determine the temperatures under the snow at which these animals are active and the relationship between temperature and their activity, (4) to compare winter and summer fauna of the area, (5) to examine some of the more common species in a temperature gradient, and (6) to determine whether or not the winter-active species are holarctic or nearctic by comparison with Fenno-Scandanavian fauna.

II. DEFINITIONS

The term SUBNIVEAN will be used to describe the animals, temperatures and the space under the snow while the term SUPRANIVEAN will be used to describe the temperature above the snow. The term, WINTER-ACTIVE, refers to animals active under snow, or during the hiemal period. These terms are repeatedly referred to in the text.

Seasons are not classified in the conventional manner of three months per year, but according to temperature and snow conditions at the latitude of southern Manitoba, i.e. 50°N. AUTUMN is designated as September and October, WINTER as November to mid-April, SPRING as mid-April to the end of May, and SUMMER as June through August. Winter is further divided into EARLY WINTER (November and December), MIDWINTER (January to mid-March), and LATE WINTER (mid-March to mid-April).

Chapter II

REVIEW OF LITERATURE

I. INTRODUCTION

The occurrence of invertebrates in or on snow was probably first noted in the nineteenth century by European mountaineers and somewhat later by naturalists. Biologists probably did not examine these animals *per se* until about the 1940's, because of the biologists' aversion to cold temperatures. Biologists first examined the soil fauna and then turned their attention to the fauna on or under the snow.

II. SOIL BIOLOGY

Soil fauna collected in summer at high altitudes or at high latitudes contains genera and/or species that are active under snow. Historically, biologists used the methods of soil biologists to study invertebrates on or under snow. Therefore, these soil methods will be discussed first under: animals and their activity, thermal properties of the soil surface, insulation provided by both litter and snow, and animals living on the soil surface.

A) The Animals and their Activity

In England, activity of animals on the soil surface was high in summer and low in winter (Williams 1959a). Throughout the year activity in the woods was about half diurnal and half nocturnal; in scrub,it was predominantly diurnal in warmer months of the year and nocturnal in colder months (Williams 1959a). Williams (1962) mentioned the similarity between nocturnalism and winter activity. In Illinois, Holmquist (1926) noted a cessation of most invertebrate activity from mid-November to the third week in March each year, except for some protected species. Collembola seemed to exhibit normal activity all winter. Of particular significance was his statement that "Most species are not completely dormant in winter, but possess enough activity to be able to crawl to cover when exposed," (Holmquist 1926). After examining invertebrates from high altitudes in Switzerland, Diem (1902) concluded that slight changes in soil temperature occurred with time, such that many soil invertebrates remained active. He also mentioned that the subnival (subnivean) region had a richer fauna than the subalpine and alpine ones.

More recently, invertebrates were found active on the snow surface at the Arctic circle in the U.S.S.R. Novikov (1940) observed active insects and spiders on the snow, even at temperatures down to -9° C. Also some insects were collected under the snow where the temperature is significantly higher than that above the snow, sometimes as much as 25°C. Novikov (1940) concluded that the activity of insects on the snow was probably dependent upon the temperature regime of the subnivean space and not upon the thickness of snow cover. In Poland, Wolska (1957) found insects and spiders active on the snow surface, as did Chapman (1954) in Montana, Strübing (1958) in Germany, Fjellberg and Greve (1968) and Hågvar (1971, 1973) in Norway. In Sweden, Näsmark (1964) studied the invertebrates active under snow. Kühnelt (1961) in Germany mentioned that, during thaws, some ground litter inhabitants were forced to the snow surface by the water on the ground and that they returned to the litter when colder weather resumed. Kevan (1962) mentioned that mites and Collembola in eastern Canada were active under snow cover, if the ground was not previously frozen. In Manitoba, Pruitt (pers. comm.) and others noted Collembola, Diptera, Mecoptera and Araneae active on the snow surface at temperatures near 0°C.

Insects which show a high degree of adaptability to life on and under snow are the mecopterans of the genus _Boreus_. Mecopterans are wingless, moss feeders which copulate on the snow surface. Adults are cold-resistant; larvae occur in sand under spruce groves in Germany (Strubing 1958). Fjellberg and Greve (1968) found _Boreus_ _hiemalis_ L. and _Boreus_ _westwoodi_ Hag. in Norwegian alpine conditions. In Germany, Strübing (1958) collected them on the snow surface during windless, sunny days at about -1°C. Pruitt (pers. comm.) captured _Boreus_ _nivoriundus_ Fitch (one pair _in_ _copula_) at -4°C on fresh snow during February near the Taiga Biological Station (51° 03' N, 95° 21' W), Wallace Lake, Manitoba. In western Montana, Chapman (1954) found Boreus unicolor Hine and Boreus reductus Carpenter jumping on the snow surface at 0°C and saw more individuals at -1.7°C. At -0.6°C they copulated; at -5.6°C they moved slowly; and at -12.2°C they were motionless (Chapman 1954).

B) Thermal Properties of the Soil Surface

It is well known now that soil temperatures are much more stable than those of the air (MacKinney 1929, Mail 1932, Heydemann 1956, Pruitt 1957, Kevan 1962, Ylimäki 1962, Geiger 1965, Wallwork 1970). Many soil animals have narrow thermal preferenda and seek these ranges in the soil (Heydemann 1956, Wallwork 1970). Two sources of insulation may buffer the stenothermic invertebrates on the soil surface from extremes of ambient air temperature: the litter layer and the snow cover.

1) Insulation from the litter layer:

Even in summer, the soil surface temperature under a litter layer remains below that of the ambient air (MacKinney 1929, Pruitt 1957, Ylimäki 1962, Geiger 1965, Huhta 1965, Wallwork 1970). Holmquist (1926), MacKinney (1929), Cloudsley-Thompson (1967), and Fuller et al. (1969) mentioned the added insulation in winter due to the litter layer; in the Alps, Diem (1902) discussed the small changes in soil temperature due to thick vegetation and probably a thick litter layer also. Heydemann (1956) noted less temperature fluctuation under litter during winter, and Todd

(1949), Ylimäki (1962), Huhta (1965), and Cloudsley-Thompson (1967) also mentioned the dampening effect that litter has upon temperature changes. In Scotland, Edgar and Loewen (1974) monitored litter temperatures in winter and ascertained that they were higher than those of both the bare soil surface and the ambient air. These authors also suggested that the spider Pardosa lugubris Walckenaer used the leaf litter as an overwintering habitat. Wallwork (1960) maintained that the seasonal changes in temperature in North America stimulated movement by mites from the litter to the humus as autumn progressed, and vice versa. Deeper litter also provides more structural micro-habitats in which more species may be present (Huhta 1971, Uetz 1975).

2) Insulation from Snow Cover:

During winter a blanket of snow insulates the soil surface from ambient air temperatures (Diem 1902, Holmquist 1926, MacKinney, 1929, Coulianos and Johnels 1962, Ylimäki 1962, Mellor 1964, Geiger 1965, Huhta 1965, Formosov 1969, Fuller et al. 1959, Pruitt 1970, Wallwork 1970, Aitchison 1974), such that the soil temperature remains near 0°C while the ambient air temperature fluctuates considerably (Strubing 1958, Geiger 1965). Thus the soil surface habitat is a thermally stable environment throughout the year. Both Kühnelt (1961) and Kevan (1962) acknowledged the insulating property of snow cover. This property is discussed further in Appendix 3-1(Aitchison1974).

C) Animals Living on the Soil Surface

Animals that live on the soil surface were extensively studied by Diem (1902), Kühnelt (1961), Kevan (1962), Burges and Raw (1967) and Wallwork (1970). The invertebrates reported include: Protozoa, Acoelomata, Pseudocoelomata, Annelida, Mollusca, Onychophora, Crustacea, Myriapoda, Tardigrada, Arachnida, and many Insecta. Many niches are present in the litter on the soil surface (Uetz 1975), and in the soil. Food for the saprophagous and fungivorous species is readily available in moist litter, and species preying upon these types of invertebrates may find their requirements of habitat, temperature, relative humidity, and food provided in the litter. Detailed discussions of particular groups and species will be found in subsequent chapters.

III. WINTER ECOLOGY

In Canada differences of up to 75°C occur in the Arctic in mean annual maximum and minimum temperatures. In order to explain survival in this severe environment, meteorologists and physicists examined the properties of snow, while biologists studied adaptations of plants and animals that enhance survival in winter. Aspects that will be considered in this thesis are meteorology as modified by snow, the properties of snow, and reactions of invertebrates to low temperatures. Scientists throughout the northern hemisphere have made contributions to snow ecology.

A) Pure Meteorology

In Finland Keränen (1920) wrote a comprehensive and classical paper on snow. He discussed in detail the geothermal heat and its effect on frost penetration, sublimation and condensation, and heat conductivity. His conclusions were based on measurements of snow density and temperature in the soil and in the snow cover. MacKinney (1929) in Connecticut and Pruitt (1957) in Alaska measured soil temperatures throughout the year, noting the insulation provided by both litter and snow cover. In Germany, Geiger (1965) published an extensive meteorological work on the micro-climate near the ground. By examination of this micro-climate in the annual cycle, the effects of ground cover and standing vegetation upon snow depth and frost penetration, and the characteristics of snow such as its albedo (reflectivity), its thermal properties, and light penetration were considered. The long wavelengths of light (reds) penetrate snow more readily than the short ones; also denser snow is more readily penetrated by light than less dense snow (Geiger 1965). In the United States, Porter (1943) measured light transmission through low density, fluffy snow at about -12°C by discs of a Weston Illuminometer; he found 2.4% light transmitted through 3.5cm of snow and only 0.8% through 8.5cm. Another worker in the United States, Mellor (1964), and Rikhter (1954) in the U.S.S.R., considered snow properties from a physical viewpoint, taking into account crystal shape, metamorphism and other details of snow physics.

B) Snow Ecology

The basic properties of snow are dealt with in Appendix 3-1 (Aitchison 1974). While studying the subnivean environment of small mammals in Sweden, Coulianos and Johnels (1962) examined the differences in temperature between the subnivean air space and that 10cm above the snow surface, and found the former much more stable than the latter, e.g. a change in the ambient air temperature of 10°C produced a change in the subnivean temperature of 2°C. Similar differences were noted by Ylimäki (1962) in Finland, and Mail (1932), Pruitt (1957) and Mellor (1964) in the United States. Furthermore, Coulianos and Johnels (1962) found that large amounts of vegetation produced larger subnivean spaces.

1) Snow Density:

One of the major parameters of snow is its density (Aitchison 1974). Williams and Gold (1958) discussed the effect of wind upon snow which causes an increase in snow density by packing snow crystals closer together. The density of snow affects its insulating power; low density is associated with good insulation while high density is associated with poor insulation (Rikhter 1954, Williams and Gold 1958). In exposed locations on the prairies, wind action causes hard-packed, dense snow; in sheltered areas, the snow is soft, less dense and friable. As snow has much air enclosed between the crystals and has a low thermal conductivity when it is light and fluffy, it is a good insulator (Rikhter 1954, Williams and Gold 1958, Coulianos and Johnels 1962, Formosov 1969, Fuller *et al*.1969, Pruitt 1970, Aitchison 1974).

2) Snow Thickness:

Pruitt (1970) considered 20cm to be the thickness of snow at which the subnivean temperature is stabilized from the effects of the ambient air temperature, a thickness that he named the "hiemal threshold". Ylimäki (1962), who studied snow in southern Finland, stated that as little as 15 to 20cm of snow was adequate protection for the soil from excessive heat loss, while Keränen (1920) ascertained in northern Finland that 25 to 30cm of snow cover in early winter maintained a soil surface temperature of about -7°C. The hiemal threshold maintains a temperature of about 0°C in the subnivean micro-climate (Coulianos and Johnels 1962, Ylimäki 1962, Geiger 1965, Pruitt 1970).

C) Reactions of Invertebrates to Low Temperatures

Temperature measures energy, in the form of heat, which affects the speed of metabolic processes in poikilotherms. Also, the transfer of heat acts as a stimulus in the behaviour of invertebrates (Fraenkel and Gunn 1961). Heat may be transferred by: (1) radiation, both solar and infra-red; (2) conduction; (3) convection; and (4) evaporation (Carthy 1958, Fraenkel and Gunn 1961, Moen 1968).

Invertebrates react by altering their behaviour in response to the first three, but rarely to evaporation (Fraenkel and Gunn 1961).

Temperature regulates all the physiological processes and the general activity of invertebrates and other poikilotherms. The distribution of invertebrates is governed by temperature (Messenger 1959), and most animals congregate in areas of favourable temperature for all their life processes (Carthy 1958, Wallwork 1960, Fraenkel and Gunn 1961).

A multitude of factors affect an animal's response to temperature change (Moen 1968), and several will be mentioned. The types of behavioural response to temperature by invertebrates will be examined, as will reactions of different animals to changing temperatures and to cold.

Reactions of invertebrates to low temperatures were studied by Wolska (1957) and Strubing (1958). Both observed snow invertebrates in thermal preferenda, while Strubing found that Chionea lutescens Dalm. had a thermal preferendum down to -5°C. In Minnesota, Mail (1930) examined survival of the elaterid Melanotus communis Gyll. in the soil during the winter, and found that cold-sensitive species overwintered deep in the soil while hardier species were near the surface. He concluded that snow cover can affect the survival of insects.

In Saskatchewan, Riegert (1967) found that mortality was low in the eggs of three species of grasshoppers in areas where minimum temperatures were below -35°C. He concluded that this was due to the insulation of the snow cover and also observed high winter mortality in areas with insufficient snow cover.

In the natural habitat, the thermal preferendum is significant and is usually close to temperatures in which insects develop. Generally, animals in a gradient avoid temperatures greater or less than the optimum temperature for development, which is more or less equivalent to the preferendum (Carthy 1958). Fraenkel and Gunn (1961) defined the temperature preferendum as that temperature range which gave "the range within which 50 to 80% of the observations occur." The temperature effect on metabolism or on the central nervous system affects behaviour, by changing the speed of a manoeuvre or by increasing avoidance (Carthy 1958). Poikilotherms control their body temperature almost entirely by behavioural means, often by locomotory reaction. The temperatures to which the animals are acclimated also affect the preferendum (Fraenkel and Gunn 1961).

D) Reactions of Invertebrates to Varying Temperatures

Cloudsley-Thompson (1953) stressed the importance of fluctuating temperatures. Most researchers hold animals at a constant temperature, really an abnormal situation. This may be close to the normal condition for homeotherms , but this is not true for poikilotherms. Cloudsley-Thompson (1953) discussed the deleterious effects of constant temperatures and gave examples of a number of insect species, in which development was accelerated at a constant temperature, but survival, longevity and productivity were reduced. Constant temperatures appear to inhibit activity, as some species depend on sudden decreases in temperature to stimulate orthokinetic (speed of movement) locomotion (Cloudsley-Thompson 1953).

Changes in temperatures affect activity of many insects. Social insects exhibit behavioural mechanisms to keep their colonies at optimal temperatures (Carthy 1958). At 16°C or lower, bees form a cluster with their heads toward the middle. Those individuals in the middle wiggle and produce heat which protects the others from low ambient air temperatures(Carthy 1958).

Gunn (1934), in a classic experiment, placed weighed cockroaches, <u>Blatta orientalis</u> L., in a thermal gradient of 2° to 40°C. He also realized that a humidity gradient existed within the thermal one and ascertained that normally the cockroach was unaffected by the moisture gradient. An animal that desiccated to 70% of its original weight preferred a lower temperature range of 12° to 23°C (versus the normal 20° to 29°C.), due to the greater relative humidity in that range. After a drink of water, the desiccated animal returned to its previous preferendum (Gunn 1934). This is an example of interaction of more than one stimulus.

Other examples of interaction of several stimuli have been found. In some groups of animals (Mollusca, Coleoptera), it was agreed in the past that activity was induced by changing temperatures (Bentley *et al*. 1941, Dainton 1954, Karlin 1961). Some researchers found recently that the stimulus of light intensity affects the behaviour of their test animals more than temperature (Newell 1968, Lewis 1969).

E) Basic Reactions and Examples

Reactions of invertebrates to cold are less definite than those to heat. At temperatures markedly above or below the preferred range, stupor and immobility occur prior to death (Carthy 1958, Wallwork 1960). Cold torpor may occur between 0° and 15°C, thus producing an aggregation of animals where the temperature is low enough to produce cold torpor (Fraenkel and Gunn 1961). The parameter of locomotion, in the form of klinokinesis or change in the rate of turning, is most important for measuring the effect of low temperature. Temperature produces behavioural effects often by direct action upon the central nervous system, which will, in turn, produce changes in metabolism that induce locomotory activity (Fraenkel and Gunn 1961). Some insects occur in habitats near 0°C, while a few cannot tolerate temperatures much over 0°C, usually due to direct physiological effects (Fraenkel and Gunn 1961). By behavioural and physiological means, winter-active and overwintering invertebrates can survive low temperatures. Physiological mechanisms will be considered later in the section on cold-hardiness.

Bertram (1935) compared the low temperature limits of activity in a variety of insects and spiders in eastern Greenland and Finland. He determined the point of cold stupor, above which the animal is active and below which it loses its normal activity, and concluded that in Greenland invertebrates withstood cold better than those of Finland, which were active at 10°C (Bertram 1935).

Mellanby (1940) examined the activity at low temperatures of certain Arctic insects in Finnish Lapland. He found that acclimation could occur in 24 hours or less and thus could produce dramatically different results in the measurements of cold stupor temperatures. Stone-fly nymphs, Dictyopterygella subfissa Bingtsson, collected at 7°C, were active at 0°C even without acclimation. Acclimation of adults at high temperatures altered their cold stupor temperatures.

Specific papers dealing with each phyletic group discussed in this thesis are considered in subsequent chapters.

In conclusion, the responses of terrestrial invertebrates to temperature may be classified as appetitive behaviour. The responses may be easily recognized, especially avoidance reactions or klinokinesis; or because several stimuli may produce a 'synergistic' response under certain conditions, where the response to a single stimulus may only be observed when it is measured in combination with one or more other stimuli, e.g. the effects of humidity superimposed upon those of temperature (Gunn 1934). Furthermore, temperature causes several types of change in the bodies of poikilotherms through direct effects on the central nervous system, through indirect effects on the speed of metabolism, and by an interaction of both effects, producing behavioural reactions.

IV. COLD-HARDINESS

Some insects survive in temperatures of less than -30°C, with their body fluids in a supercooled, unfrozen state (Carthy 1958). Supercooled body fluids contain a high percentage of colloids, and a lower proportion of water than in the summer, enabling the insects to tolerate the formation of small, isolated ice crystals in their tissues (Carthy 1958, Wigglesworth 1972). Cold-hardiness is dependent upon the water content of the body, and most overwintering animals keep it at a lower level in winter than in summer, e.g. 65% versus 79% (Carthy 1958)). Effects of temperature on all aspects of insect life histories, including cold-hardiness, are discussed by Uvarov (1931).

Wigglesworth (1972) equated cold-hardiness with avoidance of freezing. Insects may be grouped into two classes: a freezing-resistant (F-R) group that tolerates freezing of body tissues; and a freezing-sensitive (F-S) group which avoids freezing of its tissues by depression of freezing and supercooling points of the haemolymph and/or accumulation of a cryoprotective substance such as glycerol (G) (Salt 1961, Asahina 1966, Sømme 1967b, Wigglesworth 1972). Relatively few insects, usually larvae, can survive ice formation in their bodies, while many F-S insects overwintering in exposed habitats can supercool (Sømme 1967b, Ashwood-Smith 1970). F-S species which supercool may overwinter in the larval or the pupal stages (Salt 1961, Asahina 1966, Ashwood-Smith 1970), or may be active as adults (Ohymama and Asahina 1972). Factors determining cold-hardiness that will be discussed here are: (1) the ability to survive freezing (freezing-resistance), (2) the ability to supercool, and (3) the ability to survive long exposures at low temperatures (Asahina 1966).

B) Factors Determining Cold-Hardiness

1) Ability to Survive Freezing:

The initiation of freezing occurs spontaneously or after 'inoculation' by external ice crystals. Before a solution will freeze, a nucleus is needed in the solution around which an ice crystal can form. Nucleation depends upon molecular orientation, the size of the water mass, time, and the presence of nucleating sites such as dust particles (Salt 1961). Food particles covered with dust provide ideal nuclei for inoculation in the foregut of an insect (Salt 1953, 1961). Ohymama and Asahina (1972) noted that for some insects, cessation of feeding and emptying the gut of ice crystals nucleators in the autumn brought on an increase in supercooling ability, and that the reverse occurred in spring with the resumption of feeding. Östbye and Sømme

(1972) also found that the beetle *Pelophila borealis* Payk. lost its supercooling ability when it began to feed in spring. By contrast, Kaufmann (1971) observed that *Pterostichus brevicornis* Kirby ceased feeding in the early Alaskan winter, then resumed feeding in mid- and late winter. Its survival was not hampered by this feeding. Spontaneous freezing is dependent upon the size of the crystal nuclei, and inoculation by external ice crystals is a faster way to induce freezing (Asahina 1966).

Freezing of the haemolymph of an overwintering insect may be slow, while in summer it may occur easily. Freezing may be intracellular or extracellular. F-S species may have much intracellular freezing via 'flashing', or rapid ice formation, that damages cells, while F-T species have extracellular freezing. In the latter case, thawing produces cells with normal appearance and activity (Asahina 1966).

The relationship between temperature and freezing for a large, intact insect is exemplified in Figure 2-1. The rise in temperature (A) occurs when the latent heat of fusion is released as intracellular freezing sweeps through the body cavity of the insect (Wigglesworth 1972, Stöver 1973). The plateau, B (present only in large insects), represents the end of freezing. If cooling ceases here, the insect may survive; if it continues, death is certain for F-S insects (Kirchner and Kestler 1969, Stöver 1973). The gradual fall (C and D) represents progress towards extracellular freezing, accompanied by a concentration of the frozen blood and dehydration of the tissues (Asahina 1966, Wigglesworth 1972).

Mechanisms of freezing resistance are avoidance of intracellular freezing and the process of frost hardening. A large volume of body water retards intracellular freezing. All known F-R insects are in the larval or the pupal stage, stages with high blood volumes. Haemolymph may also have the characteristics of "the formation of a concentrated blood layer around ice crystals," retarding further inoculation (Asahina 1966). Extracellular freezing may be resisted by having little unbound water in the insect's body and by the presence of cryoprotective, neutral compounds with small molecular weight such as glycerol (G). Frost-hardening may be accomplished by chilling or by exposure to moderately cold temperatures (Asahina 1966).

Freezing-resistance was demonstrated in the parasitic wasp, Bracon cephi Gahan, and the slug caterpillar, Monema flavescens Walker. Both are highly F-R species containing some G (Asahina 1966). In Alaska, an overwintering adult carabid, Pterostichus brevicornis, tolerated freezing below -35°C. Adults contain some G, while immatures have none; nevertheless, both are F-R (Miller 1969, Kaufmann 1971). In northern Japan, Ohymama and Asahina (1972) studied seven species of adult insects, all of which exhibited poor ability to supercool (supercooling points between -6° and -10°C), and thus they were classified as F-R adults. An ant that they studied had two supercooling points. If it was rewarmed before it reached the second one, it resumed normal activity; but it could not survive if it was cooled to the second supercooling point. As a result of preparing histological sections of the whole, frozen ant at -10°C and at -20°C, Ohymama and Asahina (1972) ascertained that cooling of -10°C for 15 hours only produced ice in the foregut; colder temperatures produced ice throughout the ant. Stöver (1973) found that a terrestrial snail from the mountains of Austria, <u>Arianta</u> <u>arbustorum</u> L., could tolerate ice in certain tissues for short periods of time, until the plateau on the freezing curve was reached (see Figure 2-1). She thought that the freezing was "almost certainly extracellular". The inactivity of this snail during winter, causing slower freezing, also enabled it to tolerate subzero temperatures (Stöver 1973).

2) Ability to Supercool:

Many investigators examined supercooling, and foremost in this field are Salt (1953, 1956, 1957, 1959, 1961) and Sømme (1964, 1965a, 1965b, 1966, 1967a, 1967b). Earlier researchers were Payne (1927) and Sacharov (1930), who felt that dehydration of overwintering specimens and dehydration plus the amount of fat in insects, respectively, were responsible for cold resistance. Aspects of supercooling being considered here are the accumulation of cryoprotective compounds, lowering of supercooling and freezing points, and dehydration, with examples.

The accumulation of cryoprotective compound(s) was discovered in numerous overwintering insects, the majority of which hibernate in exposed places and are in diapause (Salt 1961, Somme 1967b). Wigglesworth (1972) gave a synopsis of supercooling, which might occur by a hydrophilic cryoprotectant. He stated: "Ice crystals forming in solutions rich in hydrophilic colloids are liable to become covered with a sheath of dehydrated colloid, and thus fail to 'seed' the entire solution." Cryoprotective substances include low molecular weight, polyhydric alcohols such as glycerol (G), sorbitol and mannitol, and possibly lipids (Salt 1961, Sømme 1964, Ashwood-Smith 1970, Baust and Miller 1970). All these low molecular weight substances contain groups forming hydrophilic bonds, thus increasing the viscosity of the haemolymph and affecting supercooling (Sømme 1967b). Sømme (1967a) stated that "the effect on supercooling exhibited by glycerol is not unique, but that a number of solutes in the haemolymph may have a similar effect." He cited those solutes as being G, sorbitol, trehalose, glucose, lactate, alanine, ninhydrin-positive substance, and acid-soluble phosphorus (Sømme 1967a).

A correlation between G concentration and supercooling points in which an increase in G produces a depression of the supercooling point has been determined (Sømme 1964, 1965a, 1967b; Ashwood-Smith 1970; Baust and Miller 1970; Ohymama and Asahina 1972). Sometimes this correlation is not linear, indicating several substances (Baust and Miller

1970). 'Protection' by a cryoprotectant is not always complete, and some other cold defence mechanisms may operate (Salt 1959; Sømme 1964, 1965a, 1965b, 1967b; Asahina 1966; Ashwood-Smith 1970). "The amount of protection (from freezing) is proportional to the relative concentrations of neutral solutes and electrolytes," (Salt 1959). A depression of the melting point of haemolymph occurs with a high concentration of G (Sømme 1964). Baust and Miller (1970) suggested that G may accumulate preferentially in certain organs, while Asahina (1966) indicated differential freezing in an ant.

Baust (1973) discussed freezing with and without G; with no G, intracellular freezing, rapid growing conditions, membrane and protein denaturation, and migratory recrystallization occurred with lowered temperatures; the presence of G increased the solute concentration, depressed the freezing point, increased viscosity, and prolonged the liquid phase. G modifies ice structure by blunting crystals and, in general, produces a decrease in the supercooling point (Baust 1973). Salt (1957) called G a good antifreeze "because of its high solubility in aqueous salt solutions, its ability to permeate the cell rapidly, its low molecular weight, and its absence of toxicity even when in great excess". G does not always prevent freezing. None the less, survival of frozen larvae of _Bracon_ _cephi_ is more likely if G is present (Salt 1959). One unusual quality of G in the haemolymph is that it causes a lower supercooling point than that of a G-water solution (Somme 1964). Some insects with G become F-R while other do not (Somme 1965a), which leaves the role of G unclear (Somme 1964). Studies indicated that there are seasonal and other changes in G concentration. G often increases in diapausing insects and in overwintering spiders during autumn and subsequently decreases after diapause is broken; there are, of course, a few exceptions (Salt 1959, 1961; Sømme 1964, 1967b; Kirchner and Kestler 1969; Ashwood-Smith 1970; Baust and Miller 1970, 1972).

One of the most notable and most frequently occurring phenomena associated with the accumulation of G is the depression of supercooling and freezing points. Asahina (1966) reported that some species accumulate G. Seasonal variations in supercooling points of Pelophila borealis in Norway show that a linear correlation exists between the amount of supercooling and percentage of G (Sømme 1964, Baust and Miller 1972, Östbye and Sømme 1972). For Panonychus ulmi Koch, a linear correlaton exists between supercooling points and sorbitol content (Sømme 1965a). The concurrent accumulation of G (or sorbitol) and depression of supercooling points may be induced thermally by artificial methods in specimens collected in the autumn; likewise, elevation of temperature will reverse the process for most species (Salt 1961, Sømme 1965b, Miller 1969, Baust and Miller 1970, 1972). Sømme and Östbye (1969) examined some winter-active insects and found that the freezing point of the haemolymph was higher than the chill-coma temperatures; hence these insects were able to move when supercooled. Boreus westwoodi was active until it was frozen (Sømme and Östbye 1969).

Supercooling was also noted in centipedes and scorpions in New Mexico, but it was not correlated with a cryoprotectant (Crawford and Riddle 1974).

Kirchner (1973) examined cold-hardiness in spiders from central Europe and concluded that they died at temperatures less than 0°C due to ice crystal formation in their bodies. In addition, he concluded that cold resistance was species-specific and that the degree of cold-hardiness was dependent upon the nature of the winter quarters. Cold-hardiness varied with season and with age. Neither G nor the protein content of the haemolymph of Araneus cornutus Clerck was important in supercooling. This species is very F-R, with a supercooling point between -16° and -30°C, overwintering outdoors in vegetation and having a reduced metabolic rate in winter. These factors probably promote survival when food is scarce (Kirchner 1973).

It was postulated that dehydration of an insect prior to entering diapause facilitated its ability to survive cold temperatures (Payne 1927, Sacharov 1930). Ashwood-Smith (1970) stated that "A correlation exists between the amount of water in an insect and its frost hardiness," while Wigglesworth (1972) reported previously that this was not so. Salt (1956) experimented with four species of insects and ascertained cold-hardiness increased when desiccation was nearly severe enough to cause death. In natural conditions, a reduction of body moisture in the animal prior to hibernation produces more concentrated body fluids and a lower freezing point. He concluded that desiccation was "occasionally important in cold-hardening insects" (Salt 1956). Later he confirmed this viewpoint and added that gut evacuation prior to hibernation resulted in less body water and was accompanied by a decrease in secretory activities and by an accumulation of fat (Salt 1961, Kaufmann 1971). Stöver (1973) noted that specimens of the snail, *Arianta arbustorum*, contained less water in winter than they did in summer. Two of my lumbricid species, *Allobophora turgida* Eisen and *Lumbricus rubellus* Hoffmeister collected in the autumn, were noticeably dehydrated (Reynolds, pers. comm.). Dehydration still seems to aid cold-hardiness to some extent.

The ability to survive long exposures at low temperatures was examined by Salt (1950), who stated that the "Probabilty of freezing is dependent upon temperature and time." Using larvae of *Cephus cinctus* Nort., he froze them over a period of 82 days, with periodic examinations and found an increase of mortality with time. Also, low temperatures enhance the chances of ice nuclei formation (Salt 1950), and fluctuating temperatures increase the probability of nucleation (Salt 1961). He also mentioned that the time-freezing curve could be determined for a population but not for an individual

(Salt 1956). Sømme (1967b) also cited decreasing temperatures and increased exposure times as deleterious to insects, with survival dependent upon temperature and the time over which freezing occurred.

V. CONCLUSIONS

The study of soil biology led to studies on winter ecology and subnivean invertebrates. Responses of terrestrial invertebrates at low temperatures may be classified as appetitive behaviour. These responses may be easily recognized, especially avoidance reactions or klinokinesis. Alternatively, several stimuli may evoke a 'synergistic' response which would not have been observed had only one stimulus been present, e.g. the effects of humidity superimposed upon those of temperature (Gunn 1934). In some instances, the response to a second variable (such as relative humidity) overrides the response to changing temperature. Invertebrates tend to congregate in their thermal preferenda. Decreasing temperatures stimulate activity in some invertebrates.

The phenomenon of cold-hardiness is not exclusive to insects; in this review reports on cold-hardiness in molluscs, myriapods, scorpions, mites and spiders were included. The accumulation of a cryoprotectant lowers the supercooling point of haemolymph enough to allow survival to occur at low temperatures. Many areas of investigation are not yet clear and offer many fascinating research possibilities.

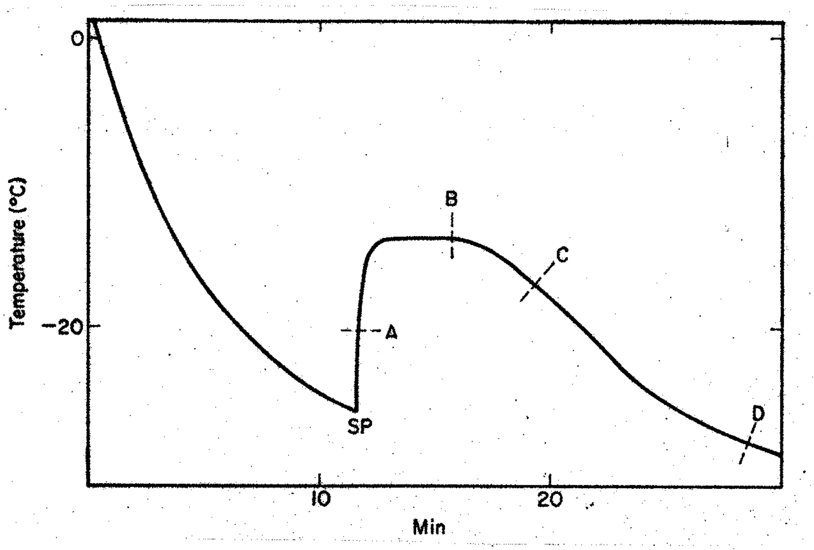


Figure 2-1

Freezing curve of an overwintering pupa of Papilio xuthus. SP, Supercooling point. If the temperature measuring element to measure the body temperature is in contact with the outside surface of an insect body, any point on the freezing curve is usually lower then the true body temperature of the insect, particularly when the cooling is more rapid (Asahina 1966).

Chapter III

MATERIALS AND METHODS

I. STUDY AREA

This study was conducted in southern Manitoba, Canada, at Fort Whyte, two miles west of Winnipeg (97° 13' 30" W, 49° 49' N). The climate is continental, with an annual variation of 34°C between mean temperatures in January and July, and snow cover lasting for up to six months per year. The study area was in the aspen parkland eco-system composed of a mixture of aspen groves and long grass prairie.

A. Habitats

Pitfall traps were placed in the fenced property of Canada Cement Lafarge Ltd., Fort Whyte, in three different habitats. Representative areas of natural vegetation were present on the property, and three habitats were chosen as follows: (A) an exposed, grassy ridge running east-northeast to west-southwest and rising about 1.5m above the dredged ponds on either side; (B) an aspen-bur oak woods; and (C) a damp, grassy meadow surrounded by the woods described in (B). The location of transects is shown in Figure 3-1. Tables 3-1 to 3-3 contain a list of the dominant species of plants found in these different habitats (Scoggan 1957). Vegetation in the woods is approaching or is in a climax condition, while that of the ridge and of the meadow is in a transitional stage, with fewer species present. The ridge was the area most disturbed by human activities, and the woods the least disturbed.

In all habitats, the percentage of vegetation cover was taken after leaf fall from the mean of 20-1/4m² quadrats taken at regular 6m intervals on the ridge, and from the mean of 100-1/4m² quadrats taken at regular 10m and 6m intervals in the woods and the meadow, respectively. The percentages of ground cover, of grass cover, of shrub cover, and of area occupied by tree stumps were estimated and are presented in Table 3-4. It must be borne in mind that the percentages of cover refer to three dimensions.

B. Position of Sampling Transects

A transect of eight traps was placed in each habitat. The transect on the ridge (A) ran east-northeast to west-southwest, to the east of some tall willows, with traps 6m apart (Figure 3-2). The one in the woods (B) ran south-southeast to north-northwest, and the traps were 10m apart as the habitat was more extensive (Figure 3-3). The transect in the meadow (C) ran southeast to northwest with traps 6m apart (Figure 3-4).

C. Construction of Traps

Simple pitfall traps of the Barber (1931) type were used and modified according to Näsmark (1964) and Breymeyer (1966). A detailed description of the ring and lid with attached handle covering each trap is given in Appendix 3-1 (Aitchison 1974). A 100+cm stake (marked at 10cm intervals) was driven vertically into the ground at the edge of the ring (Figure 3-5). The length of the handle was carefully determined in relation to the snow thickness and the effect of wind on the snow cover observed during the first winter. The exposed ridge was subjected to strong wind action, the meadow to moderate wind action, and the woods to virtually no wind action. As the critical insulating thickness of snow is 20cm (Pruitt 1970, Aitchison 1974 in Appendix 3-1), the handles at the ridge and the meadow were 17.5cm and 20cm long, respectively. In these two habitats the length was of importance since the wind action on the snow will form a hollow, or aŋmaŋa (Pruitt 1970), around any obstruction. The aŋmaŋa in turn will decrease the insulating power of the snow by decreasing the thickness. Fortunately, no aŋmaŋas developed, and the problem did not arise in the exposed habitats. In the woods, the handles were 30cm long, and no aŋmaŋas formed.

II. TEMPERATURE MEASUREMENTS

In the winter of 1973-1974, two thermistors were fixed in an undisturbed location beside each transect. One was 1cm above the ground surface in the upper portion of the subnivean space, and the other on the soil surface. Temperature readings were taken with an ohmmeter (disadvantages of which are discussed in Appendix 3-1, Aitchison 1974). In the winter of 1974-1975 three pulsed temperature telemeters (MacKay 1968), hereafter referred to as "clickers", as described in Appendix 3-1 (Aitchison 1974), were placed at each site; the first as a control 2m away from the transect; the second at a trap that had not produced unusual results during the first winter; and the third at a trap which had produced unusual results in the first winter. Temperatures were determined from the number of pulses emitted per minute, which were referred back to the calibration curve for that individual clicker. Accuracy of the temperature readings is ± 1°C. Temperature readings were taken each day that collections were made.

In addition to the above temperature readings, during the second winter eight-inch stem dial thermometers (Tel-tru Manufacturing Co., Rochester, N.Y.; range of -50°C to +25°C) were inserted under the ring of the trap cover into the subnivean space while a trap was being cleared. The thermometer equilibriated by the time the trap was cleared, and the temperature was recorded.

During the winter of 1974-1975, temperatures within snow profiles were taken once a week in early and late winter and once every two weeks in midwinter at each collection site. A clean vertical face of snow must be exposed from the soil surface to the top of the snow surface to do a snow profile; this profile consisted of the maximal, minimal, and modal thicknesses of snow and temperatures at intervals throughout the snow layer, whose separate layers were also measured.

In March of each year, snow station measurements were done with a standard National Research Council snow kit (Science Workshop, Lakehead University, Thunder Bay, Ontario, and Sargent-Welch catalogue) in undisturbed snow adjacent to the transect. Once a snow profile was exposed, hardness was determined by pushing discs of various sizes into a snow layer until the snow collapsed under a specific, measured pressure; to determine density, a specific volume of snow was extracted and weighed on a spring balance. Measurements of ambient air temperature in °C, snow thickness in cm, snow hardness in g/cm^2 and snow density in g/cm^3 at various thicknesses, plus observations of wind speed and surface conditions were recorded.

III. REMOVAL OF SPECIMENS

In order to minimize disturbance and compaction of the snow cover, I used cross-country skis when removing specimens from traps. Established trails were followed at each visit to avoid extensive packing of the snow, which would increase its density.

To collect the specimens, the inner removable cup was lifted out, and the invertebrates visible to the naked eye were removed with either a wooden-handled probe which had a minute loop of a few strands of fine copper wire at its tip, or with leather-shanked forceps to reduce heat loss from fingers. Specimens from each trap were put into a glass shell vial partially filled with ethylene glycol, stoppered, and returned to the laboratory.

In the winter of 1974-1975, snow density over the trap increased only in the area penetrated by the cylinders (see the section on snow properties in Appendix 3-1). Despite the narrow clearance of 1cm between the walls of the two cylinders, a sizeable volume of snow sometimes fell into the trap and clouded the ethylene glycol. Nevertheless, the crystals melted in several minutes, and despite this inconvenience, much less snow cascaded into the traps than in the previous winter when the cylinders were not used. The outer cylinder and a trap are shown in Figure 3-6. In the spring of 1975, two of the 24 handles on the lids came loose when hoarfrost on the underside of the lid froze to the snow underneath. In one instance, a crowbar was needed to pry off the lid.

General meteorological conditions were considered prior to each collection day. When the temperature was below -35°C with a wind in excess of 35 km.p.h., collections were postponed until the wind chill factor was less severe. Even so, it was often necessary to re-warm my hands intermittently throughout the collection period of one day in the first winter and a half day in the second winter.

IV. LABORATORY PREPARATION OF SPECIMENS

In the laboratory each sample was filtered through a "kimwipe" tissue, washed with distilled water, and specimens were removed from the tissue with a fine camel-hair brush. Specimens were temporarily stored in a shell vial filled with 70% ethanol. Later they were sorted to family and counted. Representative individuals were prepared according to Beirne (1955) and sent to various taxonomic authorities for more precise identification.

In March of each year six representative samples consisting of snow immediately above the subnivean space, or "pukak" (Pruitt 1970), and about 1 cm of soil and litter were removed 2m away from each transect. These samples provided an indication of activity, variety, and density of animals present on the soil surface. During the first winter, these samples were stored in a cold room at 2°C and lower for two days prior to extraction in modified MacFadyen funnels with a cool collection chamber for seven days (MacFadyen 1961). In the second winter the samples were placed in the extraction funnels immediately after arrival at the laboratory and left for one week.

Figure 3-1

Map of nature reserve and transects in the grounds of Canada Lafarge Cement Co., Fort Whyte, Manitoba.

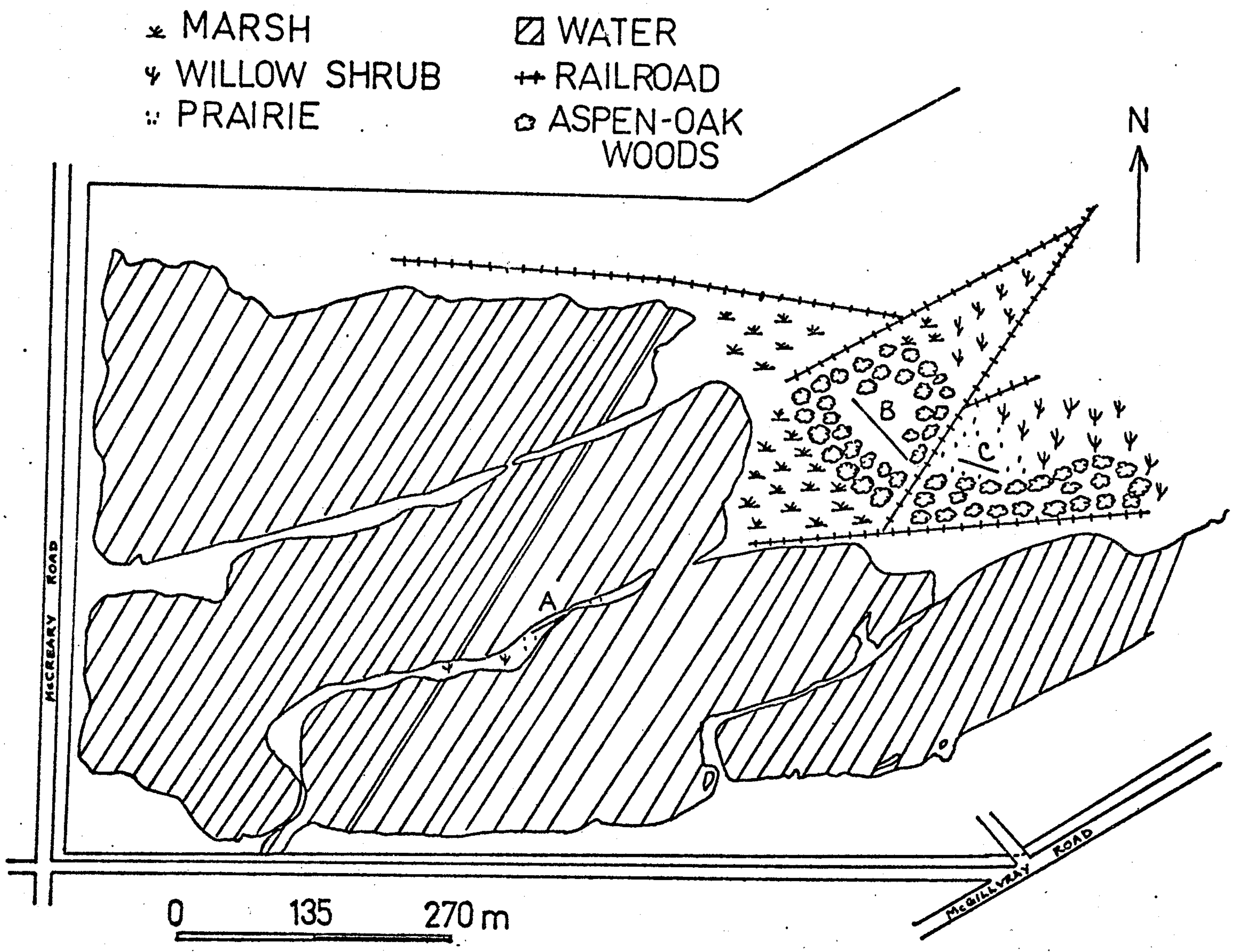

MARSH
WILLOW SHRUB
PRAIRIE
WATER
RAILROAD
ASPEN-OAK WOODS
N
A
B
C
McCREARY ROAD
McGILLVRAY ROAD
0
135
270 m

Figure 3-2

Ridge transect (A) looking west south-west in early autumn.

Figure 3-3

Woods transect, showing trap B4, looking north.

Figure 3-4

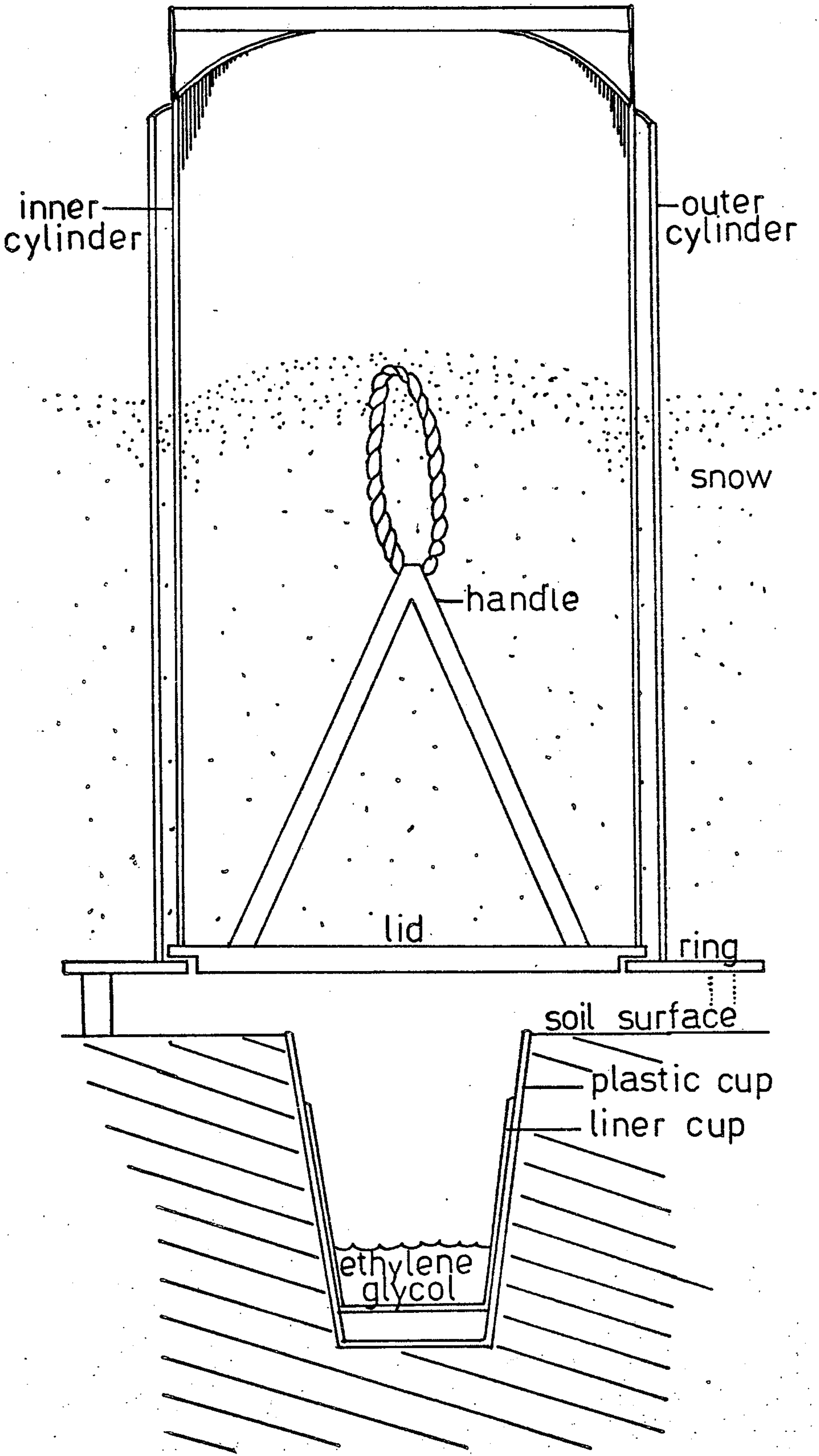
Meadow transect, showing trap C8, looking south.

Figure 3-5

Trap A2 on ridge transect, showing ring and lid.

Figure 3-6

Diagram of the pitfall trap, ring and lid, and inner and outer cylinders in place in the snow cover as seen from the side.


inner cylinder
outer cylinder
snow
handle
lid
ring
soil surface
plastic cup
liner cup
ethylene glycol

Appendix 3-1

A Sampling Technique for Active Subnivean Invertebrates in Southern Manitoba by C. W. Aitchison (1974).

The Manitoba Entomologist Vol. 8 (1974) :

A SAMPLING TECHNIQUE FOR ACTIVE SUBNIVIAN INVERTEBRATES IN SOUTHERN MANITOBA

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ABSTRACT: A technique for sampling subnivian invertebrates has been devised for Manitoba conditions based on a method used originally in Scandanavia. A pitfall trap containing a removable cylinder is set in the soil and covered with a ring holding a lid to keep out moisture and snow. To avoid excessive changes in the physical properties of the snow cover, two metal cylinders are inserted into the snow. The cylinder with the largest diameter is pushed to the top of the ring; the other with the slightly smaller diameter fits on the lid and allows the snow above the lid to be removed without compaction.

Among the invertebrates collected in the traps have been three new records for the fauna of Manitoba.

INTRODUCTION

Many researchers in the past have thought that insects and other invertebrates were not active during the winter, but Näsmark (1965) found otherwise. In the past twenty years techniques have been devised to study winter activity in the boreal regions (Heydemann 1956, Nâsmark 1964, Breymeyer 1966). A modification of the method of sampling previously used in Scandanavia is discussed here. This modification was necessary because of the different snow characteristics in Central Canada. Apparently the properties of snow cover create an environment in which certain invertebrates can remain active throughout the winter.

Those conditions which favor invertebrate activity during winter are temperatures near 0°C and a high relative humidity. Snow cover, when at a certain thickness, insulates the ground from severe temperature changes and maintains a temperature near 0°C. Also under the snow the relative humidity is high (Coulianos and Johnels 1962, Nâsmark 1964).

PROPERTIES OF SNOW COVER

Snow cover is really an ecotone between two very different environments: the dry, very cold, and sometimes rapidly moving atmospheric air, and the moist, relatively warm, and stable air of the microenvironment under the snow (Coulianos and Johnels 1962, Pruitt 1970). Formosov (1969) defined snow cover as "an emulsion of air and snow flakes . . .". A blanket of snow insulates the subnivian space (i.e. the space between the soil surface and snow cover (which may be 3 to 8 cm high, Coulianos and Johnels 1962), from the macroenvironment.

The first parameter which has a major effect on the insulation of snow cover is density. Snow with a low density provides greater insulation than snow with a high density (Rikhter 1954, Formosov 1969, Pruitt 1970). Due to the low thermal conductivity of snow, a temperature gradient develops in the snow cover between the source of heat in earth and the supranivian air (Formosov 1969). The movement of water vapor along the temperature gradient produces condensation on the colder crystals, changing their structure by making them larger and more rounded (Rikhter 1954, Geiger 1965). Metamorphorosis of snow crystals occurs with time, causing an increase in density. (Snow density may be defined as the ratio of the amount of ice in relation to the amount of air in a given volume, and snow hardness may be defined as the amount of force needed to collapse the intercrystalline bonds.) Furthermore, the snow cover may increase in both hardness and density (Rikhter 1954, Williams and Gold 1958). Snow density is also affected by air and snow temperatures. Williams and Gold (1958) found that higher snow densities were associated with shallow snow cover and extremely variable wind and temperature conditions, such as those on the prairies and on the arctic tundra. In these conditions there is a maximum heat exchange from the ground to the air.

The second parameter which affects the insulation provided by snow cover is thickness. When snow thickness is 20 cm approximately or more, the subnivian environment is stable and independent of the macroenvironment (Williams and Gold 1958, Coulianos and Johnels 1962, Geiger 1965, Formosov 1969, Pruitt 1970). Pruitt (1970) has labelled this crucial thickness factor as the "hiemal threshold", i.e. the snow cover thickness at which the subnivian environment is insulated from the diel fluctuations in ambient temperatures. Snow thickness in excess of 20 cm does not increase the insulating power of the snow cover significantly, unless density decreases and thus decreases the heat loss from the ground (Coulianos and Johnels 1962, Geiger 1965, Pruitt 1970).

To quantify these data on snow cover in the present study, a National Research Council standard snow kit was used. The parameters of snow thickness, grain size, surface condition, wind speed, snow profiles with density, hardness and temperature readings from top to bottom in the snow cover are obtained.

CONSTRUCTION OF PITFALL TRAPS

Barber (1931) devised pitfall traps consisting of a jar filled with a non-repellent preservative for cave-inhabiting insects, and modified Barber traps were used in this project. Modified Barber traps were used by Näsmark (1964) and Breymeyer (1966), who fitted a small, inner, removable cup containing a small amount of preservative, inside an outer cup whose upper rim was level with the soil surface. Näsmark (1964) also placed a cover over the trap site to keep it free of snow. The cover consisted of a ring of plywood supported by three small legs (4 cm high), and a central masonite lid (see Figure 1). The preservative used in Manitoba was ethylene glycol, since it is non-repellent, does not freeze at -30°C (when pulled out of the outer cup to remove the specimens), and does not deteriorate over a long period of time.

During the winters of 1973-1974 and 1974-1975 invertebrates have been sampled using the method described above, at the fenced property of the Canada Cement Lafarge, Ltd. in Fort Whyte, Manitoba. Because snow conditions are very different in Manitoba than those in Scandanavia, modifications for removing the invertebrates from the traps were made in the winter of 1974-1975.

During the winter of 1973-1974, the disturbance of the snow on the lid of a trap at each sampling occasion led to a considerable increase in snow hardness at the trap site. This change in hardness probably resulted in heat loss. Hence each trap site was probably colder than the surrounding soil surface, and this may have affected the catch. Towards spring the snow cover was so dense and hard that it was necessary to saw out wedged-shaped blocks of snow to uncover the lids. Snow density was found to also have increased at the trap sites.

To minimize this change in snow hardness in the winter of 1974-1975, a pair of thin galvanised iron cylinders have been used. In very soft, friable snow both are used; the outer one whose diameter is slightly greater than that of the lid prevents the surrounding snow from falling into the trap, while the inner one whose diameter is less than that of the lid retains the soft snow immediately over the lid. A handle about 20 or 30 cm long has been fitted in the centre of the lid. By pulling it to remove the lid, the inner cylinder and the snow inside are removed with minimal disturbance. In hard spring snow, it is expected that only the inner cylinder, with saw-toothed edges, will be needed. In this way the hardness of the snow above the lid remains much the same as that of the surrounding snow cover. The only disturbed area is above the ring where the cylinders have penetrated.

In late winter and early spring, hoar frost accumulates on the underside of the lid, freezing the lid to the ring. The longer handles allow more leverage to be applied and thus make it easier to remove the lids than in the winter of 1973-1974.

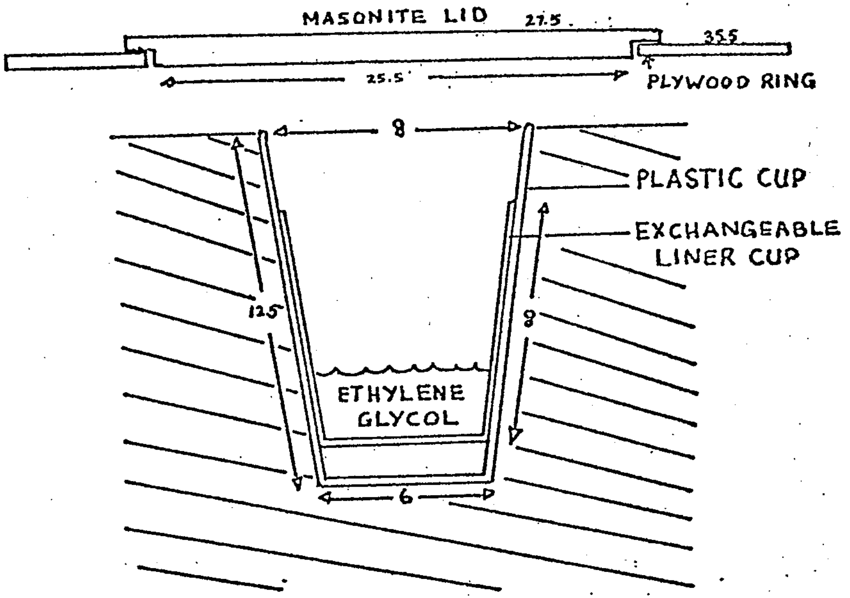

Figure 1: Transverse section through the trap. Measured in cm (after Näsmark (1964).

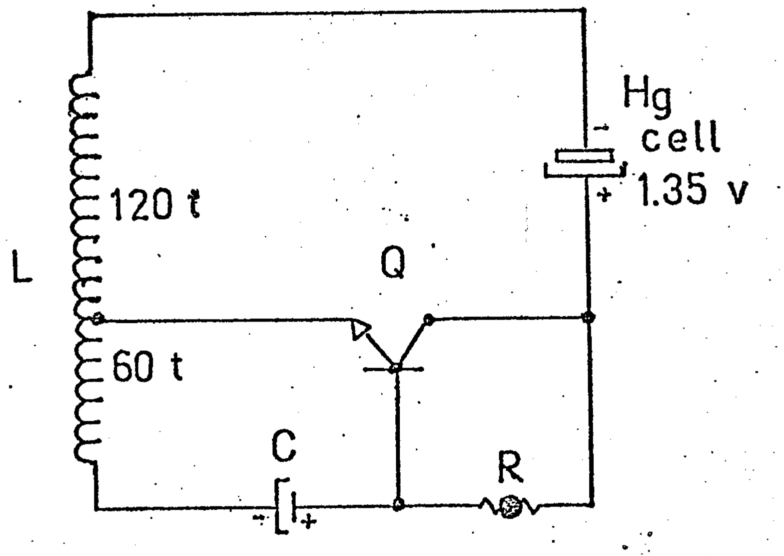

Figure 2: Circuit diagram of "clicker" telemetry transmitter component schedule:

Q: MPS 3704 (Motorola) Silicon general purpose NPN transistor
Cell: 1.35 volt mercury cell (one cell of type TR 133R battery, manufactured by Mallory).
C: 1.5 microfarad tantalum electrolytic capacitor (15 W.V.D.C. rating)
R: YSI #44014 (Yellow Springs Instruments) precision thermistor bead, 300 kohms at 25°C.
L: Coil of 180 turns, single layer closely wound #32 wire, 0.5 cm diameter by 1.5 cm long. Approximately 2.2 millihenries.

TEMPERATURE MEASUREMENT

During the winter of 1973-1974, thermistor probes and an ohmmeter were used for temperature measurement. Since ohmmeters become inaccurate at temperatures below 4°C, they were replaced during the winter of 1974-1975 by a simple radiotelemetric device called a "clicker". It is an untuned simplification of the circuit used by Spencer (1968), (see Figure 2 for specifications). A transistor radio, tuning to 535 to 1605 kHz, makes a suitable receiver for the broad-beam AM radio frequency pulse emitted by the "clicker". The number of clicks emitted per minute varies directly with temperature (MacKay 1968). Each clicker has a range of about 60 cm, so that readings may be taken above the snow cover, without disturbing the snow.

INVERTEBRATES COLLECTED

The invertebrates collected in the traps have been mainly Collembola, Acarina, Araneae, and Staphylinidae in the mid-winter. Other groups were also caught in autumn and spring. The value of this method can be demonstrated by the fact that three new records for Manitoba have been recorded. They are as follows:

1) *Neanura muscorum* (Templeton), (Collembola: Poduridae), determined by W.R. Richards, Biosystematics Research Institute, Ottawa, taken 17 October 1973 from a ridge between 2 ponds.

2) *Stenamma diecki* (Emery) (Hymenoptera: Formicidae), determined by G.L. Ayre, Canada Agriculture Research Station, Winnipeg; taken 17 October 1973, from scrub oak-aspen woods.

and 3) *Lamycetes* sp. (Chilopoda: Henicopidae) determined by R.E. Crabill, Jr., Department of Entomology, Smithsonian Institute, Washington, D.C., U.S.A.; taken 24 October 1973, from a small meadow.

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Table 3-1

Dominant Plant Species on the Ridge (A)

SCIENTIFIC NAME	COMMON NAME
Andropogon gerardi Vitman	big bluestem
Elymus sp.	wild rye
Juncus sp.	rush
Poa pratensis L.	Kentucky blue grass
Achillea millefolium L.	yarrow
Aster sp.	aster
Astragulus goniatus Nutt.	purple milk-vetch
Cirsium arvense (L.) Scop.	Canada thistle
Helianthus maximillianus Schrad.	narrow-leaved sunflower
Meliotus alba Desr.	white sweet-clover
Potentilla anserina L.	silverweed
Solidago nemoralis Ait. var. *decemflora* Fern	showy goldenrod
Sonchus arvensis L.	sow-thistle
Rosa blanda Ait.	smooth rose
Salix interior Rowlee	sandbar willow

Table 3-2

Dominant Plant Species in the Woods (B)

SCIENTIFIC NAME	COMMON NAME
Poa pratensis L.	Kentucky blue grass
Anemone sp.	anemone
Aster junciformis Rydb.	rush aster
Cirsium arvense (L.) Scop.	Canada thistle
Cypripedium calceolus L. var. *parviflorum* (Salisb.) Fern	small yellow lady's slipper
Galium boreale L.	Northern bedstraw
Hieracium canadense Michx.	Canada hawkweed
Meliotus alba L.	white sweet-clover
Mentha arvensis L. var. *villosa* (Benth.) S.R.Stewart	wild mint
Ranunculus sp.	buttercup
Sanicula marilandica L.	snakeroot
Solidago canadensis L.	graceful goldenrod
Sonchus arvensis L.	perennial sow-thistle
Thalictum venulosum Trel.	veiny meadow-rue
Zizia aptera (Gray) Fern	heart-leaved alexandra
Cornus stolonifera Michx.	red osier dogwood
Rhus radicans L. var. *rydbergii* (Small) Rehder	poison ivy
Rosa blanda Ait.	smooth rose
Salix bebbiana Sarg.	beaked willow
Salix petiolaris Smith	basket willow
Viburnum lentago L.	nanny berry
Amelanchier alniflora Nutt.	saskatoon
Corylus americana Walt.	American hazelnut
Populus tremuloides Michx.	trembling aspen
Prunus virgiana L.	red-fruited choke cherry
Quercus macrocarpa Michx.	bur oak

Table 3-3

Dominant Plant Species in Meadow (C)

SCIENTIFIC NAME	COMMON NAME
Juncus balticus Willd. var. *montanus* Engelm.	Baltic rush
Poa pratensis L.	Kentucky blue grass
Achillea millefolium L.	yarrow
Aster pansus (Blake) Cronquist	many-flowered aster
Cirsium arvense L. Scop.	Canada thistle
Glycyrrhiza lepidota (Nutt.) Pursh	wild licorice
Lathysus venosus Muhl. var. *intonous* Butt. and St. John	wild pea vine
Meliotus alba Desr.	white sweet-clover
Sonchus arvensis L.	perennial sow-thistle
**Populus tremuloides* Michx.	trembling aspen
Rosa acicularis Lindl.	prickly rose
***Symphoricarpos occidentalis* Hook.	Western snowberry

* At south end of transect only.

** Several plants in clump at middle of transect, 0.25m from the fourth trap.

Table 3-4

Percentage of Vegetation Cover After Leaf-Fall

HABITAT	% GROUND COVER	% GRASS COVER	% SHRUB COVER	% TREE COVER
Ridge (20 quadrats)	79.25	46.75	9.60	0.0
Woods (100 quadrats)	97.70	73.49	28.97	7.5
Meadow (100 quadrats)	97.80	69.75	14.55	0.0

Chapter IV

TEMPERATURE MEASUREMENTS UNDER SNOW AND THERMAL GRADIENTS WITHIN THE SNOW LAYER

I. RESULTS AND DISCUSSION

A) Calibration of Temperature-Measuring Devices

Observations on temperature were made under and in the snow cover during the two winters of research. During the first winter, thermistors were calibrated prior to and after field work. Calibration was made by using a standard curve; the relationship between temperature and resistance in ohms being non-linear. This is particularly noticeable in the wide range in resistance at low temperatures such as -20°C, or lower, when readings may be inaccurate (see Appendix 3-1, Aitchison 1974).

During the second winter "clickers" were calibrated prior to and after field work. The threshold of low temperature activity of the "clickers" ranged from -1°C to -12°C. As one clicker of the three on the ridge did not function below -1°C, it emitted pulses only at the start and end of the winter. Figure 4-1 shows a linear relationship between the number of pulses per minute and temperature. At low temperatures, the mercury batteries have a life of more than twelve months. Also there was greater variability of readings at low temperatures for thermistors than for clickers.

B) Subnivean Temperature and Supranivean Temperature

The subnivean temperature, T(s), is that of the subnivean space under the snow. The supranivean temperature is that above the snow, or the ambient air temperature, T(a). The ohmmeter was not available on the 12 and 27 of December, 1973, so that T(s) could not be taken on those dates. All clickers at control stakes in undisturbed snow remained functional throughout the second winter. As readings of T(s) were not made daily or continuously, results may be distorted. Mean daily T(a) is given here, and variation in T(s) recorded whenever possible.

Due to the low frequency of observations of temperature readings in this study, the associations of a specific T(s) with a somewhat earlier-recorded T(a) must be regarded as relative, not absolute, due to the time lag in days as the temperature moves through the snow cover. Low temperatures, storms, and high winds on the study area strongly influenced observations, which therefore were biased in favour of rising or higher T(s)'s. Hence correlations between activity of invertebrates and T(s) are relative and may not be valid. Continuous recordings of T(s) and the known presence or absence of invertbrates would have eliminated this problem.

In 1973-1974, the mean daily winter supranivean temperature, T(a), varied greatly in contrast to the small fluctuations in the mean T(s) for all habitats. Subnivean temperatures were recorded once snow cover became established on November 1. Generally, the winter was cold, with a mean temperature in January of -22.49°C, 4.29°C below the usual mean for that month. During the remainder of the winter and early spring (snow lasting until the 19th of April), T(a) approached the normal range.

Drops in T(a) were usually followed several days later by dips in T(s). During the first winter,the T(s) ranged between 0° and -9°C (excluding mid-April temperatures) and averaged about -4° to -5°C for all habitats, while the T(a) ranged between +0.6° and -35.6°C (Figure 4-2).

The T(s) on the ridge fell below 0°C in late November to -7°C by mid-December, and stayed low until mid-March, with a minimal T(s) of -9°C recorded after each T(a) of -31.7°C and -20°C, respectively (Figure 4-3a). These readings may not be representative as the thermistor was located in an area which had reduced snow cover because of wind. Snow thickness was below the hiemal threshold on the 19 December, 1973, and 9 January, 1974.

In the woods, the T(s) remained just below 0°C until late November and fell to -5°C on December 5th, concurrent with a drop of T(a) to a mean of -20.0°C on the 4 December (Figure 4-3b). At that time the snow thickness varied from 15 to 20cm (Figure 4-11b), which is less than the hiemal threshold. From then on, the T(s) stabilized between -3.5° and -5°C, until it began to rise towards the end of February.

On the 28 March, the T(s) fell to -6°C, after a mean low T(a) of -27.8°C on the 23 March. T(s) rose in the late winter/early spring.

In the meadow, the T(s) was the highest and most stable of those measured (Figure 4-3c). A sudden drop in T(a) to a mean of -33.9°C in early January saw the T(s) drop to -5°C two days later, and again in early February a drop in T(a) to -31.7°C preceeded a drop in T(s) to -5°C two days later. The same relationship was seen again in late March, with a lag of five days before the dip in T(s). In late February/early March, the general rise in T(a) was followed by a rise in T(s) to -0.5°C.

In the 1974-1975 winter snow cover was not permanent until December 14th and lasted until the 17th of April. Generally the early and midwinter period was mild with occasional drops in T(a) to below -20°C. T(s) for all habitats were colder than the previous year, ranging from 0° to -10.5°C, and averaging about -5° to -6°C, while T(a) ranged between -5°C to -29.4°C. Lows in T(s) of -9°C and -10.5°C occurred two and four days after drops in T(a) to -27.8°C, -29.4°C and -23.9°C, respectively. A warm period with T(a) of -3.9°C occurred in late February, followed by a cold March and early April, with temperatures hovering between -16.7°C and -29.4°C. None the less, snow melt was almost complete by April 17th.

Mid-December marked the first T(s) for the winter. In early December, the T(a) began to drop, once down to -15°C, and the bare soil surface temperature fell to -9°C on the ridge (Figure 4-4a). As the snow cover gradually increased from the time it became permanent, the T(s) rose and was steady at around -6°C for midwinter. Despite the low T(a)'s in March, the T(s)'s continued to rise and showed a relationship to T(a) in late March and early April.

Both woods and meadow revealed a similar pattern (Figures 4-4b and 4-4c), though the T(s) were slightly higher throughout the midwinter (about -5°C) and fluctuated more in amplitude. T(s) in late winter rose more markedly in the woods than in the meadow.

Many researchers noted that T(s) is more stable than T(a), which fluctuates widely (Keränen 1920, Mail 1932, Rikhter 1954, Williams and Gold 1958, Coulianos and Johnels 1962, Ylimäki 1962, Geiger 1965, Pruitt 1970). This relationship also occurred in this study. Sudden drops in T(a) were followed by corresponding small decreases in T(s), two to five days later, a delayed response of T(s) similar to that reported by other workers (Keränen 1920, MacKinney 1929, Pruitt 1970). Fuller _et_ _al_. (1969) mentioned T(s) was never completely independent of T(a), as is substantiated by the results given in this chapter (see Figures 4-3 and 4-4).

C) _Thermal Gradient in Snow Cover_

A thermal gradient was established in the insulating snow layer (see Figure 4-5). During mid- and late winter in

1975, these temperatures were measured in undisturbed snow cover in all habitats. The method of measurement of temperatures by long stem, dial thermometer is shown in Figures 4-6 and 4-7. Temperatures in the top of the subnivean space and closest to the ground were taken in "pukak" or large depth hoar crystals (Pruitt 1970), and are marginally lower than T(s).

On the ridge T(s)'s varied considerably in mid- and late winter, while the temperature in the top 5cm of snow was between that of T(s) and T(a) (supranivean) (Figure 4-8a). In late January, the snow proved a reasonable insulator against the T(a) of -25.0°C. At 30cm in the snow cover the temperature dropped to -18°C from a T(s) of -7°C, a difference of 11°C in 30 cm of snow. Towards late March, the snow had a homogeneous texture, and no thermal gradient occurred in it; all temperatures were -2°C. This particular area was exposed and had the most dense snow, with the poorest insulation compared to the other two habitats. The temperature difference between T(a) and T(s) is a function of the insulating power of the snow cover; a greater temperature difference is associated with greater insulating capacity (Figure 4-8b).

In the woods T(s)'s were more stable (Figure 4-9a), and the insulating capacity of the snow greater, as shown by greater temperature differences between T(a) and T(s). In both the woods and the meadow, the snow was less dense than on the ridge and hence had a greater insulating capacity

(Figures 4-9b and 4-10b). In late January the temperature in the snow cover 40cm above the soil surface was -18°C, while the T(s) was -3°C, a difference of 15°C. At that time the T(a) was -25°C. From then on, snow became denser, until in early April the temperature difference was 24.5°C, with a T(s) of -1°C (Figure 4-9b). Throughout the late winter, the insulating power of the snow decreased as its density increased, until mid-April when all layers within the snow cover were at 0°C.

The snow was also a good insulator in the meadow as shown by the large temperature differences (Figure 4-10).

The presence of a thermal gradient in snow cover is well-documented (Keränen 1920, Rikhter 1954, Mellor 1964, Geiger 1965, Pruitt 1970), and indicates the insulation provided by the snow cover. Here a large temperature difference (exceeding 15°C) implied good insulating properties, while a small temperature difference implied poor ones.

D) Subnivean Temperature and Snow Cover Thickness

The amount of snow cover during the winter of 1973-1974 was 2.5cm more than average for last thirty years. It occurred over the usual span also, from late October to mid-April.

On the ridge T(s) dropped steadily and remained at -7°C to -9°C in midwinter, also a period of intense cold (-20° to -30°C) (Figure 4-11a). Wind action on the ridge above the ponds caused snow deposition to be uneven, varying by 40cm. Some parts of the transect had 20 to 25cm of snow while other had over 60cm, due to drift formations around isolated shrubs at the western end. This snow was hard and dense wind slab. The snow melted in early April in about ten days.

In the woods where wind was minimal, snow cover was less variable (the usual variation was 5 to 10cm) and less dense (Figure 4-11b). The variation in T(s) was especially large and noticeable in early December when the snow cover was below the hiemal threshold, and in early March when the snow density increased due to metamorphism. The T(s) was stable at -3°C for most of the winter; colder temperatures were usually recorded by the thermistor 1cm above the soil surface.

The meadow was the area of most snow accumulation, with up to 70cm (Figure 4-11c). T(s) varied more with T(a) than in the woods, yet was maintained at roughly -3° to -4°C during most of the cold midwinter. Temperature fluctuations occurring in late winter appear to be influenced more by T(a) than by snow cover thickness; however, at that season the snow had increased considerably in density.

During the winter of 1974-1975 little snowfall occurred in early winter, but 41.3% of the total snowfall fell during January. By the end of the winter the total snow cover was only 3.5cm less than the average of 126.5cm. As a consequence of the late appearance of permanent snow cover, the soil surface temperature was low beforehand.

On the ridge the snow cover increased in December and January, but generally was thin (not more than 45cm) (Figure 4-12a). Even so, in mid-January and late March the snow cover in places was below the hiemal threshold of 20cm. In January a corresponding drop to -10°C in T(s) ensued, while in late March the T(s) rose to +2°C, perhaps due to insolation of the snow cover as the T(a) was low (-20.3°C). From February until late April, T(s) rose, except for a dip in early April.

In the woods snow cover accumulated less rapidly than on the ridge, due to reduced wind action (Figure 4-12b). By midwinter the thickness reached a maximum of 55cm. In late March snow thickness decreased again, and an increase in T(s) occurred as on the ridge. Generally the T(s) varied between -3° to -6°C throughout mid- and late winter. By mid-April T(s) began to rise; then in the third week of April the soil surface temperature had risen to +3.5° and +4°C, accompanied by a simultaneous disappearance of snow cover. This is the usual pattern of events in spring in each habitat (Figure 4-12b).

In the meadow the snow cover accumulated gradually in midwinter, up to a maximum of 50cm (Figure 4-12c). The greatest snow thickness each winter accumulated around snowberry bushes in the middle of the transect. In some areas along the transect the snow thickness did not exceed the hiemal threshold until the end of January. Previous to that time in late January, T(s) fluctuated more widely, by about 3° or 4°C, reaching a minimum of -9°C. The general T(s) throughout midwinter ranged between -4° and -9°C, intermediate between T(s) in the woods and that on the ridge. Again in mid-March a sudden decline to -9°C in T(s) occurred without a change in snow thickness. In the third week of March, T(s) rose sharply as the snow thickness decreased. At the end of March a fall of T(s) to -9°C occurred three days after a drop in T(a) to -24.5°C. April was characterized by a steady increase in T(s) and soil surface temperature as the snow melted.

Generally the snow thickness was greater during the first winter (40 to 60cm) than during the second (30 to 50cm), and T(s) were also higher in the first with the exception of the ridge. This latter discrepancy is probably partly explained by the location of the thermistor stake (which was often below the hiemal threshold) and partly by the greater snow density. Figures 4-11a to 4-12c reveal that a snow thickness greater than 20cm gave some protection against T(a), while that less than 20 cm (Figures 4-11b, 4-12a and 4-12c) provided much less.

The variability of snow thickness differs from year to year (as seen here) and from place to place, e.g. in anmanas (Pruitt 1957, Fuller _et_ _al_. 1969). Less snowfall is encountered in areas with trees, while fields and thick brush may have heavy drifts (Rikhter 1954). More snow occurred in the meadow due to the "shadow effect" of the trees catching snow in the woods, as described by Geiger (1965). The most variable deposition occurred on the ridge which was subjected to wind action.

Snow is usually hard-packed in exposed areas, while loosely packed in forests and fields (Rikhter 1954), which corroborates the data presented here. Increased density resulting from strong wind action produced a higher thermal conductivity and greater heat loss (Williams and Gold 1958). This, in turn, results in low T(s). Coulianos and Johnels (1962) observed a decrease in the size of the subnivean space in areas exposed to strong wind. This relationship may partially explain the low T(s) and low catches seen on the ridge in this study.

E) Properties

In March, 1974, complete snow stations were done for each habitat (Table 4-1). The ridge had the most severe subnivean habitat, with wind-packed snow. T(s) of -6.5°C, a hardness of 600 g/cm^2, and a density of 0.300 g/cm^3. By contrast the woods and meadow were more favourable habitats, with T(s) of -0.5°C and -0.25°C, snow hardnesses of 15 to 25 g/cm^2 and 20 to 27.5 g/cm^2, and snow densities of 0.260 and 0.280 g/cm^3, respectively. Most important here were the readings of snow hardness at the trap sites: 1000 g/cm^2 on the ridge, 400 g/cm^2 in the woods, and 550 g/cm^2 in the meadow. The weekly disturbance of digging in the snow cover down to the lids caused considerable sublimation and recrystallization of snow crystals, thus increasing its hardness. Density is not synonomous with hardness (see Appendix 3-1, Aitchison 1974).

In March of 1975, partial snow stations were taken at each habitat, and the pertinent parameters measured (Table 4-2). The snow was exceptionally heavy and wet on that day, giving high density readings for all habitats. Thus the T(s) for all habitats were not representative of temperatures encountered during most of the winter. With the use of cylinders to empty traps, the snow cover above the lids was much less disturbed, and gave snow densities of 0.310 g/cm³ on the ridge, 0.340 g/cm³ in the woods, and 0.300 g/cm³ in the meadow. These results were slightly greater than those taken from undisturbed snow adjacent to the transect. These snow morphology observations were too few to be of significance.

Although the hardness readings at trap sites were taken in 1974 and density readings in 1975, the order of magnitude of differences between undisturbed snow and that above the trap sites varied substantially. In 1974 the hardness of snow above the trap sites was almost twice that of undisturbed snow on the ridge, and 16 to 20 times greater in the woods and meadow. In 1975 the differences in snow density between the two types of snow were not of the same magnitude (largest difference was 0.290 g/cm³ versus 0.340 g/cm³ in the woods).

The use of the cylinders during the second winter prevented a large increase in snow density at the trap sites. During the first winter the weekly uncovering of each lid led to a considerable increase in hardness of that snow, such that it became necessary to saw out wedges of snow (Table 4-1). Consequently there must have been an appreciable heat loss . During the second winter the circle of snow penetrated by the cylinders became hard, but the cylindrical volume of snow above the trap site remained at much the same density as that of the undisturbed snow cover (Table 4-2). Thus it seems probable that there was less heat loss from the traps the second winter.

Williams and Gold (1958) calculated the mean Winnipeg snow density to be 0.279 g/cm³ ±0.050 g/cm³, the highest in Canada except for the Arctic and alpine tundra. The measurements taken in March each year varied from a low of 0.265 g/cm³ (Table 4-1: woods, 1974) to a high of 0.340 g/cm³ (Table 4-2: trap-site in woods, 1975). Geiger (1965) stated that old snow density ranged between 0.3 to 0.5 g/cm³, which compares favourably with the results here. It must be emphasized that density measurements were taken in late winter. At this time snow cover is most dense after metamorphism (Formosov 1969).

The relative humidity in the subnivean space is high, usually 100% (Coulianos and Johnels 1962, Formosov 1969, Pruitt 1970). This factor would be beneficial to many invertebrates, especially those with large surface-to-volume ratios such as Collembola.

Penetration of solar and sky radiation into snow occurs (Näsmark 1964, Geiger 1965); in fact Mellor (1964) stated that "Absorption of solar radiation in snow affects the temperature distribution layers just below the surface." This explains the characteristic of the thermal profiles in snow cover observed in the spring in which the temperature in the top 5cm was relatively high, about -1°C, even though the T(a) was low, about -15° to -20°C (Figures 4-8a and 4-9a). Approximately 1 to 7% of light is transmitted through 20cm of snow cover (Geiger 1965). The greater the density of the snow cover, the greater is the light penetration by long wavelengths, i.e. solar and sky radiation (Rikhter 1954, Geiger 1965). Table 4-3 (Budyko 1963) demonstrates the seasonal changes in radiation intensity at different latitudes, with southern Manitoba at about 50°N. This increase in light intensity and penetration would occur in the late winter when the snow cover was most dense.

One interesting parameter which was not measured in this study is the accumulation of carbon dioxide under snow. As the snow cover increases in density, it becomes less permeable to air. Loose, porous snow is somewhat permeable to air, while ice layers in snow cover reduce that permeability (Rikhter 1954). Since the subnivean space contains active small mammals, invertebrates and respiring dormant vegetation (Pruitt 1957, 1970; Coulianos and Johnels 1962, Ylimäki 1962, Näsmark 1964, Formosov 1969, Fuller *et al.* 1969), the carbon dioxide accumulation may increase under snow as winter advances (Pruitt 1970). Probably, the effect on invertebrates is minor, compared to that on small mammals which actually construct ventilation shafts to the snow surface in late winter (Pruitt 1970). Permeability of snow to air is not well understood (Geiger 1965), but is is presently being investigated (C. Penny, pers. comm.).

In late winter of each year, problems caused by the formation of depth hoar, or "pukak" (Pruitt 1970), were encountered. As mentioned in Appendix 3-1 (Aitchison 1974), the pukak accumulated on the underside of the lids, frequently freezing to the snow on the ring in temperatures near 0°C. A crow bar was required to uncover the traps.

The accumulation of pukak in late winter is due to metamorphism occurring above the subnivean space (Keränen 1920, Rikhter 1954, Geiger 1965). Evaporation of snow crystals at the relatively warm soil surface in the saturated atmosphere, vapour diffusion along the thermal gradient in the snow cover, and recrystallization caused the formation of pukak on the underside of the trap lids that froze them to the snow on the ring (Rikhter 1954, Mellor 1964, Pruitt 1970).

The periods immediately prior to the first snowfall in autumn and after the snow cover has disappeared in spring may be called the autumn and spring critical periods for small mammals (Pruitt 1957, 1970; Fuller et al. 1969), and for ectothermic invertebrates also. At those times T(a) may be low, and no insulating snow cover is present for protection, though some protection may be provided by the litter. These periods are defined in relation to the thermal overturn in the soil and the arrival of the hiemal threshold thickness of snow cover. Their length, amount of precipitation, especially of rain, determine the survival of many small organisms (Pruitt 1957, 1970).

II. SUMMARY

Because clickers show less variablity in readings at low temperatures than thermistors, clickers were more satisfactory for measuring temperatures under snow than thermistors.

During the first winter T(s) in all habitats remained fairly constant at about -4° to -5°C while T(a) fluctuated widely. The T(s)'s on the ridge were lowest, due to dense snow and probably a smaller subnivean space. Minimal T(s)'s of -9°C were recorded on the ridge. Sudden drops in T(a) were followed several days later by a small decline in T(s).

In the second winter permanent snow cover was established in mid-December, and the hiemal threshold attained at all habitats in late January. Consequently the soil surface temperature reached a low of -9°C prior to snowfall; the mild autumn prevented even lower temperatures. Minimal temperatures of -10.5°C in the meadow were recorded in January, owing to the thin snow cover. For all habitats T(s)'s averaged about -5° to -6°C, somewhat colder than the previous winter.

Thermal gradients within snow cover indicate the amount of insulation provided by the snow. The larger the temperature difference between T(a) and T(s), the more insulation provided.

Snow cover thickness during the first winter was slightly greater than average, while a less than average snow cover thickness occurred during the second winter. The T(s) was directly proportional to the thickness of the snow cover. The most variable snow thicknesses occurred on the exposed ridge, while the most snow accumulation was encountered in the meadow.

Snow density determines the insulating power of snow cover. The dense, wind-packed snow on the ridge provided less insulation than the same thickness of loosely-packed snow in the woods. The use of cylinders greatly reduced snow hardness above trap sites during the second winter.

Light penetration into snow cover increases as the amount of light (radiation) available increases in intensity and as the density of snow increases. Hence the subnivean space in March is probably no longer dark.

III. CONCLUSION

In southern Manitoba, fluctuations of T(a) have an effect upon T(s). T(s) fluctuates considerably less in amplitude and exhibits a lag effect of two to five days. The temperature profile within snow cover demonstrates the insulation which snow provides. As snow increases in density by metamorphism in late winter, it loses much of its insulating power, and T(s) fluctuates more widely than in midwinter. Also in late winter penetration by long wavelength light is greater in dense snow cover. During the second winter the use of cylinders prevented a large increase in snow density and hardness above the trap sites, and thus insulation in the snow cover above the lid was better.

Figure 4-1

Calibration curves for all nine clickers(a to i), with number of pulses emitted per minute versus temperature in °C.

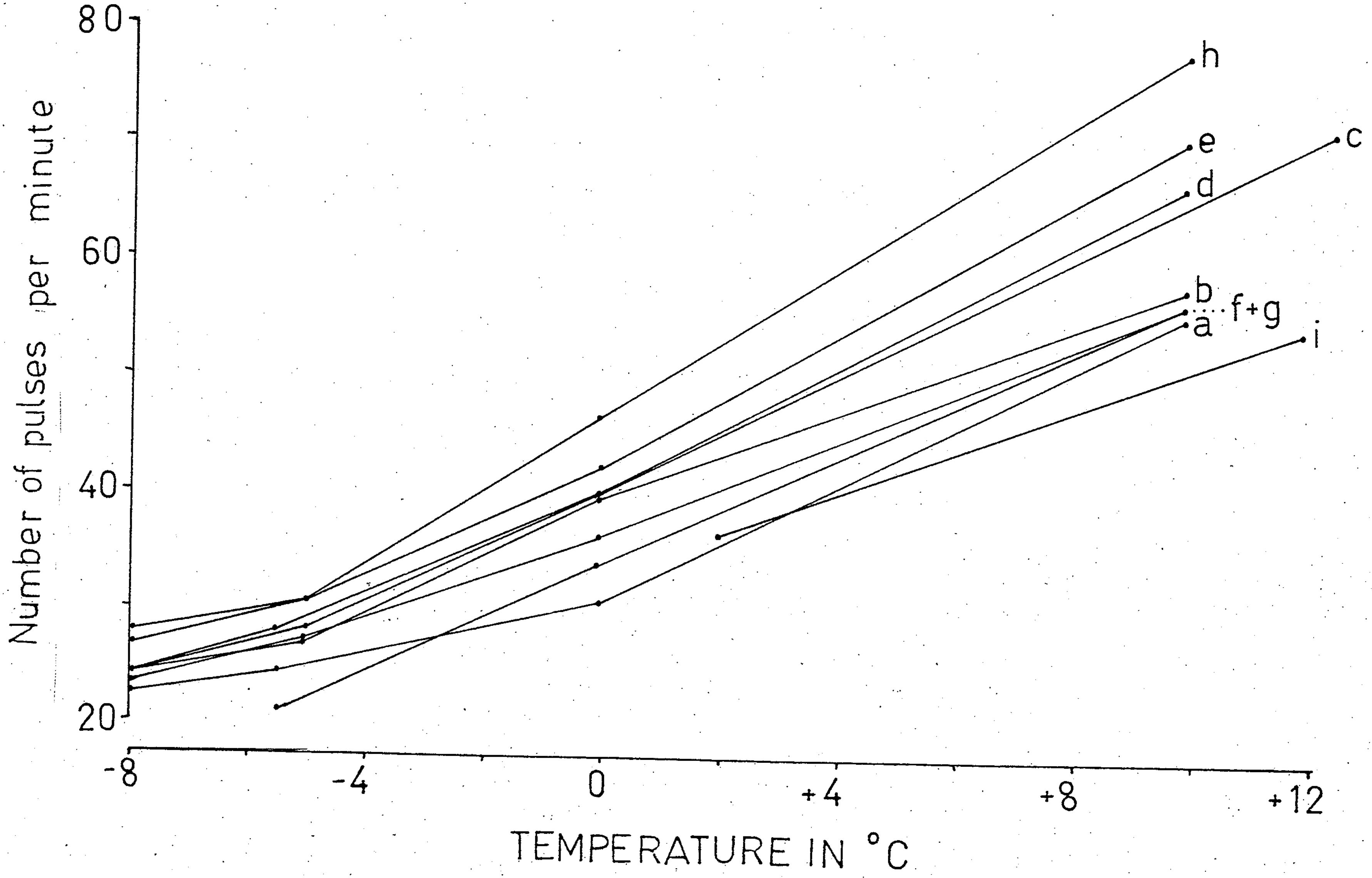
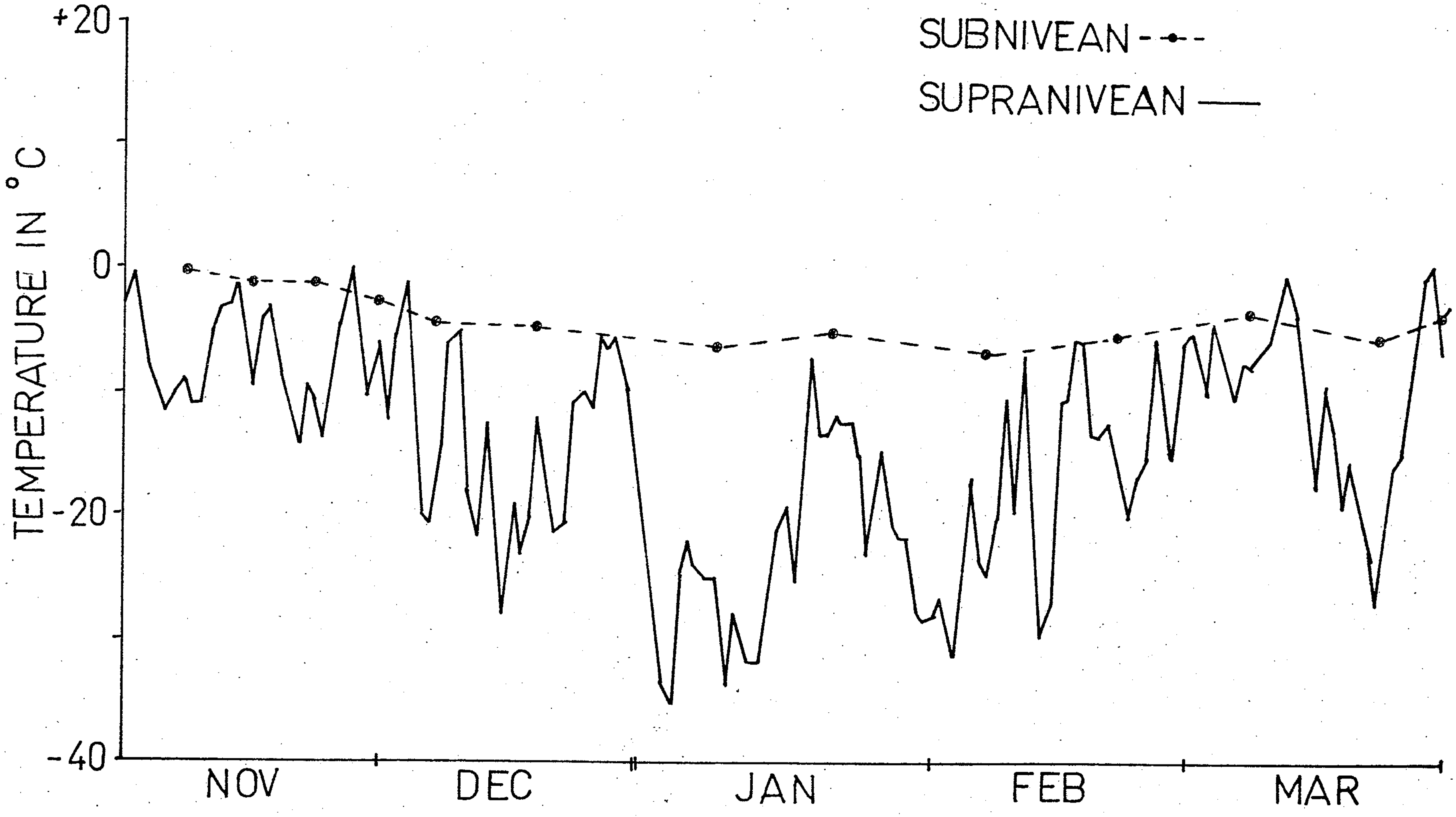

80
60
40
20
Number of pulses per minute
-8
-4
0
+4
+8
+12
TEMPERATURE IN °C
h
e
c
d
b
f+g
a
i

Figure 4-2

Average weekly subnivean and mean daily ambient air temperatures for all sites in 1973-1974 (solid dot indicates reading of T(s)). The latter temperatures were taken from metecrological readings of the Winnipeg Weather Office, Atmospheric Environment Service, International Airport, Winnipeg, Manitoba R2R-0S7.

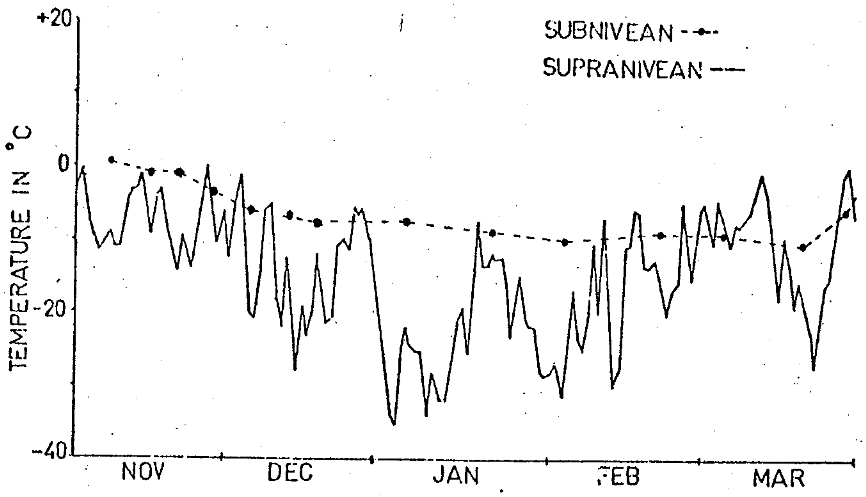


ALL SITES 1973-1974

Figure 4-3

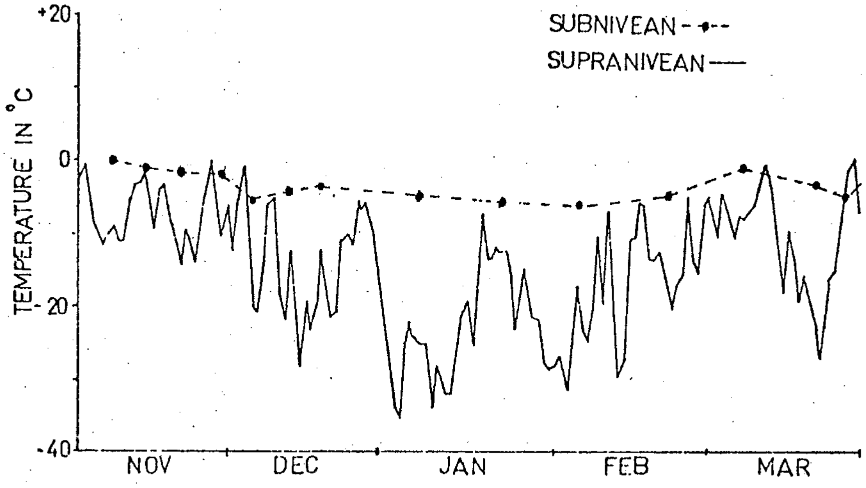
Average weekly subnivean and mean daily ambient air temperatures for each habitat in 1973-1974 (A - ridge, B - woods, C - Meadow), (dots as for Figure 4-2).

A



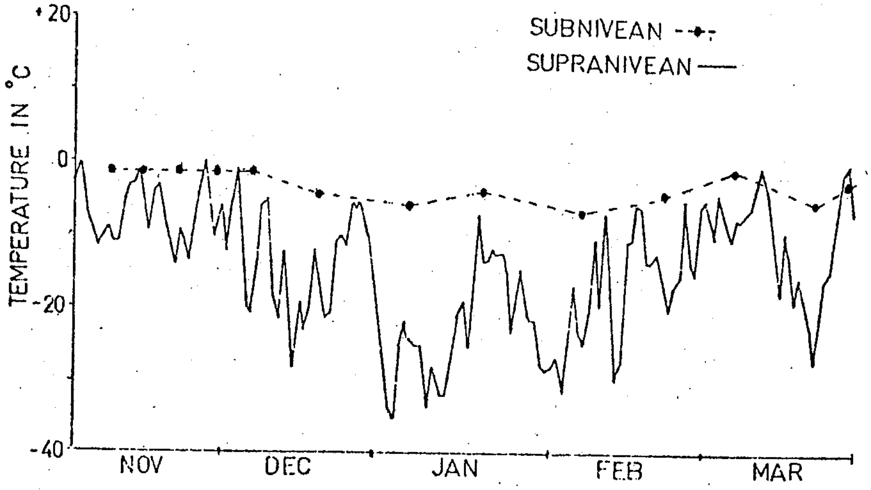
RIDGE 1973-1974

B



WOODS 1973-1974

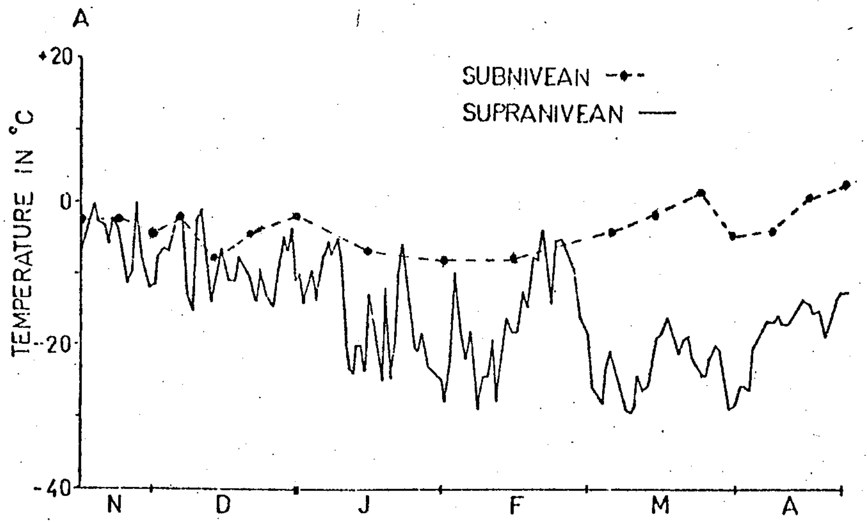
C



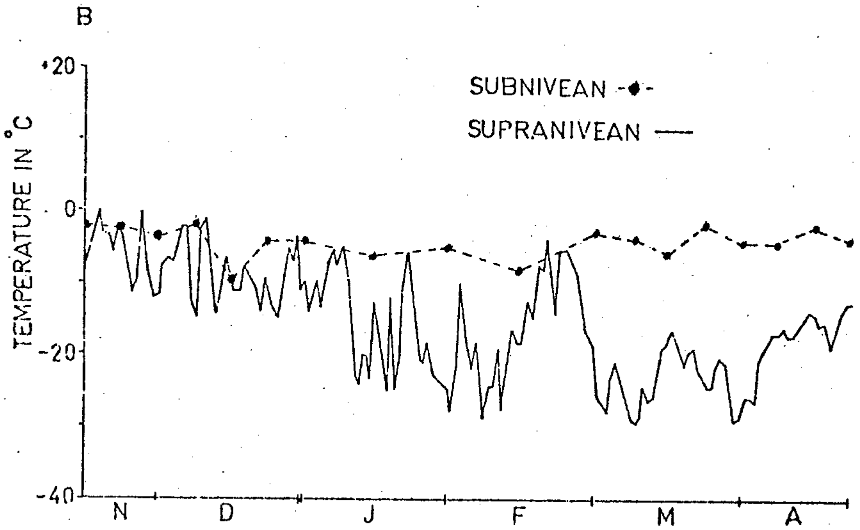
MEADOW 1973-1974

Figure 4-4

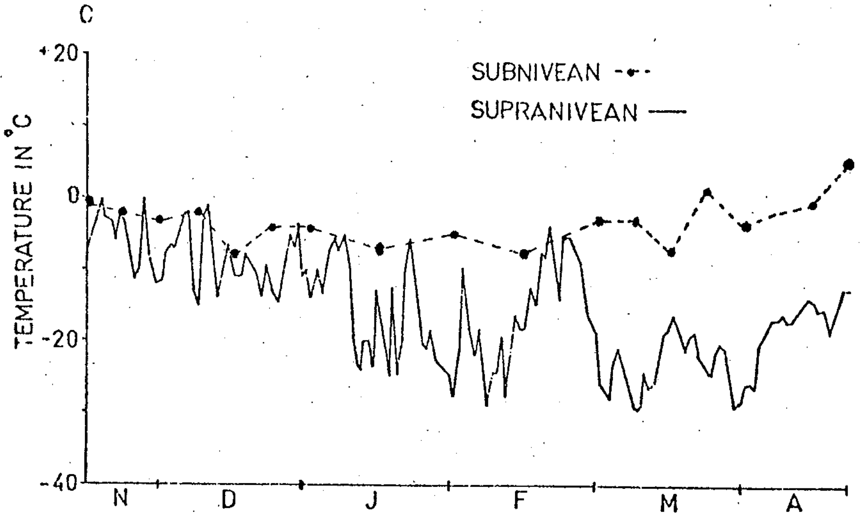
Average weekly subnivean and mean daily ambient air temperatures for each habitat in 1974-1975 (A - ridge, B - woods, C - meadow), (dots as for Figure 4-2).



RIDGE 1974-1975



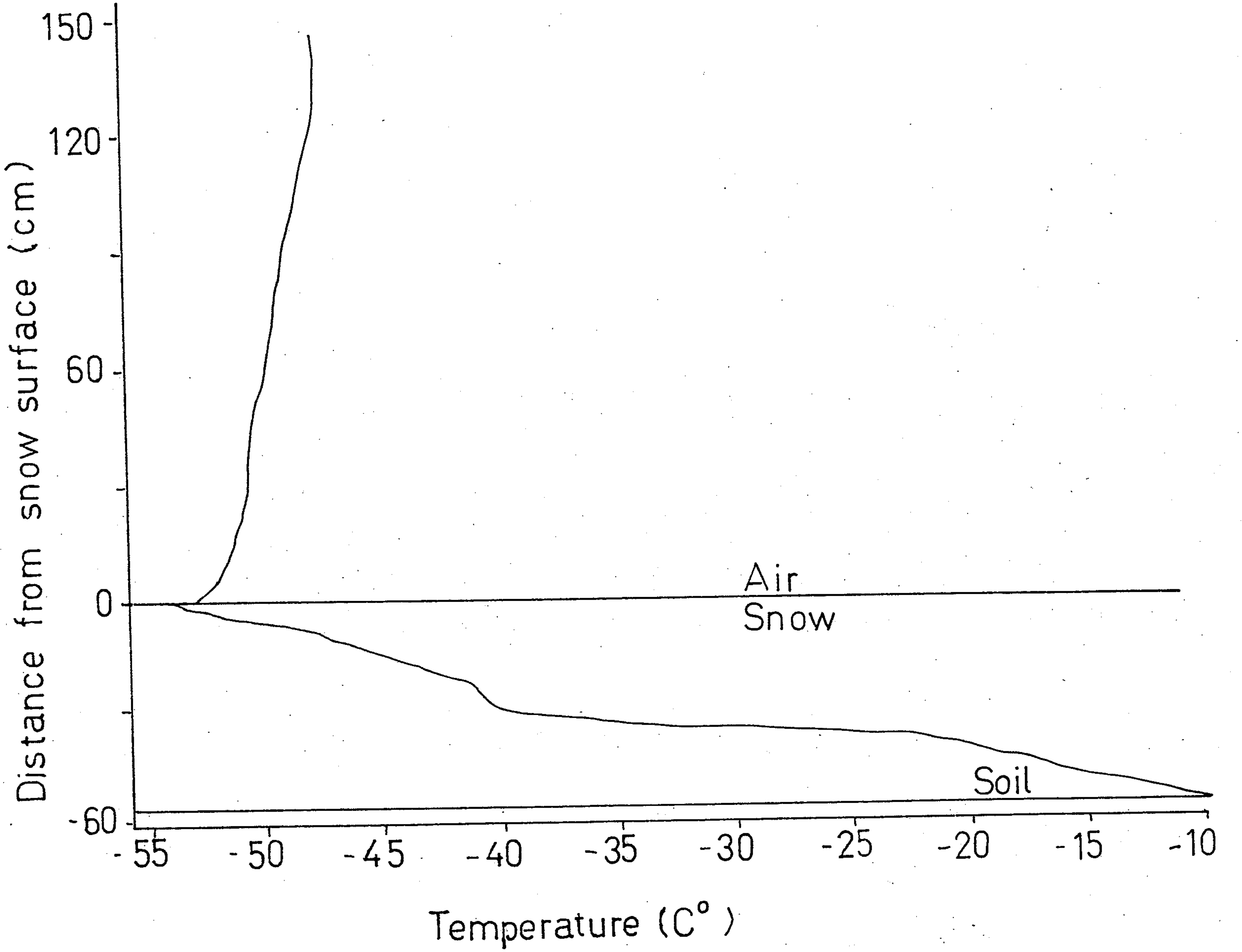
WOODS 1974-1975



MEADOW 1974-1975

Figure 4-5

Temperature gradients in air and snow in Alaska (after Johnson 1954).


150
120
60
0
-60
Distance from snow surface (cm)
Air
Snow
Soil
-55
-50
-45
-40
-35
-30
-25
-20
-15
-10
Temperature (C°)

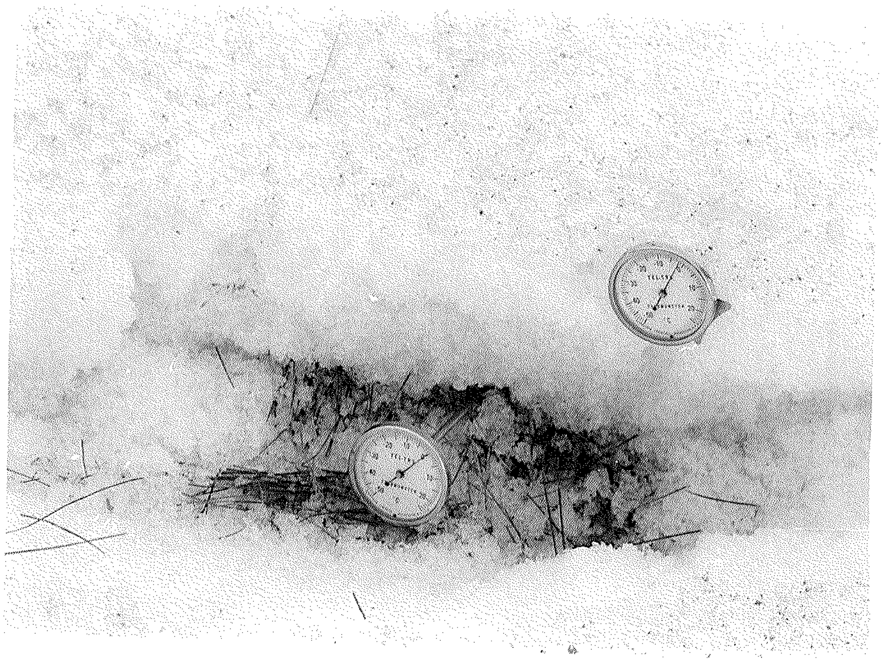


Figure 4-6

Thermal gradient in snow cover of meadow after a thaw in in March, 1975 (note large pukak crystals).

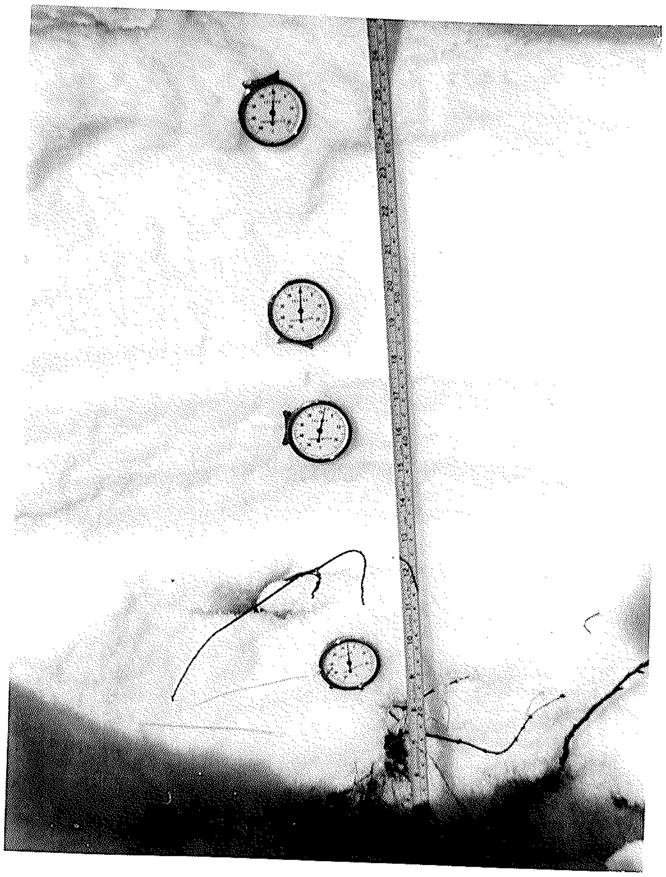
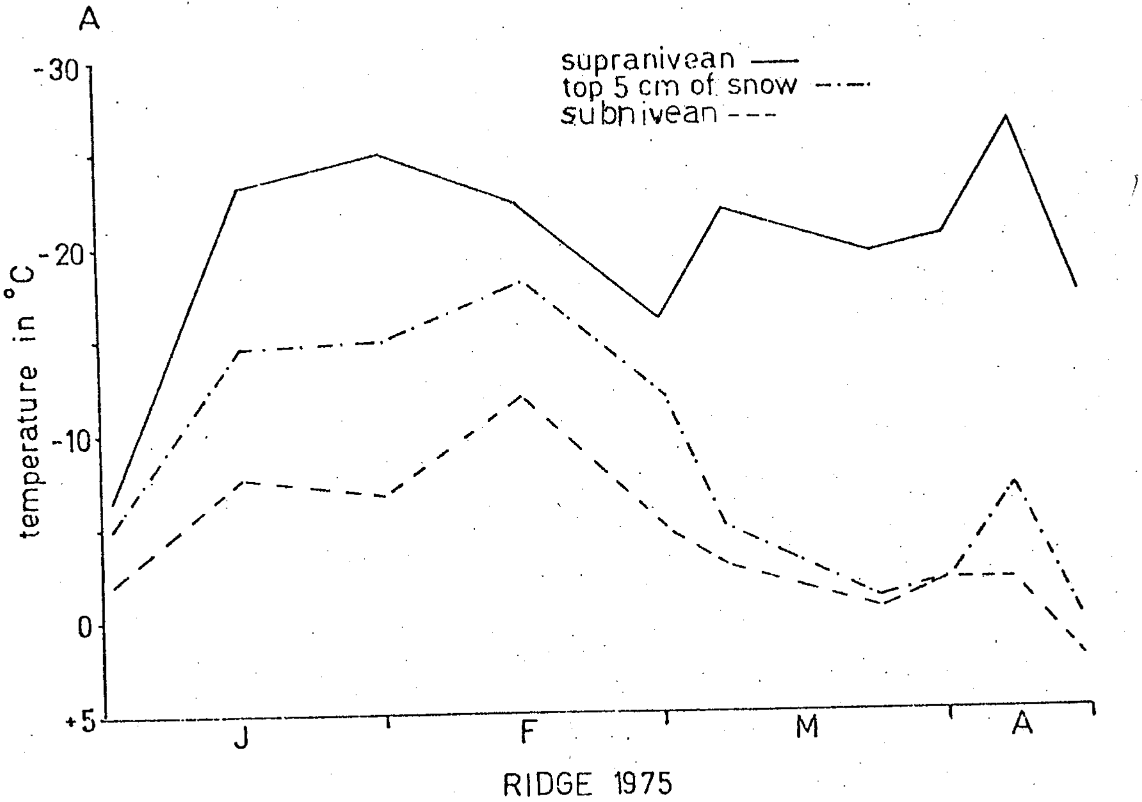


Figure 4-7

Thermal gradient in 70cm of snow in meadow in March, 1976. T(s) is -2°C.

Figure 4-8

(A) Supranivean, top 5cm of snow, and subnivean temperatures in snow cover of ridge in 1975, and (B) the temperature difference between T(s) and T(a) on the ridge in 1975.


A
supranivean ——
top 5 cm of snow -·-·-
subnivean ---
-30
-20
-10
0
+5
temperature in °C
J
F
M
A
RIDGE 1975

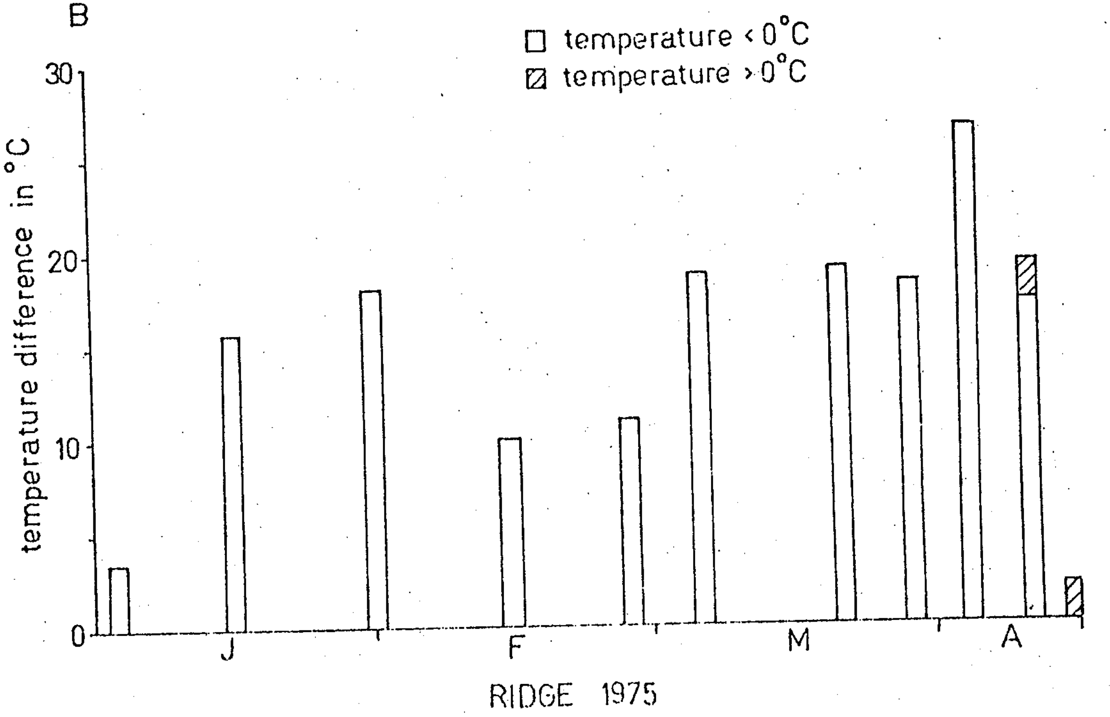
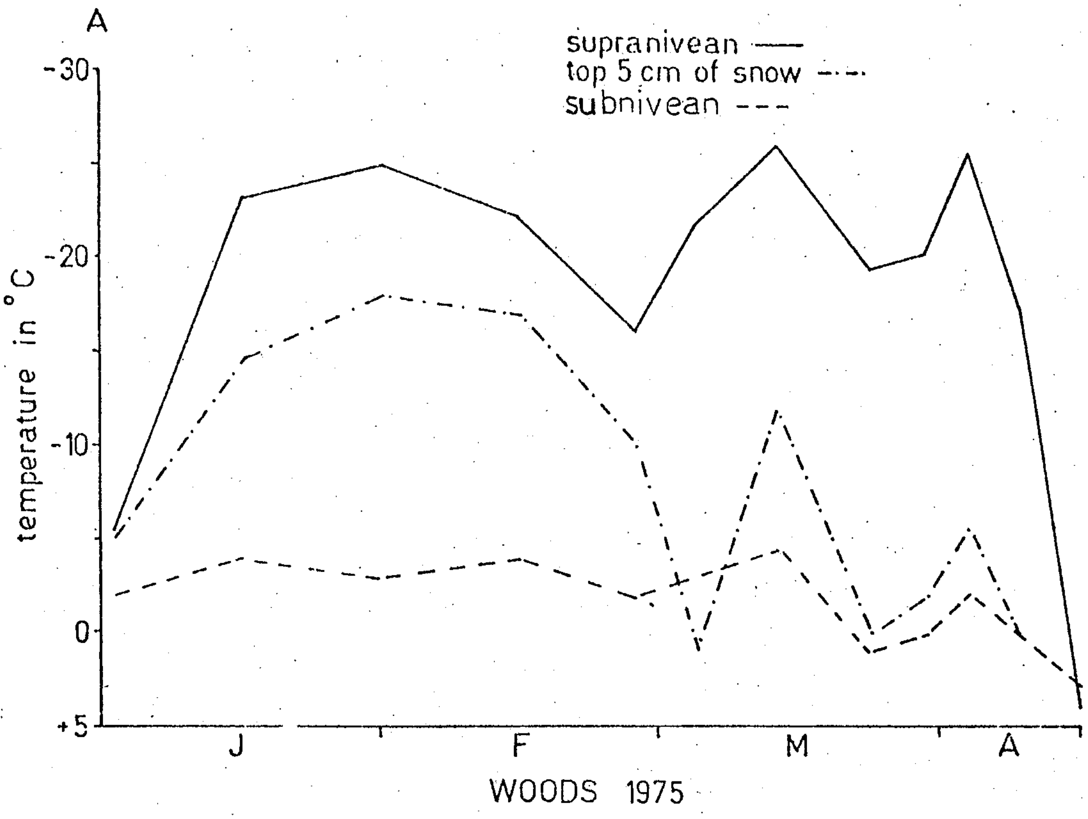

B
☐ temperature < 0°C
▨ temperature > 0°C
30
20
10
0
temperature difference in °C
J
F
M
A
RIDGE 1975

Figure 4-9

(A) Supranivean, top 5cm of snow, and subnivean temperatures in snow cover of the woods in 1975, and (B) the temperature difference between T(s) and T(a) in the woods in 1975.


A
supranivean ——
top 5 cm of snow -·-·-
subnivean - - -
-30
-20
-10
0
+5
temperature in °C
J
F
M
A
WOODS 1975

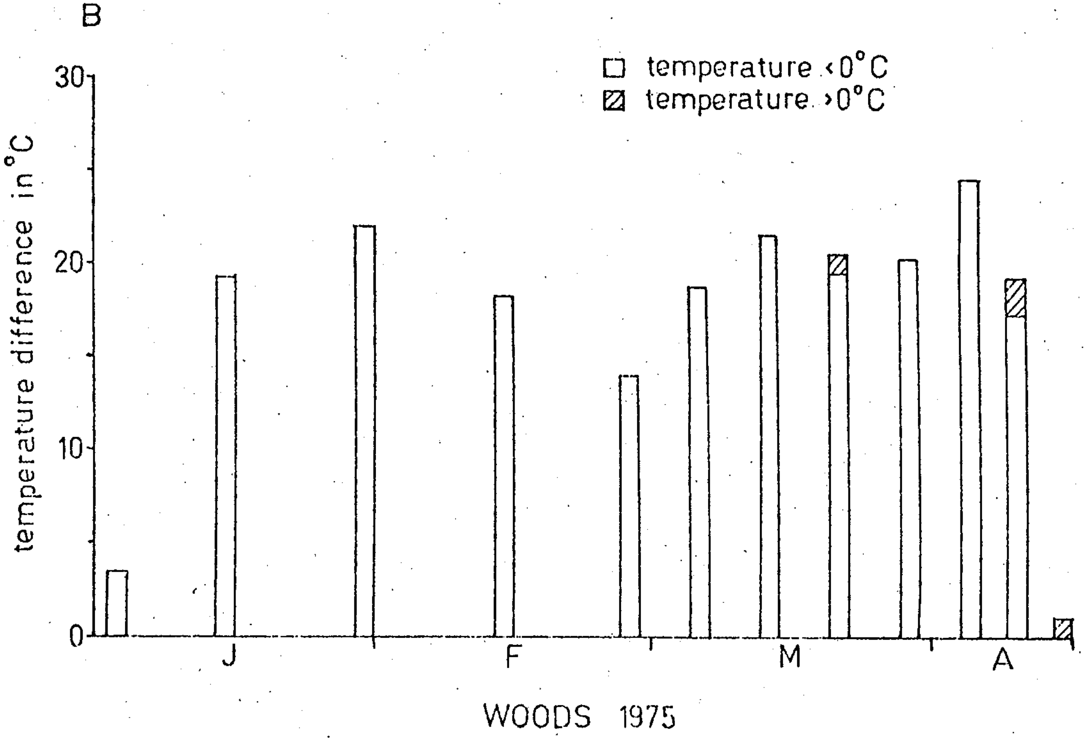
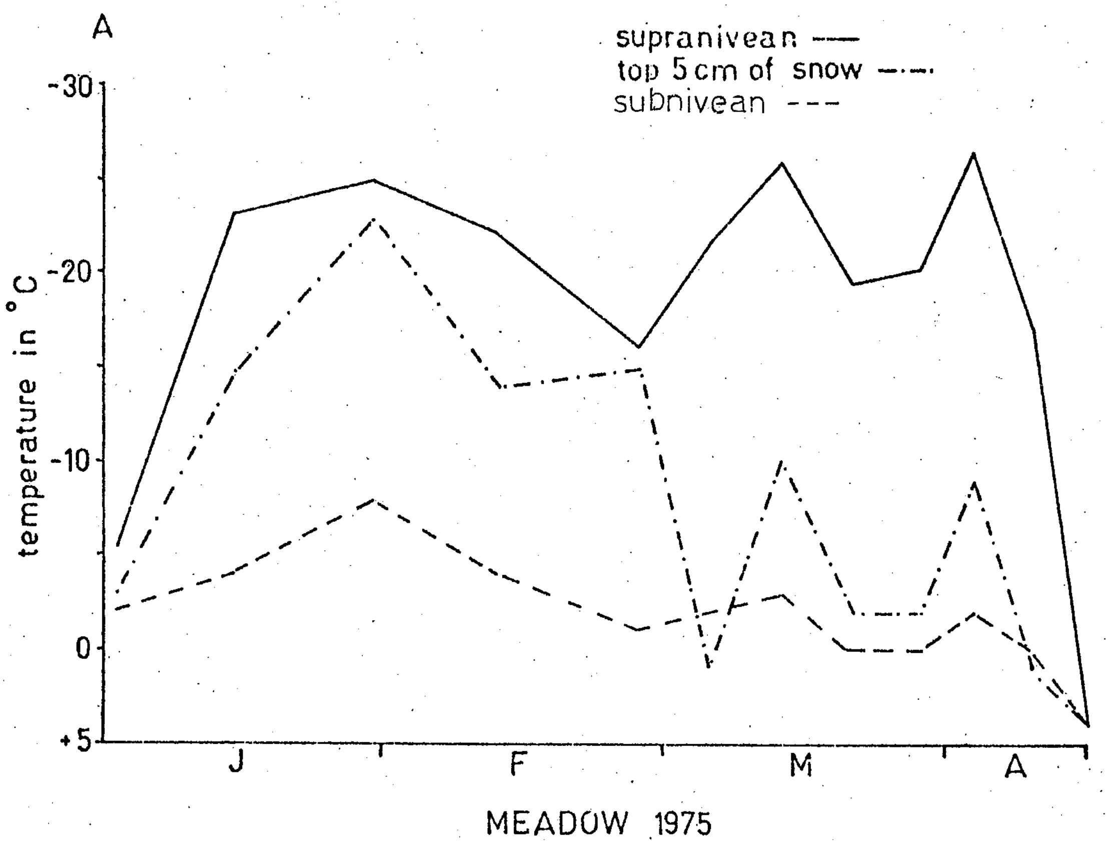

B
☐ temperature <0°C
▨ temperature >0°C
30
20
10
0
temperature difference in °C
J
F
M
A
WOODS 1975

Figure 4-10

(A) Supranivean, top 5cm of snow, and subnivean temperatures in
snow cover of the meadow in 1975, and (B) the temperature difference between T(s) and T(a) in the meadow in 1975.


A
supranivean
top 5 cm of snow
subnivean
-30
-20
-10
0
+5
temperature in °C
J
F
M
A
MEADOW 1975

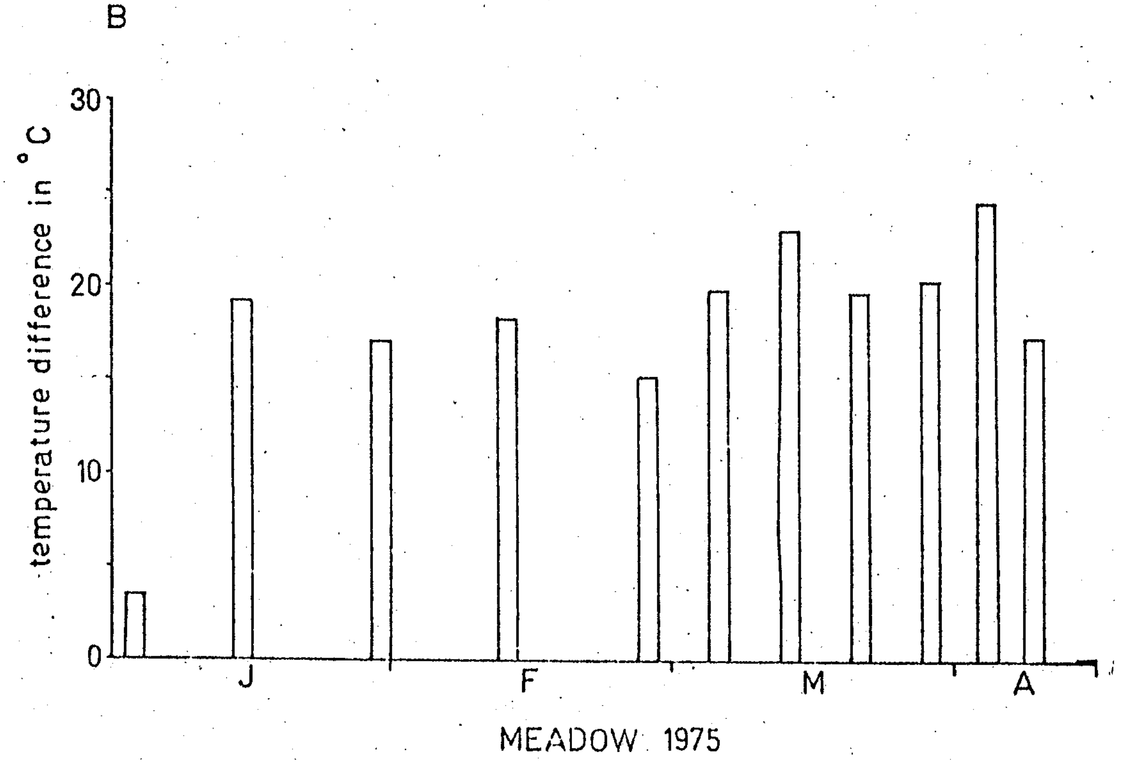
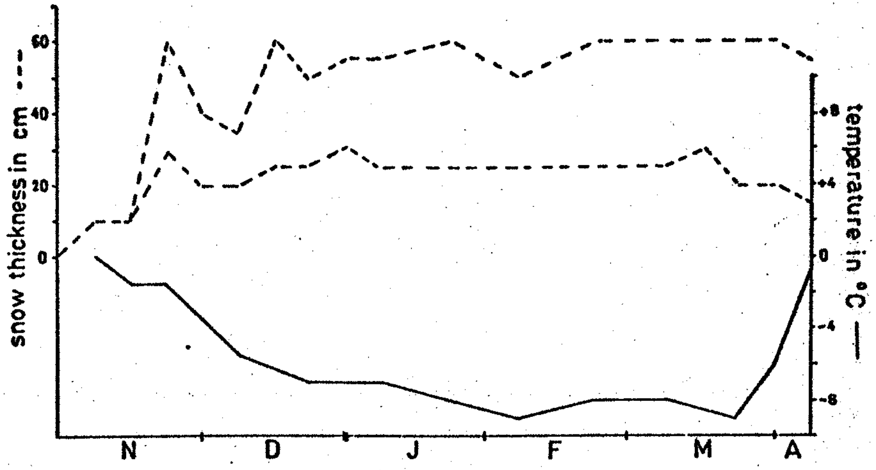

B
30
20
10
0
temperature difference in °C
J
F
M
A
MEADOW 1975

Figure 4-11

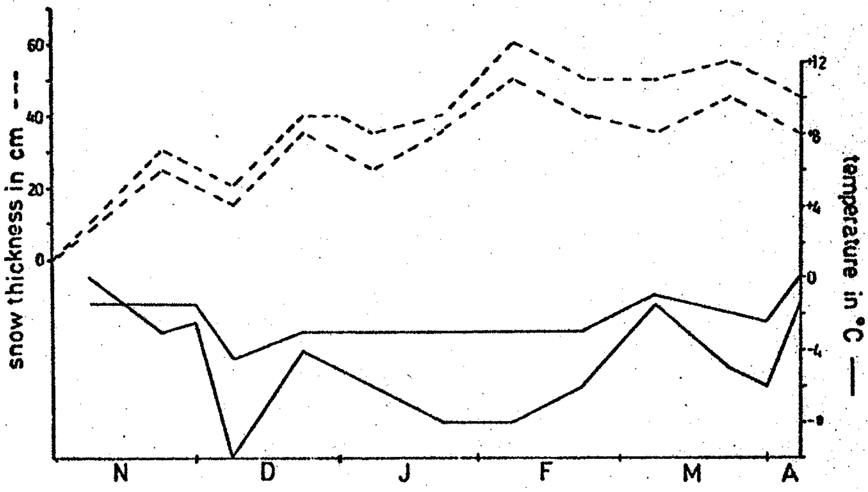
The variations in snow thickness and T(s) in 1973-1974 (A - ridge, B - woods, C - meadow). The two dotted lines indicate the maximal and minimal snow thicknesses, while the two solid lines indicate the maximal and minimal T(s)'s.

A



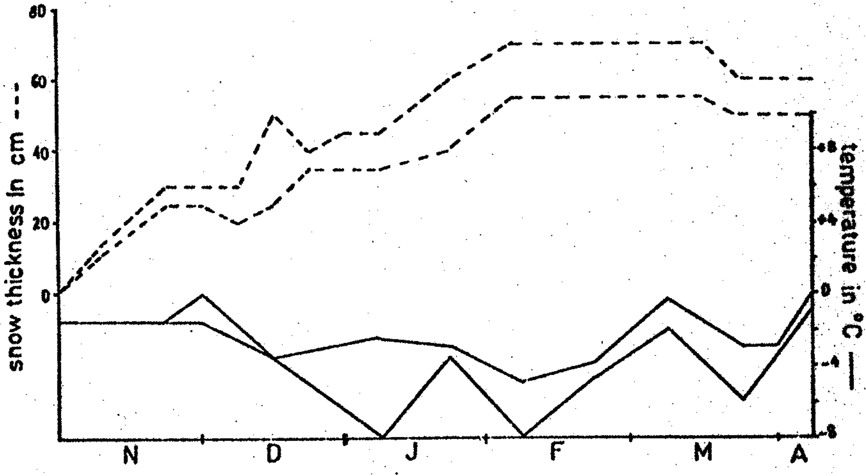
RIDGE 1973-1974

B



WOODS 1973-1974

C

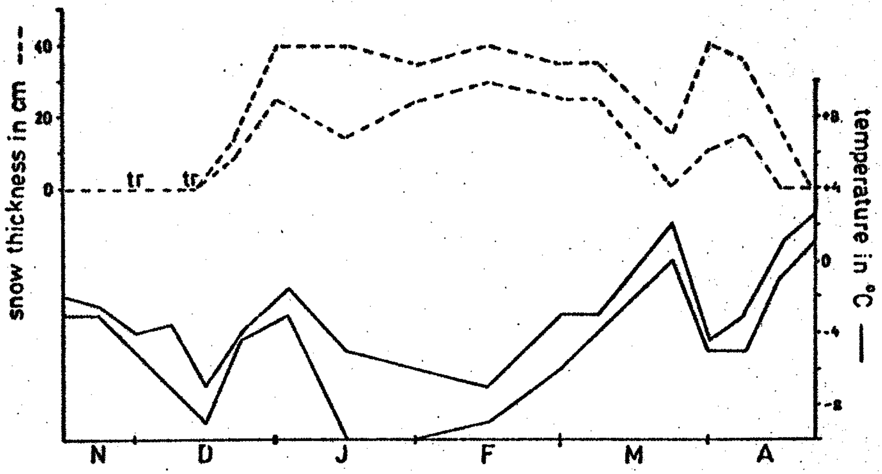


MEADOW 1973-1974

Figure 4-12

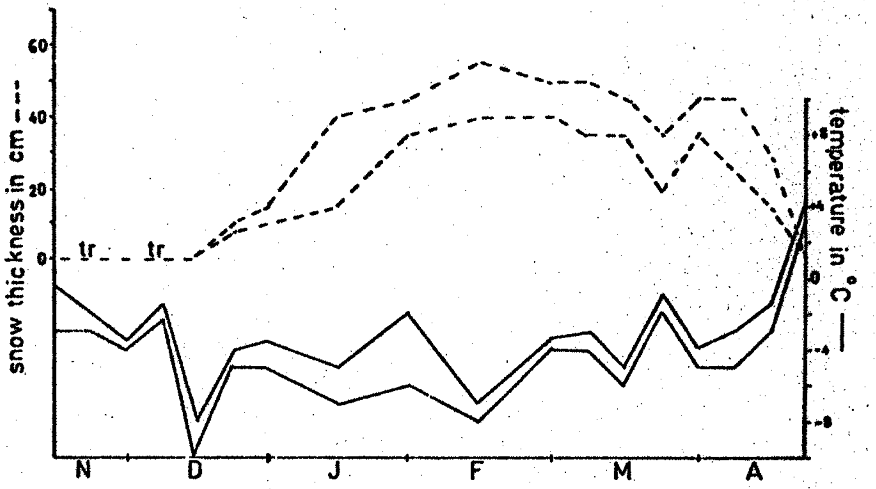
The variations in snow thickness and T(s) in 1974-1975 (A - ridge, B - woods, C - meadow). Lines as for Figure 4-11.

A



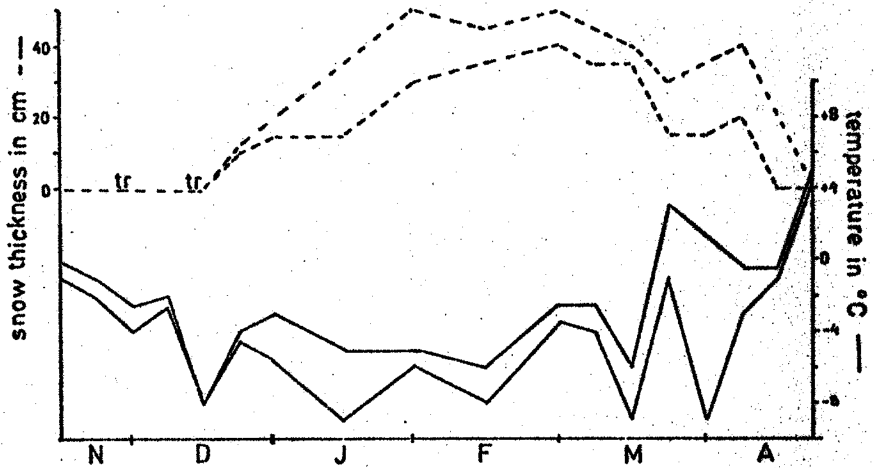
RIDGE 1974-1975

B



WOODS 1974-1975

C



MEADOW 1974-1975

Table 4-1

Meteorological measurements at Snow Stations Taken 9 March, 1974 at all Sites

	Ridge	Woods	Meadow
Air temperature	-5°C	-5°C	-2.5°C
Wind speed	5-20 m.p.h.	5 m.p.h.	10-15 m.p.h.
Snow thickness	20cm	56cm	59cm
Surface condition	wind slab, spotty new snow	6cm new snow	wind blown, 3cm new snow
Snow temperature	all depths: -6.5°C	3cm*: -0.5°C 20cm: -2.5°C 40cm: -3°C	3cm*: -0.25°C 25cm: -2°C 45cm: -2.5°C
Snow hardness in g/cm²	all depths: 600 trap site: 1000	20cm*: 15 40cm: 25 trap site: 400	5cm*: 27.5 45cm: 20 trap site: 550
Snow density in g/cm³	all depths: 0.300	20cm*: 0.265 40cm: 0.280	in old snow: 0.260

* These measurements refer to distances above the soil surface.

Table 4-2

Meteorological Measurements at Snow Stations Taken 20 March, 1975 at all Sites*

	Ridge	Woods	Meadow
Air temperature	+1°C	-5.6°C	-2.2°C
Wind speed	5-10 m.p.h.	--	5 m.p.h.
Snow thickness	15cm	35cm	30cm
Snow temperature	2cm**: +0.5°C 15cm: +1°C	2cm**: +1°C 11cm: 0°C 20cm: 0°C	2cm**: 0°C 13cm: -2°C
Snow density in g/cm^3	in old snow: 0.310	20cm**: 0.29 trap B5: 0.340	15cm**: 0.28 trap site: 0.300

* Surface condition and snow hardness deleted since they do not significantly expand the description of the thermal properties of snow.

** These measurements refer to distances above the soil surface.

Table 4-3

Radiation Balance at Earth's Surface in Relation to Latitude and Season in Langleys Per Day (after Budyko 1963)

°Lat.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.
30-40	175	163	108	81	115	125	193	259
40-50	178	96	33	1	8	40	113	206
50-60	123	55	-21	-28	-29	-17	54	145

Chapter V

CLASS OLIGOCHAETA

I. REVIEW OF LITERATURE

Temperature affects the biology of the oligochaetes, both lumbricids and enchytraeids, and in particular their activity, metabolism, development, respiration and reproduction (Dash and Cragg 1972, Edwards and Lofty 1972). The number of lumbricids on the soil surface is positively correlated with temperature; the optimal temperature for activity is 10.5°C (Satchell 1967, Edwards and Lofty 1972). The same correlation is true for the enchytraeids, though the optimal temperature is probably lower (Dash and Cragg 1972). *Lumbricus terrestris* L., which feeds on surface litter, remains active in autumn until the temperature reaches 5°C and resumes activity in late winter at 0.4°C (Arthur 1965, Reynolds 1973). In Germany, *L. terrestris* is active at grass-air temperatures down to 2°C (Satchell 1967), and ceases burying leaves in orchards at 2°C (Arthur 1965).

Grant (1955), who studied *Allobophora caliginosa* Savigny and *Pheretima hupeiensis* Michaelsen in New Hampshire, U.S.A., noted that earthworms had low thermal tolerances, avoided high and low temperatures, and congregated in optimal zones. In particular, *A. caliginosa* was active in the range of 10° to 23°C, avoiding lower and higher temperatures. In a study of *A. caliginosa* and *Pheretima californica* Kinberg in Egypt, *A. caliginosa* was active in the range of 2° to 37°C, with an optimal temperature range from 8° to 28°C (El-Duweini and Ghabour 1965). *P. hupeiensis* in New Hampshire congregated in the range of 15° to 23° (Grant 1955), whereas *P. californica* from Egyptian gardens exhibited a narrow temperature preferendum of 26° to 35°C (El-Duweini and Ghabour 1965). The American species died in several days after exposure to 3°C or less (Grant 1965). All authors concluded that the species were well adapted to their environments.

Lumbricid activity is seasonal, with maximal activity in spring and autumn in England and in the eastern United States (Satchell 1967, Edwards and Lofty 1972). Activity is correlated with soil temperature and soil moisture (Satchell 1967). Dispersal occurs slowly, and as ice and snow present barriers to lumbricids, they do not occur in recently glaciated areas (Reynolds 1973). In winter, earthworms near the surface are probably killed as soon as the soil surface freezes (Edwards and Lofty 1972). Vertical dispersal occurs seasonally, and lumbricids are usually found in the top 15cm of soil in winter (Edwards and Lofty 1972), while enchytraeids were collected from the top 3 to 6cm of soil in the Kananaskis Valley of Alberta in winter (Dash and Cragg 1972).

Adequate moisture is a requirement for activity (Satchell 1967, Reynolds 1973), and thus lumbricids inhabit generally moist soils (Edwards and Lofty 1972). A deficiency of moisture produces quiescence or the initiation of diapause in some species (Edwards and Lofty 1972).

Enchytraeids, small dark ice worms, occur in glaciers on the west coast of North America from Alaska to Washington and in Greenland, but no species of ice worms have been found in inland regions (Dash 1970, Tynen 1970). They may survive only in permanent snow, thereby being limited in their dispersal. Ice worms may spend the winter season below snow at temperatures around 0°C; snowless, cold areas probably have no ice worms (Tynen 1970). Dash and Cragg (1972) collected many immature forms during winter in the Kananaskis Valley, and found that the maximum populations occurred from April until June in aspen woodland.

Colourless enchytraeids, or pot worms, have a wider distribution than ice worms, and have been taken in Manitoba. Some unidentified enchytraeids were taken from northern Lake Winnipeg in summer (O.Saether, pers. comm.) and from greenhouse soils containing peat moss in Winnipeg (J. M. Mills, pers. comm.).

II. RESULTS

The number of oligochaetes collected at Fort Whyte are presented in Table 5-1. Most activity appears to take place in the cooler seasons of autumn and spring. Two species of lumbricids and one of enchytraeids were identified and are tabulated in Table 5-2.

No oligochaetes were taken when snow cover was permanent. The latest captures were made in late October 1973, and the earliest in mid-April 1974 (Table 5-1). On the 28 April, 1974, thirteen specimens of enchytraeids, possibly *Henlea nasuta* Eisen (Dash pers. comm.), were found in one trap on the ridge but not at any other time.

Lumbricids which appeared in May were trapped when the soil was water-logged. Summer specimens were taken on or soon after days on which rain had fallen. For example, two specimens were trapped two days after the rainfall on 20 May, 1975. Traps were set out for three consecutive days, once every two weeks in summer, and thus were open at that time. The correlation between rainfall and the capture of lumbricids was observed in summer.

Some autumn specimens of lumbricids were small and noticeably dehydrated, a condition that occurs prior to hibernation (Reynolds, pers. comm.). The species were *A. turgida* Eisen and *Lumbricus rubellus* Hoffmeister (Table 5-2). More specimens of these species were collected in spring and summer. *L. rubellus* has a holarctic distribution.

No comparison between activity and temperature was possible in late 1973 as temperature readings were not taken. During the second trapping period (1974-1975), activity occurred at temperatures relatively close to 0°C, i.e. 5° to 7.2°C. The active specimens in early spring (May, 1975) were taken at temperatures from 2° to 4°C.

These results support the theory that oligochaetes are restricted in their activity by temperature. The thermal threshold for activity is in the region of 5° to 7°C in autumn and about 2° to 4°C in the spring.

Trapping of summer specimens was related to the high relative humidity associated with rainfall, which is favourable to activity on the soil surface (Satchell 1967). Lumbricids that appeared in May were probably forced from the water-logged soil to the surface.

Numbers of individuals taken were insufficient to indicate any population trends. The unique appearance of enchytraeids in late April, 1974, suggests a population peak, especially since it occurred at a time when peaks are known to occur in Alberta (Dash and Cragg 1970).

III. DISCUSSION

Dash (1970) in the Kananaskis Valley of Alberta, Ryan (1973) on Devon Island (75°N) and Kauri _et al_. (1974?) in southern Norway found _H_. _nasuta_ in the soil, and this is possibly the species that was collected on the ridge. Perhaps this species normally lives in the ponds and not in terrestrial habitats. Many species of this family spend much of their time between freshwater and terrestrial habitats and thus could be classified as "amphibious" (Barnes 1963). In late April when enchytraeids were taken, the ponds overflowed on parts of the ridge transect after the snow melted. This record is then clearly an exception to the theory that enchytraeids do not exist in mid-continental regions (Dash 1970, Tynen 1970). Enchytraeidae have been collected in greenhouse soil in Winnipeg and others from northern Lake Winnipeg.

IV. CONCLUSION

Lumbricids are restricted in their activity by low temperatures, the threshold being about 5° to 7°C in autumn and about 2° to 4°C in spring. They are not active in winter. A few individuals of possibly H. nasuta were taken in late April, which may alter theories on distribution of enchytraeids.

Table 5-1

Numbers of Oligochaeta Active Seasonally at Fort Whyte, Manitoba; 1973 to 1975

Date	Autumn	Winter	Spring	Summer
1973-1974	4*	0	13**	0
1974-1975	17	0	11	7

* Trapping occurred only in the last three weeks of October

** One collection only.

Table 5-2

Species of Oligochaeta Taken at Fort Whyte, Manitoba

Lumbricidae:*

Allobophora (Aporrectodea) turgida Eisen
Lumbricus rubellus Hoffmeister

Enchytraeidae:**

possibly *Henlea nasuta* Eisen

* Determinations by: John W. Reynolds, c/o Faculty of Forestry, University of New Brunswick, Fredericton, New Brunswick.

** Determinations by: Madhab C. Dash, Reader and Head, Department of Biological Sciences, Sambalpur University, Burla, Sambalpur, Orissa, India.

Chapter VI

CLASS GASTROPODA

I. REVIEW OF LITERATURE

Several researchers have investigated the activity of slugs with respect to temperature. Rising and Armitage (1969) found that a change in temperature was a major stimulus for inducing activity in Limax maximus L. and Philomycus carolinianus Bosc., and that the rate of locomotion varied directly with temperature. Besides the effects upon behavioural response, the authors found that the metabolic rate of these species of gastropods was lower in the spring and higher in the autumn. When placed in a thermal gradient, the slugs located themselves in the "least stressful part" of the environment (Rising and Armitage 1969).

Dainton (1954) noted that the slug Agriolimax reticulatus Muller showed a rise in activity with generally decreasing temperatures of less than 24°C. In winter the slugs sought their preferenda in cracks in the soil, movong and feeding normally at 0.8°C but more slowly than at higher temperatures. These observations were confirmed by Mellanby (1961, in Newell 1967). Above 21°C, the slugs remained active, especially at night. At constant temperatures, their rhythm of activity persisted, and in a gradient the slugs exhibited a preference for the region at 17° to 18°C (Dainton 1954).

Some controversy recently centred on the role of temperature on activity of slugs and snails. It was previously thought that decreases in temperature initiated activity (Dainton 1954, Karlin 1961). Newell (1968) mentioned that *A. reticulatus* was sensitive to changes in light intensity, activity being initiated at high intensities. Lewis (1969) showed that decreases in light intensity initiated activity in *Arion ater* L., which was consistent with the known nocturnal activity of slugs. In contrast, Karlin (1961) reported that *P. carolinianus* was active at various light intensities, but the two other species which he examined became active only when they were kept in darkness. None the less, Karlin (1961) concluded that decreasing temperature initiated activity, as Dainton (1954) had previously stated. Lewis (1969) conclusively showed that the slug, *Arion ater*, is active only in the dark phase of the photoperiod.

Thus the statement that temperature change was the prime factor in inducing activity in gastropods was proven wrong. Experiments on which these statements were based served as further examples of studies in which the possible interaction of several variables was ignored. Lack of evidence for interaction clearly identifies change in light intensity as a stimulus for activity.

At low temperatures, the Austrian terrestrial snail, *Arianta arbustorum* L., probably tolerates extracellular ice formation in its tissues. This ability is facilitated by its inactivity in winter (Stöver 1973). The slug, A. reticulatus, and its eggs can tolerate prolonged exposure to cold, e.g. two adults survived -5°C for two hours (Newell 1967). The same species is usually active between 0° and 15°C, whereas constant conditions inhibit its activity (Newell 1968).

II. RESULTS

During the first winter, gastropods consisting of slugs and a few snails, were collected most often in the woods site; the ridge site had the fewest gastropods (Table 6-1). This may be related to the greater amount of ground cover in the woods and meadow (Table 3-4). The last captures for 1973, five Agriolimax and one snail, occurred on November 7 in the woods. Activity was not detected again until late April, when five specimens were taken in the woods and one in the meadow.

During the autumn and early winter of the second year of sampling, gastropods were collected most frequently in October (Table 6-1). The highest catch was on October 10. In the first week of November, some activity still occurred, though no snow was on the ground. No further activity was noted until the third week in March, when one Discus was taken in the woods. In early May, the number of captures increased considerably. On the first of May, two Agriolimax and one Discus were trapped in the woods, and three Agriolimax and one Catinella in the meadow. In the second week of May, *Agriolimax* and *Discus* formed the largest proportion of the captures in the woods.

A list of six species taken is given in Table 6-2. *A. laeve* and *V. costata* both have holarctic distributions (Lindroth 1957).

III. DISCUSSION

Activity by gastropods was greatest on the soil surface in spring and autumn, which concurs with the results of Dainton (1954) and Rising and Armitage (1969). The activity of slugs and snails varied directly with temperature. Apparently, gastropods were not active during winter, with the exception of *Discus cronkhitei* Newcomb. At the beginning of the first winter, six individuals were taken one week after the first snowfall (T(s) = -1.5°C), but no other slugs or snails were collected when snow was on the ground. As no soil surface temperatures were available until most activity had ceased, a detailed analysis of correlation could not be made.

The statements of Newell (1967, 1968) that the slug *A. reticulatus* was active at 0.8°C and 0°C were supported in this study. In the autumn, including the first week of November, 1973, and in late March, 1975, when T(s) was about -1.5°C, some activity occurred in the woods. Five of the seven individuals of *A. laeve* were active at these low temperatures.

IV. CONCLUSION

Generally, gastropods were not active in winter, though they were relatively active in spring and in autumn, when daily temperatures were low. Their activity decreased directly with falling temperatures and ceased near 0°C. Two species have holarctic distributions.

Table 6-1

Numbers of Gastropoda Active Seasonally at Fort Whyte, Manitoba; 1973 to 1975

Date	Autumn	Winter	Spring	Summer
1973-1974	123*	6	6	35
1974-1975	45	4	49	94

*Trapping occurred only in the last three weeks of October.

Table 6-2

Species of Gastropoda Taken at Fort Whyte, Manitoba

Order Stylommatophora:

Fam. Limacidae:*

Agriolimax (Deroceras) laeve Muller
Vitrina limpida Gould**

Fam. Endodontidae:**
Discus cronkhitei Newcomb

Fam. Vallonidae:**
Vallonia costata Muller
Oxyloma cf. *haydeni* Binney
Catinella n. sp. of *stretchiana* Bland

---

* Determinations by: Lyle F. Chichester, Department of Biological Sciences, Central Connecticut State College, 1615 Stanley Street, New Britain, Conn. 06050, U.S.A.

** Determinations by: Muriel F. T. Smith, Malacology, National Museum of Canada, Ottawa, Ontario K1A 0M8.

Chapter VII

ORDER CHILOPODA

I. REVIEW OF LITERATURE

The thermal preferenda of millipedes has received limited study. Cloudsley-Thompson (1951) noted three classes of temperature reactions in two species of millepedes: (1) an orthokinetic response, affecting the speed of locomotion; (2) responses to sudden drops in temperature which act as stimuli for activity; and (3) the behavioural response of high and low temperatures being avoided by klinokinesis; and a preference is shown for about 15°C in both species. They also become more active in cool weather (Cloudsley-Thompson 1968). Striganova (1972) determined that Sarmatiulus kessleri Lohmander in the eastern Ukraine fed between temperatures of 1° to 34°C, with feeding reaching a maximum at 21°C and declining throughout the sub- and supraoptimal temperature zones. "At subthreshold temperatures (2° and 33°C) both the rate of food consumption and the assimilation of food increased significantly"; hence both vary with temperature. The activity of juveniles and adults was similar but assimilation differed (Striganova 1972).

In New Mexico supercooling down to -7.5°C was noted in the centipede Scolopendra polymorpha Wood. Even after acclimation at 5°C, at least half of the exposed animals had died after 12 hours exposure to -7°C (Crawford and Riddle

1974).

II. RESULTS

The number of Chilopoda found active seasonally is presented in Table 7-1. The meadow was the habitat with the most individuals (37), and the ridge with the least (4) in the autumn of 1974 (Table 7-1).

During the first winter, seven animals were collected when snow was on the ground; the majority of them were active in early November, when T(s)'s were around -1.5°C. An exception was one specimen of Strigamia chionophila Wood taken on 21 March, 1974, in the meadow when the T(s) was -3.5°C. In the second winter only one individual was taken in mid-November, prior to snowfall, at a soil surface temperature of -1°C.

The peaks of activity of this group appear to occur in summer and autumn. The majority of autumn activity occurred in October, 1974, in the meadow. The T(a)'s during that month ranged between -3° and +13°C. On the last day of October, the T(a) dropped to -1°C, and only two individuals were caught. No activity was detected in spring. The two species taken are presented in Table 7-2. Lamyctes, a holarctic genus usually present in cold climates, was recorded in Manitoba for the first time (Crabill, pers. comm.). L. fulvicornis Meinert is a cosmopolitan, parthenogenetic species with an affinity for stream banks (Summers, pers. comm.). Strigamia chionophila is a holarctic genus occurring in temperate and cold North America (Crabill, pers. comm.).

III. DISCUSSION

Low and decreasing temperatures were reported to act as stimulants for activity (Cloudsley-Thompson 1952); autumn activity in this study, especially in 1974, certainly supports this conclusion. Activity decreased at low temperatures. Activity was recorded at 2°C for millipedes and even as low as -7°C for centipedes (Striganova 1972, Crawford and Riddle 1974). In Manitoba, activity of centipedes was detected at -1.5°C on many occasions and once as low as -3.5°C for *S. chionophila* (the specific name means "snow-loving").

IV. CONCLUSION

Generally, centipedes and millipedes are not winter-active. Their activity appears to be restricted at low temperatures, e.g. -1.5°C. Peaks of seasonal activity occur in summer and autumn.

Table 7-1

Numbers of Chilopoda Trapped Seasonally at Fort Whyte, Manitoba; 1973 to 1975

Year	Autumn	Winter	Spring	Summer
1973-1974	7*	7	0**	25
1974-1975	36	1	0	16

* Trapping occurred only in the last three weeks of October

** One collection only.

Table 7-2

Species of Chilopoda from Fort Whyte, Manitoba

Order Lithobiomorpha: Henicopidae

Iamyctes sp.*
Lamyctes fulvicornis Meinert**

Order Geophilomorpha: Diagnathodontidae

Strigamia chionophila Wood*

* Determinations by: R. E. Crabill, Jr., Department of Entomology, Smithsonian Institute, Washington, D.C., U.S.A.

** Determinations by: Gerald Summers, Illinois Natural History Survey, Natural Resources Building, Urbana, Illinois 61801, U.S.A.

Chapter VIII

ORDER PSEUDOSCORPIONIDA

I. REVIEW OF LITERATURE

Pseudoscorpions are small arachnid predators which dwell largely in deciduous litter, and are cosmopolitan except in the Arctic and Antarctic (Hoff 1949, Savory 1966, Muchmore 1973, Nelson 1973). Their food consists of Collembola, mites, phalangids, immature spiders, ants and flies. Some densities of prey populations are probably regulated by these predators (Hoff 1949, Savory 1966, Cloudsley-Thompson 1968, Weygoldt 1969, Muchmore 1973). Temperature and moisture of microhabitats may limit their distribution (Hoff 1959, in Muchmore 1973).

In autumn these animals construct silken hibernation chambers in which several individuals spend the winter (Savory 1966, Weygoldt 1969, Nelson 1973). Nelson (1973), who sampled for pseudoscorpions throughout the year in Michigan, noted spring and summer peaks in numbers, as did Gasdorf and Goodnight (1963) in Indiana. There was little activity over the winter. All life stages overwintered (Nelson 1973).

II. RESULTS AND DISCUSSION

The number of individuals collected is presented in Table

8-1. In the two-year trapping period all specimens except one were trapped in the meadow. In the first winter, one specimen was found in late October, while two others were taken in November at a T(s) of -1.5°C. In March one specimen was taken on the ridge at a T(s) of -6°C. In the second winter specimens were trapped in November and December at temperatures ranging between -1° and -4°C. The two species are listed in Table 8-2.

Activity of pseudoscorpions reaches a peak in autumn, notably in November (which corresponds to a peak of the deuteronymph population in Michigan) (Nelson 1973). Weygoldt (1969) reported that in parts of Europe *Neobisium muscorum* Leach was active throughout the cold season, while some other species were active at temperatures above 0°C. Horegott (in Weygoldt 1969) found the peak of adult activity of this species in December, January and March. This observation was corroborated in the present study, with the modification that peak activity occurred in November and December (despite snow cover), at T(s) ranging from -1° to -4°C.

Microbisium confusum Hoff is widespread in North America in deciduous forest litter, while *M. brunneum* Hagen is cosmopolitan but with a discontinuous distribution as it is associated with *Sphagnum* bogs. Both species are parthenogenetic (Hoff 1949, Muchmore pers. comm.). In southern Manitoba, *M. confusum* was collected in the meadow (December, 1973), while *M. brunneum* was captured on the ridge

(October, 1973).

III. CONCLUSION

In southern Manitoba, pseudoscorpions appear to be rare, reaching peak numbers in November and December in damp meadows at temperatures between -1° to -4°C.

Table 8-1

Numbers of Pseudoscorpionida Taken Seasonally at Fort Whyte, Manitoba; 1973 to 1975

Year	Autumn	Winter	Spring	Summer
1973-1974	1*	3	0**	0
1974-1975	0	3	0	0

* Trapping occurred only in the last three weeks of October.

** One collection only.

Table 8-2

Species of Pseudoscorpionida* from Fort Whyte, Manitoba

Microbisium brunneum Hagen

Microbisium confusum Hoff

* Determinations by: William B. Muchmore, Department of Biology, University of Rochester, New York 14627, U.S.A.

Chapter IX

ORDER ARANEAE

I. REVIEW OF LITERATURE

A variety of topics will be covered in this section. The effects of temperature upon metabolism, life cycles, thermal preferenda, and cold-hardiness will first be discussed. Then activity, migration, species diversity and density, and reproductive periods will be considered. Following these general topics, the major cursorial families will be discussed in detail.

A. Effects of Temperature

Effects of temperature on metabolic rates of spiders depend on rapid temperature changes in the range of 10° to 30°C. At 10°C oxygen consumption did not increase adaptation "since low temperature would also inhibit activity of the prey of spiders" (Anderson 1970). Anderson (1974) noted a significantly lower metabolic rate for *Lycosa lenta* Hentz than for other poikilotherms of similar size, being further lowered by 30 to 40% during starvation. Miyashita (1969) noted concurrent drops of carbon dioxide output and temperature, and found a three to six times greater respiratory energy loss during activity than during rest, with a further decrease when fasting.

The length of a spider's life cycle seems dependent upon the primary productivity and temperature of the area. In those areas with long, cold winters the rate of development is slow and may take up to two years (Vlijm *et al*. 1963). For most spiders the life cycle lasts one to two years, though six to seven years may be required at 82°N. In Canada, the average life span is probably two years (Schmoller 1969). The longer life span is accompanied in northern, autumn-mature species by a longer period of sexual maturity, explainable by cold temperature (Huhta 1965).

Thermal preferenda are low in winter-active species. Experiments by Buche (1966) on *Macrargus rufus rufus* Wider and *M. r. carpenteri* Cambridge "showed a mean preference for 7°C, which could not be altered by acclimation" (Huhta 1971). Examining winter-active species from Poland, *Lycosa agrestris* Westring preferred the range of 5° to 9°C, temperatures at which this species appeared on snow. Also *Linyphia phygiana* C. L. Koch and *Lepthyphantes minutus* Blackwall had thermal preferenda of -3° to +3°C and -1° to +3°C respectively, close to temperatures in their natural habitats (Wolska 1957). In Norway, *Bolyphantes index* Thorell made webs in snow crevices to catch collembolans at 0° to 2°C, and showed a preference for 4.1°C. In unfavourable conditions this spider probably retreated to the subnivean space (Hågvar 1973). In the hibernation period *Araneus cornutus* Clerck, which overwinters on vegetation, survived -18°C for two and a half days and had a supercooling point in winter of -23°C. In winter this species has 2 to 3% glycerol, determined on the basis of fresh body weight, but the amount of glycerol was not correlated with the supercooling point. Some epigeic spiders are active during winter and even multiply while others cannot tolerate temperatures less than 0°C (Kirchner and Kestler 1969).

B. Activity

Generally, activity peaks are associated with the need for food and sexual behaviour (Tretzel 1954); temperature strongly affects spider activity (Granström 1973). Activity during winter has been recorded in five species of Greenland spiders between -3° to 8°C (Bertram 1935). Using multiple regression analysis, Koponen *et al.* (1975) ascertained that spider activity was affected by solar radiation and maximum temperature. In linyphiids minimum temperature was significant, humidity greatly affected thomisids, and radiation was important for hahniids. For *Pisaura mirabilis* Clerck, the cold temperatures of winter in France appeared to induce diapause, with a suppression of metabolic rate and of development (Dondale and Legendre 1971). Inactivity during winter by *Pholcus phalangoides* Fuesslin occurred in adults more than in juveniles; adults were often found in the "winter state" (a cataleptic posture on their side with legs folded under the body), while juveniles continued feeding. Many adults died in winter (McHugh 1966). In autumn near Edmonton , the activity of spiders increased with the rise of relative humidity and decrease of temperature; as freezing set in permanently the activity decreased. Those species in litter seemed little affected by snow (Mair 1969). Wandering spiders are not fully active on the soil surface until they become adult, and their activity alternates with that of carabids and opiliones. There are many inactive spiders in litter during winter, with immatures and adults often in different niches (Breymeyer 1966).

Summer populations of spiders exhibit stratification of species in three dimensions; namely (1) in the canopy layer (species of _Clubiona_ and _Xysticus_), (2) in the shrub layer (species of _Clubiona_ and _Lepthyphantes_), and (3) in the ground layer (species of _Lycosa_), (Turnbull 1960, Huhta 1965). In spring the spider populations in the canopy consist of overwintered eggs and active forms of species that overwinter on the ground, which have moved up into the canopy in May. The ground zone population remains constant until early autumn, when a rise in numbers occurs due to vertical descent to ground overwintering sites (Łuczak 1959, Turnbull 1960, Duffey 1969).

C. _Species Diversity_

Seasonal peaks in species diversity in midsummer were greatest in habitats with more vertical strata. These peaks were correlated with abundance of prey (secondary productivity) and not with seasonal temperature, relative humidity or precipitation (Uetz 1975). Gasdorf and Goodnight (1963) also found no correlation between populations of spiders and soil moisture or temperature, and noted decreases in numbers in spring and winter. Low numbers occurred from November to February in Poland (Breymeyer 1966). The number of spiders found in winter is determined by weather conditions of late autumn and early winter (Huhta 1971).

D. Reproductive Periods

Tretzel (1954) produced a classification table based on the reproductive periods of spiders: (1) eurychronous species are sexually mature throughout the year, the warm half of the year, or the cold half of the year; (2) diplochronous species have two copulation periods per year, either both in the warm season, or one in summer and one in winter; (3) female eurychronous and male stenochronous; (4) stenochronous species have a single reproductive period in summer; and (5) those species with a reproductive period in winter. Most species are stenochronous (Tretzel 1954).

E. Cursorial Families of Spiders

The family Clubionidae, which consists of nocturnal hunters dependent upon touch and speed (Cloudsley-Thompson 1953), usually occurs in leaf litter, scrub and fields, and overwinter as adults and subadults (Holmquist 1926, Kaston 1948, Williams 1962, Duffey 1969). In Sweden *Agroeca proxima* Cambr. and *Clubiona trivialis* C. L. Koch overwinter as subadults and have life cycles of 1.5 and 2 years respectively (Almquist 1969). *A. proxima* and *Clubiona* *similis* C. L. Koch are both tolerant of cold temperatures (down to -20.9°C), but overwintering subadults are more F-R than adults (Almquist 1970).

The family Erigonidae (Microphantidae) is often considered to be a subfamily of Linyphiidae. Both families of small-sized individuals comprise 42% of terrestrial spider species (Tretzel 1954), occurring predominantly in shady, moist forests with much moss or litter (Kaston 1948, Huhta 1965, Wallwork 1970). Different litter layers contain different species. When under permanent snow cover, cold adaptation allows erigonids to tolerate "a continuous temperature of -1° to -3°C for long periods...., although a short sudden frost may destroy a large part of the population earlier in autumn" (Huhta 1965).

The family Linyphiidae is a dominant group in leaf litter in deciduous forests (Kaston 1948, Łuczak 1959, Williams 1962, Wallwork 1970), while in the Arctic and Subarctic it is the major group, comprising 73% of all spiders (Wallwork 1970). Many species of this family are winter-active, e.g *Centromerus sylvaticus* Blackwall, *Bolyphantes index* Thorell, *Linyphia phygiana* C. L. Koch, and *Macrargus rufus carpenteri* Cambr. (Holmquist 1926, Tretzel 1954, Wolska 1957, Williams 1962, Buche 1966, Kronestedt 1968, Mair 1969, Huhta 1971, Granström 1973, Hågvar 1973).

The family Lycosidae (wolf spiders) inhabits leaf litter of forests, scrub, clearings, grassy fields, and ecotones at the edge of woods (Kaston 1948), and may provide up to 78%

of the epigeic spiders in Poland (Kajak et al. 1971). They usually capture prey by means of their speed and strength; small species often wander in dry places (Cloudsley-Thompson 1953). Generally subadults overwinter in leaf litter (Holmquist 1926, Muma and Muma 1949, Williams 1962, Vlijm et al. 1963, Almquist 1969, Mair 1969, Miyashita 1969, Edgar 1971, Edgar and Loewen 1974). Species of Pardosa are numerous and exhibit many differences in phenology between species and between localities (Vlijm et al. 1963). Many lycosids are dependent upon sunshine (solar radiation) for activity (Williams 1962). Lycosa t-insignita Boes. et Str. of Japan had spring and autumn population peaks, overwintering as subadults. After November or December, decreased feeding inhibited a final moult until spring, increasing its longevity. During warm periods in winter this species was active on the soil surface(Miyashita 1969).

The family Thomisidae (crab spiders) occurs in grass, bushes and under stones in deciduous forests (Kaston 1948); most species are sedentary and wait on the ground for prey (Cloudsley-Thompson 1953). It is a dominant family in the ground fauna (Łuczak 1959). Subadults and females overwinter (Holmquist 1926, Kaston 1948, Almquist 1969, Schmoller 1969). Life cycles of some Canadian species may be twice as long as elsewhere (Dondale 1961). In Poland Kajak (1960) noted two age classes of Xysticus ulmi Hahn., X. cristatus Clerck, and Tibellus maritimus Menge throughout the whole season.

Other cursorial families include Agelenidae, Dictynidae, Gnaphosidae, Salticidae, and Tetragnathidae, and are found in variety of habitats. Frequently many of these families occur in leaf litter (Kaston 1948), overwintering as adults and/or subadults (Kaston 1948, Almquist 1969, Schmoller 1969). Tetragnathids and gnaphosids are commonly taken in scrub of southern England (Williams 1962).

II. RESULTS

The numbers of Araneae active seasonally are presented in Tables 9-1A and 9-1B. The season with the least soil surface activity was spring. Essentially linyphiids predominated in autumn and early winter; and lycosids in spring and summer. The higher numbers in the second winter appeared to be unusual. At Fort Whyte, Manitoba, 49 species of spiders were taken, ten of these species being taken only in the summer. In winter 19 species were found active under snow, and the dominant, cursorial families included clubionids, erigonids, linyphiids, lycosids, and thomisids (Table 9-2).

A. 1973-1974

Maxima in numbers and species diversity occurred in early winter of 1973. Numerous immatures were active then. At all sites *Agroeca pratensis* Emerton generally represented the clubionids; *Ceraticelus laetus* O.P.-Cambridge, the erigonids; *C. sylvaticus* Blackwall, the linyphiids; *Pardosa* moesta Banks, the lycosids; and Oxyptila conspurcata Thorell, the thomisids (Figure 9-1).

On the ridge in the early winter of 1973-1974, only adult clubionids were active, first males, then females being present in traps (Figure 9-2A). Activity ceased in midwinter and was resumed by adults in late winter. Erigonids were active during the early winter as a mixture of juveniles and females. In mid- and late winter a mixture of age classes was active. Linyphiids were active in early winter as adults, first males, then females. They were encountered at no other time. In early winter the lycosids were represented by a mixture of age classes, almost exclusively immatures. Juveniles were active in midwinter. Thomisids occurred more rarely, represented by a mixture of immatures and one female taken in early winter.

In the woods the clubionids followed the same pattern as on the ridge (Figure 9-2B), but fewer erigonids were taken than on the ridge, though they also followed the established pattern. The linyphiids were abundant in the woods, and again only adults were active in early winter. Similarly, fewer lycosids were taken in the woods than on the ridge. Thomisids were not taken.

The meadow habitat produced the highest numbers of spiders (Figure 9-2C). Adult clubionids, especially males, were active in the early winter of the first year, and one immature was taken in midwinter. More immature erigonids were active than adults. In midwinter a mixture of 16 juveniles and adults were taken, the largest winter catch. In late winter, an immature was occasionally trapped. As many as 42 adult linyphiids were taken in early winter, the only season in which they occurred. Immature and adult lycosids occurred in early winter, and a juvenile was trapped at times in late winter. Only a few thomisids were taken in early winter.

B. 1974-1975

In 1974-1975 the number of active spiders increased greatly. Linyphiids were the dominant group, active in autumn, followed closely by lycosids and clubionids (Table 9-1B). During the winter (including six weeks of unusually warm weather in November and early December), the clubionids were dominant, lycosids and erigonids being the next most active groups. Most of the catch (540 specimens) was taken in November and December, though some specimens were trapped in January. Even in spring larger numbers of spiders were caught (131 versus 6 individuals in 1974), and also in summer.

Besides the increase in numbers, species diversity also increased in 1974-1975. The dominant species in each family were as follows:

Family	Species
Clubionidae	*Agroeca ornata* Banks *Phrurotimpus borealis* Emerton
Erigonidae	*Ceraticelus laetus*
Linyphiidae	*Centromerus sylvaticus* *Neriene clathrata* Sundevall
Lycosidae	*Pardosa distincta* Blackwall
Thomisidae	*Oxyptila conspurcata* *Xysticus emertoni* Keyserling

(See also Figure 9-1).

On the ridge in the early winter, 71 immature clubionids plus some adults were taken (Figure 9-3A). In midwinter a few juveniles were trapped, but in late winter none were caught. In spring, juveniles and a few males were again active. Only the occasional adult erigonid was collected in October, but in late November and early December there was an upsurge in activity (19 males and 19 females). Adult activity continued to be detected in January and that of subadults in February. In late winter *C. laetus* was inactive, whereas in spring adults and a few subadults were again active. *C. sylvaticus* ceased activity by the end of November. In mid-December one juvenile of *Meioneta* sp. was collected. Adults of this family resumed activity in spring. Lycosids were represented by a mixture of age classes in early winter; in fact three of six females of *P. distincta* were found dragging egg cocoons in mid- and late October. In mid-December, many juveniles of the genera *Pardosa*, *Lycosa*, *Tarentula* and *Trochosa* were caught. In

January, a few subadult *Pardosa* were active, and in late winter a few more were collected. In early May, an adult male *Trochosa terricola* Thorell was caught, plus juveniles of *P. distincta* and *Lycosa*. Of the thomisids, the occasional immature *Xysticus* was active in early winter, in early January, and in mid-April. In spring juvenile and male *X. emertoni* and *O. conspurcata* resumed activity again. Activity in the other families was more pronounced in early winter; juveniles and adults of the agelenid genus *Cicurina* and the hahniid genus *Neoantistea*, and of the gnaphosid genus *Zelotes* were active. In late November and early December activity by females of *Argenna* (dictynid) and *Neoantistea* was detected. In mid-December a few juveniles and adults of the families Gnaphosidae, Hahniidae, Tetragnathidae and Theridiidae were also active. In midwinter activity ceased, and in late winter one juvenile agelenid was taken. In spring males and a few juveniles were collected.

In the woods the clubionids exhibited the same pattern as on the ridge; namely, a large increase in numbers was found in mid-December (Figure 9-3B). Again no activity occurred in midwinter, and one juvenile *Agroeca* was taken in late March. In spring adults and a few subadults were active. The erigonid activity pattern was similar to that on the ridge. The linyphiid, *C. sylvaticus*, followed the established pattern. One exception was a female *Porrhomma terrestris* Emerton taken in mid-December. Numerous juvenile lycosids of the genera *Pardosa* and *Tarentula* were active in early winter; no activity occurred in midwinter and a male *T.* *terricola* was collected in late April. In spring juveniles and adults resumed activity. Only one thomisid was collected in early winter. Both subadults and adults of the other families were active until mid-December. In midwinter a male *Hahnia* *cinerea* Emerton was taken, and in spring activity resumed.

The meadow was the most productive habitat for spiders (Figure 9-3C). Juvenile clubionids of the genera *Agroeca* and *Phrurotimpus* were numerous, particularly in early winter. Some continued activity into January and February, as demonstrated by the capture of a few female *A.* *ornata*. In spring adults and a few immatures were active. Adults of *C.* *laetus* were active from October to February, the greatest activity being recorded in early December. Spiders resumed activity in mid-April and through the spring. Among the linyphiids, adults of *C.* *sylvaticus* were mobile until late November, and then male and juvenile *N.* *clathrata* and a female *Macrargus* *multesimus* O.P.-Cambridge were collected in December. In early January and late April a few more individuals of *N.* *clathrata* were taken. The family resumed extensive activity again in late spring. A mixture of lycosids occurred in early winter, with a higher proportion of immatures than in the same period of the previous year (87.2% versus 71.4%). A few subadults were collected in mid- and late winter. In spring, activity of adults and immatures increased gradually. Mixtures of age classes occurred in other families in early winter; in early spring activity of all age classes resumed.

C. Habitats of Species

The species of spiders taken in each hatitat are presented in Table 9-3. Twenty-six species occurred on the ridge, 25 in the woods, and 23 in the meadow. *Alopecosa aculeata*, *Pardosa moesta*, *Ceraticelus laetus*, *Neoantistea agilis* and *Zelotes subterraneus* were present in all habitats, with *C. laetus* preferring the litter of the woods and meadow. Agelenids and lycosids were most often taken on the ridge, while thomisids and dictynids preferred the open habitats of the ridge and meadow. *C. sylvaticus*, *P. borealis* and mimetids were collected in the woods, and *N. clathrata* was especially prevalent in the meadow.

D. Winter-Active and Summer Species

Nineteen species of spiders were active under snow, and hence are called "winter-active". Subadults usually cannot be identified beyond genus. The winter-active species are presented in Table 9-4.

Summer trapping for a three-day period every two weeks indicated a greater species diversity than in autumn and winter. Ten species which were collected only in summer are presented in Table 9-5.

E. Correlations

For each winter period, the number of spiders active was pooled from all habitats and correlated with T(s) (Figure 9-4). In 1973-1974 a positive correlation significant at the 5% level occurred (r = 0.47), so it was concluded that their activity was directly proportional to T(s) (Figure 9-4A). For each habitat, only the correlation with spiders on the ridge was significant; the others for the woods and meadow were not significant. In the first winter T(s) dropped noticeably to a minimum of -9.5°C on the ridge by mid-December, which coincided with the cessation of activity in most families. Also in mid-March, the minimum T(s) began to increase, associated with a rise in spider activity under the snow. In 1974-1975 the number of active spiders was negatively correlated with temperature (r = -0.40), and r was significant at the 5% level (Figure 9-4B). It seems plausible that the unusually warm temperatures occurring up to late November were partly responsible, as was the late establishment of the hiemal threshold (late January). Even when the spiders taken prior to snow fall were deleted, a negative correlation (not significant) occurred (r = -0.14).

A significant negative correlation (at 1% level) occurred between the number of spiders active under snow in 1975 and the temperature difference between T(a) and T(p) (Figure 9-5; see also Figures 4-8 to 4-10B). The greater the difference in temperature, the fewer spiders that were active. Often when the temperature difference exceeded 20°C, there was no activity. In the first few weeks of permanent snow cover, the temperature difference was small, and the spiders were active. The period prior to snow melt was the reverse: the temperature difference was usually small, but spiders showed little activity.

In addition to correlations between numbers of specimens and temperature, correlations between different taxonomic groups were calculated. For spiders and mites, correlations between the two were not significant for both years on the ridge and in the woods, while they were significant at the 5% level in the meadow (in 1974-1975, $r = -0.44$). Hence some conditions in the meadow produce similar activity patterns in both groups. For collembolans and spiders, correlations were not significant in the woods and significant at the 5% level on the ridge and in the meadow in 1973-1974, and were reversed in 1974-1975. So it appears plausible that collemboles constitute a portion of the diet of spiders under snow. For coleopterans and spiders, large positive correlations were calculated (significant at the 0.5% level) in 1973-1974 at all habitats, while in 1974-1975 a significant correlation (at the 1% level) occurred only in the woods ($r = 0.79$). Therefore it is concluded that similar activity occurred between these two groups, with a possibility of predation by spiders upon beetles.

F. Experiments on Activity and Feeding at Low Temperatures

Live trapping took place in November, 1974. Two traps in the woods and two in the meadow were left with no ethylene glycol, but instead, three leaves were added to provide more niches. Live animals were then collected by an aspirator, placed in separate vials, and held in a cold room at 3° to 4°C. Cold room experiments were made on individuals held for 1, 8 or 15 days at 3° to 4°C in shell vials plugged with moist cotton. While juveniles of Agroeca spp. and Pardosa spp. were not abundant in the winter of 1973-1974, they were numerous in November of 1974. Also juveniles of Phrurotimpus spp. were tested. Table 9-6 shows the results of these experiments. After an exposure of one minute at -9.5°C (the coldest T(s) recorded), 47.83% of the individuals of all spider species lost their motor control in an average of 45 seconds. When exposed to -12°C for one minute, three of the nine individuals tested died, three lost motor control in an average of 27 seconds, and three remained active throughout the test, after being held one to two weeks at 3° to 4°C. The last three specimens appeared to have acclimated to that temperature. One individual tested on 21 November lost motor control at -9.5°C, but on 28 November this only occurred at -12°C, another indication of acclimation. Other families also seem cold-hardy, especially erigonids, thomisids and some linyphiids. The pattern of more depressed activity with progressively colder temperatures clearly demonstrates orthokinesis (Table 9-5).

Seven juvenile clubionids and lycosids that survived the cold room experiments were maintained in vials with moist cotton plugs. Each week the spiders were offered three adult Drosophila. At 3° to 4°C, no apparent feeding or frass production took place, despite mobility by the spiders. Some mortality occurred in midwinter due to desiccation of the cotton plugs, but three individuals survived until April. In mid-April as the soil surface temperatures rose, spiders were transferred to 9°C and began to feed upon one or two of the three flies and to produce frass. In late April after transfer to 15°C, the spiders ate all the *Drosophila* and produced characteristic red frass. Thus feeding may be dependent upon temperature, and at temperatures of 3° to 4°C, the basal metabolic rate is depressed such that only water and no food is necessary for activity.

Table 9-7 presents a list of known nearctic and holarctic species of spiders occurring in southern Manitoba. Six nearctic and six holarctic species are listed.

III. DISCUSSION

The erigonids, *C.* *laetus* and *C.* *laetabilis* O.P.-Cambridge, are present as adults all year (Kaston 1948), which concurs with the results in southern Manitoba. Soil surface temperatures greater than 0°C produce an increase in numbers after the spring thaw; at times a few hours per day is adequate for activity (Huhta 1965). In southern Manitoba, *C.* *laetus*, one of the most common species, was active at T(s) of about -8°C.

Linyphiids are known to be cold-hardy and winter-active. During the early winter mating period (October to December), winter-active *C.* *sylvaticus* exhibited maximal activity and was taken in pitfall traps in the woods of northern Europe, Sweden, Finland, Alberta and Connecticut (Kaston 1948, Williams 1962, Buche 1966, Kronestedt 1968, Almquist 1969, Mair 1969, Huhta 1971, Granström 1973, Hågvar 1973). Adults of this species in southern Manitoba were active in October and November, particularly in the woods and meadow, the habitats with the most litter, but were not active later in the winter. Presumably, temperature is a limiting factor in their winter activity. Almquist (1969) would classify the presence of only one age group in the overwintering period as exceptional, so it appears that the occurrence of adult C. sylvaticus in Manitoba is exceptional.

Winter activity of lycosids may be seen on warm days (Williams 1962), and Muma and Muma (1949) trapped immatures of Lycosa spp. in pitfall traps during the hiemal (winter) period in Nebraska, while Breymeyer (1966) in Poland designated Trochosa as winter-active. In southern Manitoba, this family represented one of the common winter-active groups, especially P. distincta in the second winter. In Holland, Vlijm et al. (1963) noted some small egg cocoons attached to active females of P. amenata Cl., and Kaston (1948) sometimes noted P. distincta with an egg sac in October. Hence the presence of three female P. distincta with egg cocoons in October of the second year was not extraordinary.

Winter activity of thomisids was noted by Muma and Muma (1949), especially by Xysticus fraternus Banks on the soil surface of a beech-maple forest in Nebraska. In Poland, Kajak (1960) saw two age classes of X. ulmi Hahn. and X.

cristatus throughout the whole season. In southern Manitoba, the winter activity of this family was less frequent than that of most other families taken. Kaston (1948) noted adults and subadults of *T. formicinus* overwintering, and overwintering by juveniles and females has been noted (Holmquist 1926, Kaston 1948, Almquist 1969, Schmoller 1969). This seems to be the rule in southern Manitoba. It may be humidity, not temperature, that limits the activity of thomisids, as Koponen *et al*. (1975) have suggested. Under the snow the relative humidity approaches 100%.

Cold-hardiness in spiders was recorded for the families Araneidae (Kirchner and Kestler 1969), Clubionidae (Almquist 1969), Linyphiidae (Wolska 1957, Buche 1966, Hågvar 1973), and Lycosidae (Wolska 1957). Almquist (1969) noted cold tolerance in the clubionids *Agroeca proxima* and *Clubiona similis*; in the present study, adults and juveniles of *A. ornata* and *A. pratensis* were also found cold-hardy. Although some authors found lycosids active in winter (Holmquist 1926, Williams 1962, Miyashita 1969, Granström 1973), only Wolska (1957) in Poland determined the thermal preferendum of *Lycosa agrestris* to be 3° to 13°C. Juveniles of *P. distincta* taken alive in November in southern Manitoba proved to be cold-hardy. In addition to these families, the erigonids, dictynids, agelenids and thomisids must also be cold-hardy, presumably as a result of supercooling of their body tissues.

Similar to the C-R clubionids in Sweden (Almquist 1969), males of *Agroeca* in woods around Edmonton showed a sudden burst of activity in early winter, and females showed little activity (Mair 1969). Certainly *Agroeca* spp. were active in early winter in southern Manitoba. Kaston (1948) took females of *Castianeria cingulata* C. L. Koch in the winter in Connecticut, while at Fort Whyte this species only occurred in midsummer (Table 9-4).

There are many disadvantages to using pitfall traps: namely, (1) inactive species are not taken; (2) no aerial species are taken; (3) some individuals crawl out or are eaten; (4) qualitative, not quantitative, data are obtained; (5) the catch does not reflect accurately the relative abundance of different species; and (6) in spring flooding of traps may occur (Huhta 1965, 1971; Mair 1969, Mason 1972, Uetz 1975). As a means of determining species diversity, it is one of the best methods for sampling wandering spiders, the number of each species trapped representing the product of their activity and their density (Näsmark 1964, Uetz 1975). Hence, this trapping method indicates the copulatory period in which numbers per unit area are maximal, and males outnumber females (Muma and Muma 1949, Huhta 1965). Koponen (1971) also found large numbers of different carnivorous groups in pitfall traps, indicative of their importance in the ecosystem. Almquist (1969) claimed that pitfall traps do not take linyphiids and salticids; the common occurrence of *C. sylvaticus* in pitfall traps disagrees with this conclusion (Kronestedt 1968). Also at Fort Whyte many *C.*

sylvaticus were taken in early winter. In the snowfree period, especially when a spider's basal metabolic rate was higher, I observed spiders climbing out of a trap on the silk drag line attached to their spinnerets. Mason (1972) also observed small coleopterans often avoiding pitfall traps. Traps containing spiders often had exuvia of other invertebrates that presumably had been eaten. Mason (1972) captured shrews and frogs in addition to invertebrates in his pitfall traps; at Fort Whyte in the snow-free periods young Rana sylvatica and a few Sorex cinereus were also collected.

Uetz (1975) found that temperature was not an exclusive factor that limited activity of spiders in summer; this may also be true in winter, especially prior to the time of snow melt when T(s) are relatively high, but there is little activity. Huhta (1965) mentioned that climatic conditions in late summer and autumn affect the numbers of spiders present in autumn. It appears that in 1974 conditions were favourable for production of spiders, since their numbers remained relatively high even until the following spring.

The number of animals trapped is a product of activity (horizontal movement) and density, and those animals trapped either have a high density or are particularly active in the subnivean space (Näsmark 1964). Activity of spiders on the ridge in March, 1974, was very low (0.5) compared to November, when the measurement of activity was eleven times greater (5.5). In the woods, activity was slightly above

1.0, and in November and in March was 0.13. In the meadow, activity in November was 4.3 and in March 0.10. A decrease in activity occurred progressively during winter, irrespective of the densities determined.

Those species which were described in the literature as holarctic are listed in Table 9-7. This list is not complete, compared to data from Finland (Pruitt, pers. comm.). Seven of 49 species have known holarctic distributions, and three species mentioned frequently in European literature are C. sylvaticus, T. terricola and Z. subterraneus. In addition, six species that were classified as nearctic are listed.

Winter-activity of species in Europe has been mentioned, in particular, the linyphiid C. sylvaticus (Buche 1966, Kronestedt 1968), a species that also occurred in Manitoba. A total of nineteen winter-active species in Manitoba are members of genera that have not been recorded, or have not shown winter activity in Europe.

IV. SUMMARY

Activity under snow was positively correlated with T(s) in the first winter and negatively correlated with T(s) in the second winter, presumably due to mild weather conditions in early winter. In early 1975, the number of animals active was negatively correlated with the temperature difference between T(s) and T(a).

Clubionidae were active in the early winter of both years, mostly adults in the first year and mainly immatures in the second year. In the meadow in midwinter, activity generally ceased, except by juveniles during the second winter. A small amount of activity occurred in late winter of a mixture of age classes. In spring, adults were predominantly active. Juveniles of the genus *Agroeca* were found to be cold-hardy, remaining active at -12°C. The species taken were also well-represented during summer.

Erigonidae were generally represented by adults of *C. laetus*, which were most frequently encountered on the ridge and in the meadow. This family exhibited activity throughout the year and was one of the two most winter-active families. Adults of this species were taken throughout the year, indicating that it is probably eurychronous (Tretzel 1954).

Linyphiidae were represented only in early winter by the holarctic species *C. sylvaticus* in the woods. This species has an autumn mating period and is therefore active in October and November and may be diplochronous (Tretzel 1954). Virtually no other activity by this family occurred from December to April. In May, adult activity resumed again. This species was rarely seen in summer on the soil surface, while other linyphiid species were active.

The lycosid species were active year-round, comprising the other winter-active family. Nevertheless, their main activity was in summer (Tables 9-1A and 9-1B). This family was commonly seen in sunny habitats, i.e. the ridge and the meadow. In early winter a mixture of age classes occurred, with the genus Pardosa being very abundant. Activity practically ceased in the midwinter of the first year while in the second year some juveniles, mostly Pardosa, remained active on the ridge and in the meadow. Cold room experiments determined that subadults of the genus Pardosa were active at -12°C. Probably most species are stenochronous.

The thomisids occurred less frequently than the above families. Most activity was exhibited by juveniles and females in the early winter. They were collected on the ridge and in the meadow. Occasionally, a juvenile was taken in mid- and late winter. In spring, a mixture of age classes resumed activity, including adult males; therefore, this family is assumed to be stenochronous. The species taken in autumn and winter were also present in summer.

Other cursorial families were collected in winter, but generally were rare. These species were also taken in summer. Consequently, none of the 49 species collected were exclusively winter-active.

Spring activity, as determined by pitfall traps, was low. Possibly this was because of the general wet conditions which followed snow melt. At that time three dimensions again became available to the spiders, and many species must have moved to bushes and trees to avoid the wet conditions and to pursue their prey. The meadow was the most productive habitat in terms of numbers of spiders.

The increase in winter activity in the second year was markedly greater than in the first year (540 individuals versus 176); even in spring a larger number was active (131 versus 6). Species diversity was high in autumn, low in winter, and gradually increased in spring to reach a high in summer.

V. CONCLUSION

The five major families appear to be adaptable with respect to temperature. In the first winter, the drop in T(s) by mid-December seemed to limit their activity, except for the erigonids and lycosids. Activity was positively correlated with T(s). In the second winter with its unusual snow conditions, the clubionids were also winter-active. Activity was negatively correlated with T(s), and the number of animals active was negatively correlated with the temperature difference between T(s) and T(a). Likewise as the T(s) rose in late winter, activity gradually resumed. All families, except the linyphiids, appeared to have more than one age class present in the overwintering period. Species diversity was high in autumn, low in winter, and gradually increased in spring to reach a maximum in summer. Nineteen species were found to be winter-active.

Figure 9-1

Some representatives of the principle spider families:

a) clubionid Agroeca pratensis female;

b) clubionid Phrurotimpus borealis female;

c) erigonid Ceraticelus laetabilis male, lateral view;

d) erigonid Ceraticelus laetus male, lateral view;

e) linyphiid Bathyphantes pallida male, lateral view;

f) lycosid Pardosa moesta male;

g) lycosids P. distincta male and female;

h) thomisid Oxyptila conspurcata female;

i) thomisid Xysticus punctatus female, similar to X. emertoni; and

j) hahniid Neoantistea agilis female (after Kaston 1948).

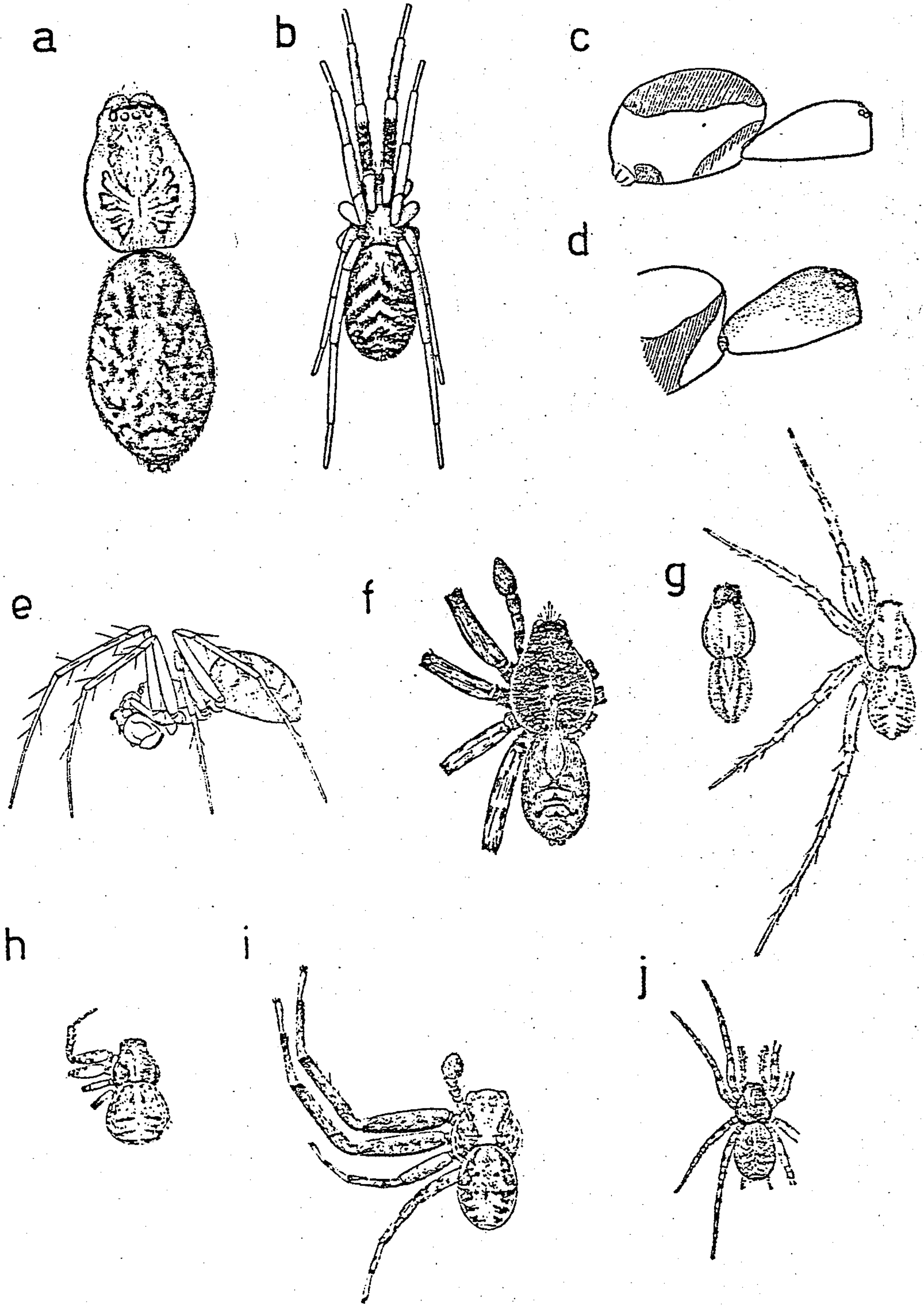

a
b
c
d
e
f
g
h
i
j

Figure 9-2

Number and families of spiders taken at each habitat in 1973-1974 (A - ridge; B - woods; C - meadow).

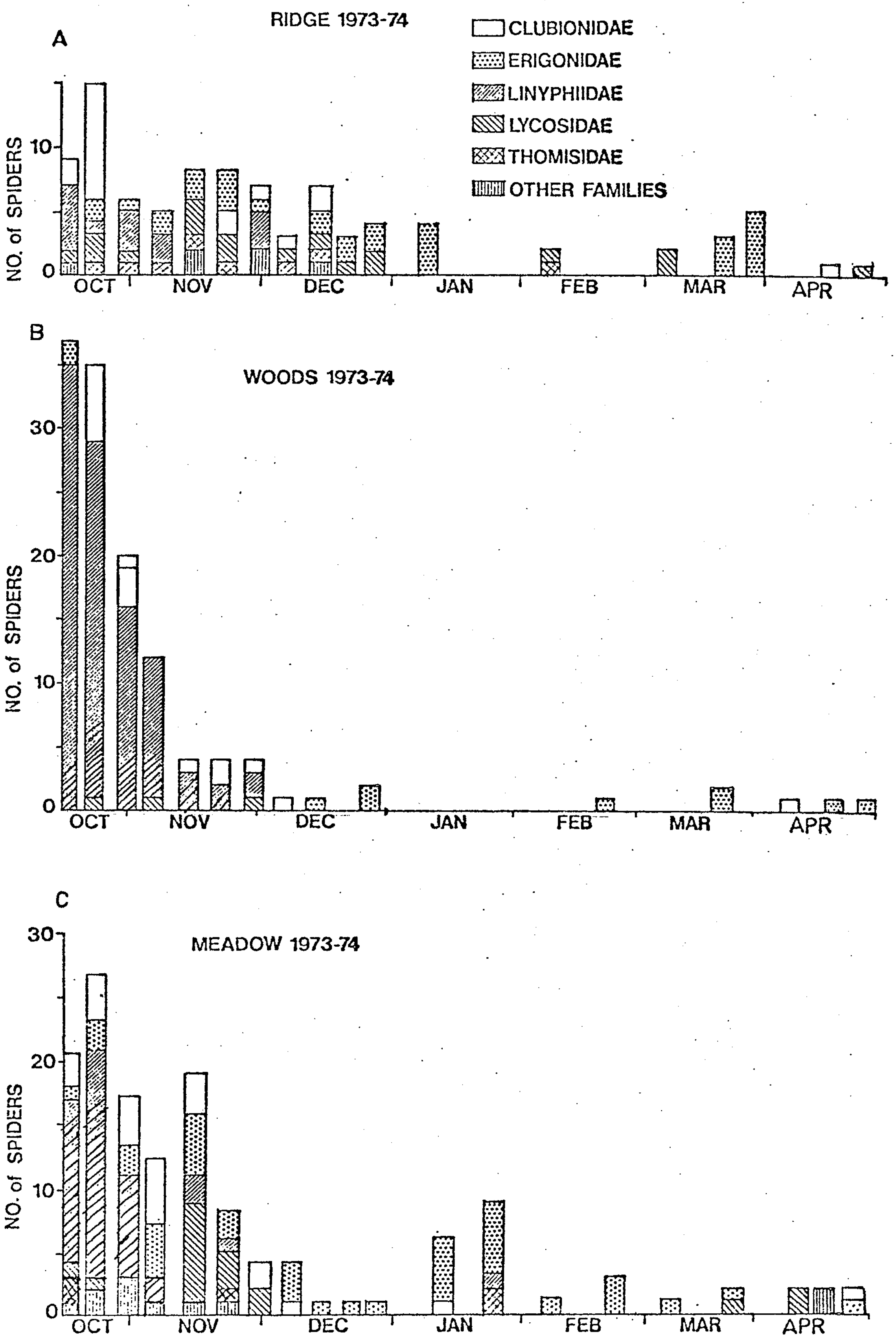

A
RIDGE 1973-74
CLUBIONIDAE
ERIGONIDAE
LINYPHIIDAE
LYCOSIDAE
THOMISIDAE
OTHER FAMILIES
NO. of SPIDERS
10
0
OCT
NOV
DEC
JAN
FEB
MAR
APR
B
WOODS 1973-74
30
20
10
0
NO. of SPIDERS
OCT
NOV
DEC
JAN
FEB
MAR
APR
C
MEADOW 1973-74
30
20
10
0
NO. of SPIDERS
OCT
NOV
DEC
JAN
FEB
MAR
APR

Figure 9-3

Number and families of spiders taken at each habitat in 1974-1975 (A - ridge; B - woods; C - meadow).

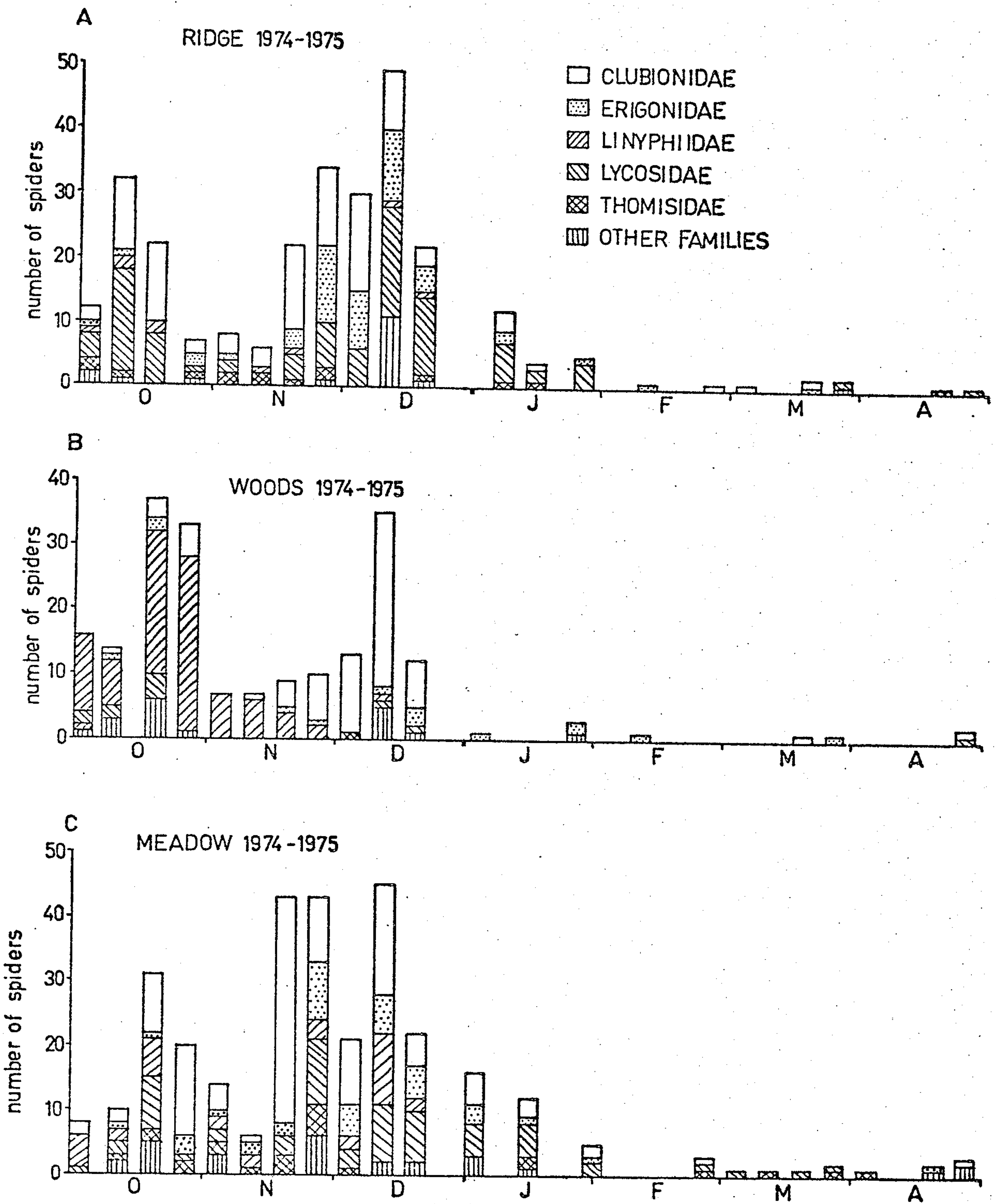
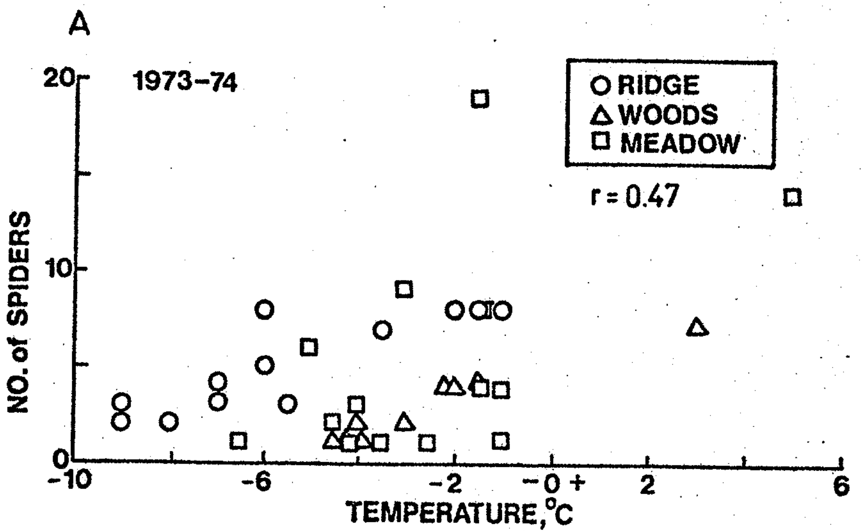

A
RIDGE 1974-1975
number of spiders
0
10
20
30
40
50
O
N
D
J
F
M
A
CLUBIONIDAE
ERIGONIDAE
LINYPHIIDAE
LYCOSIDAE
THOMISIDAE
OTHER FAMILIES
B
WOODS 1974-1975
number of spiders
0
10
20
30
40
O
N
D
J
F
M
A
C
MEADOW 1974-1975
number of spiders
0
10
20
30
40
50
O
N
D
J
F
M
A

Figure 9-4

Correlations between number of spiders trapped and T(s) (A - 1973-1974; B - 1974-1975).


A
1973-74
O RIDGE
Δ WOODS
□ MEADOW
r = 0.47
20
10
0
NO. of SPIDERS
-10
-6
-2
-0 +
2
6
TEMPERATURE,°C

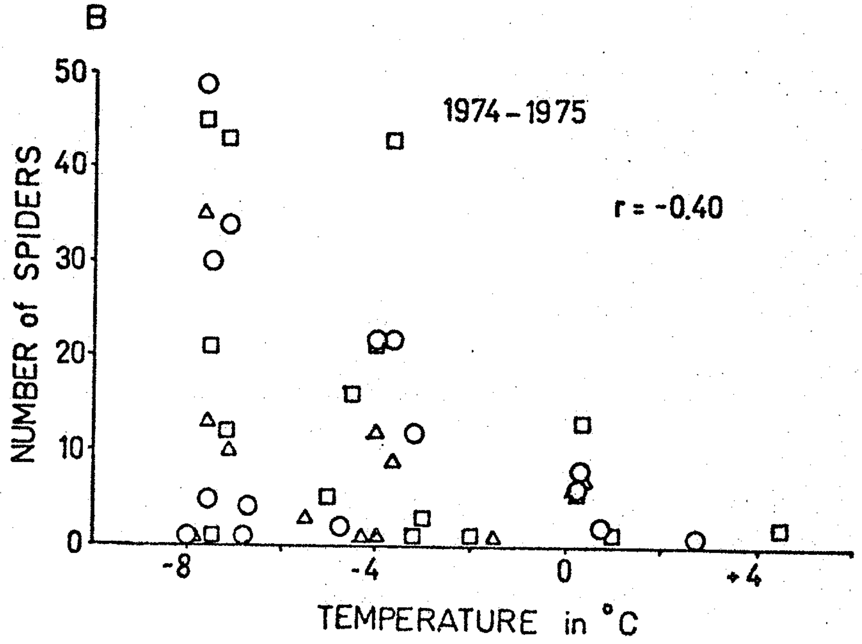

B
1974-1975
r = -0.40
50
40
30
20
10
0
NUMBER of SPIDERS
-8
-4
0
+4
TEMPERATURE in °C

Figure 9-5

Correlation between number of spiders trapped and temperature difference between T(s) and T(a) in 1975.

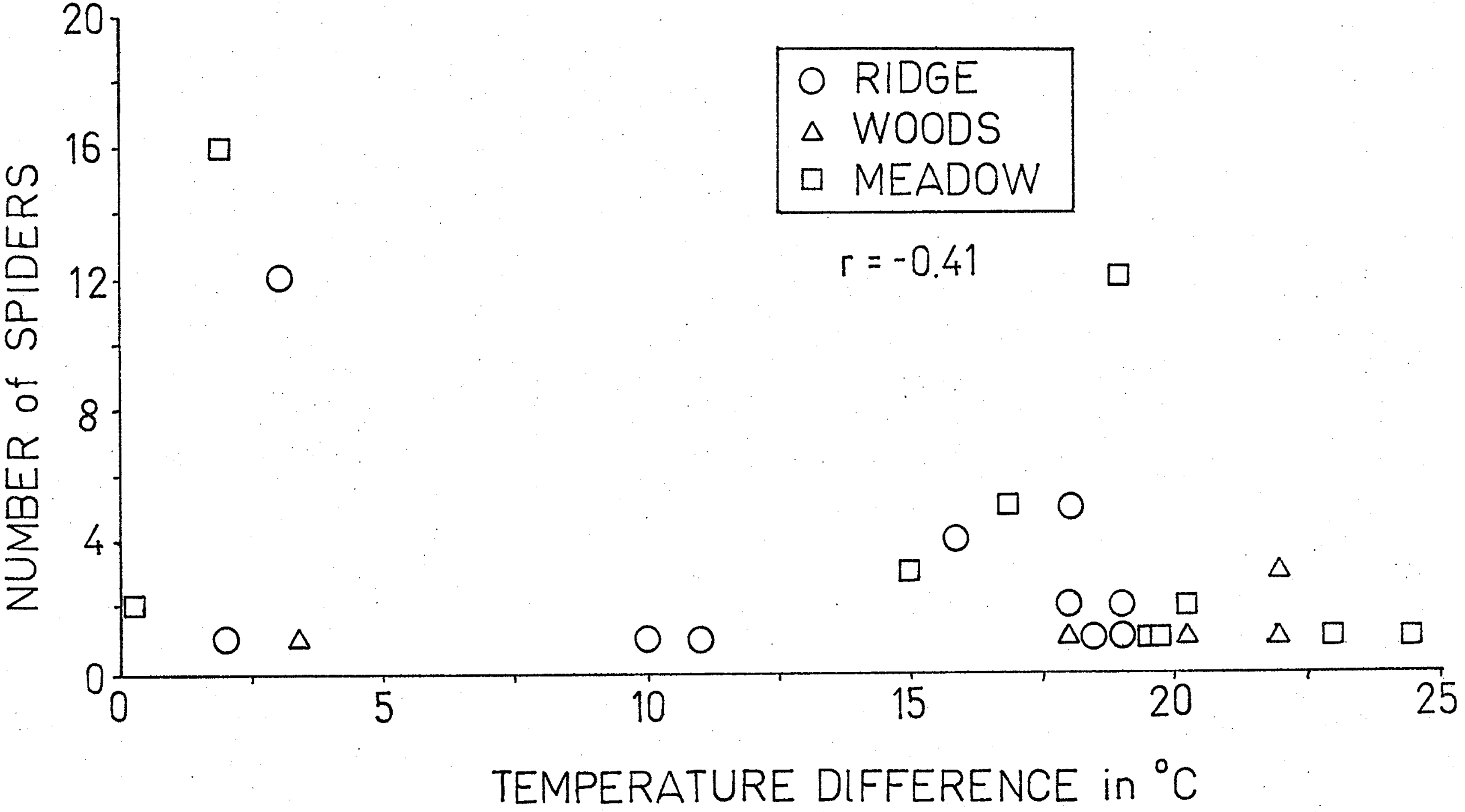

○ RIDGE
△ WOODS
□ MEADOW
r = -0.41
NUMBER of SPIDERS
0
4
8
12
16
20
0
5
10
15
20
25
TEMPERATURE DIFFERENCE in °C

Table 9-1A

Numbers of Araneae Active Seasonally at Fort Whyte, Manitoba 1973 to 1974

Date	Autumn*	Winter	Spring**	Summer
Clubionidae	27	24	3	20
Erigonidae	10	68	0	14
Linyphiidae	128	28	0	3
Lycosidae	7	29	2	113
Thomisidae	4	10	0	24
Others	10	14	4	17
Total Number	186	173	9	191

* Trapping occurred only in the last three weeks of October.

** One collection only.

Table 9-1B

Numbers of Araneae Active Seasonally at Fort Whyte, Manitoba 1974-1975

Family	Autumn	Winter	Spring	Summer
Clubionidae	75	215	16	20
Erigonidae	16	95	34	26
Linyphiidae	86	46	10	18
Lycosidae	77	112	42	155
Thomisidae	11	28	8	51
Others	34	35	30	29
Total Number	299	531	140	299

Table 9-2

Species of Araneae Taken at Fort Whyte, Manitoba*

Fam. Agelenidae:

Agelenopsis actuosa Gertsch and Ivie
Agelenopsis potteri Blackwall
Agelenopsis utahana Chamberlain and Ivie
Cicurina robusta Simon

Fam. Clubionidae:

Agroeca ornata Banks
Agroeca pratensis Emerton
Castianeira cingulata C. L. Koch
Clubiona johnsoni Gertsch
Phrurotimpus borealis Emerton
Scotinella pregnata Emerton

Fam. Dictynidae:

Argenna obesa Emerton

Fam. Gnaphosidae:

Drassodes sp.
Zelotes subterraneus C. L. Koch

Fam. Hahniidae:
Hahnia cinerea Emerton
Neoantistea agilis Keyserling
Neoantistea riparia Keyserling

Fam. Linyphiidae:

Centromerus sylvaticus Blackwall
Lepthyphantes sp.
Macrargus multesimus O.P.-Cambridge
Meioneta sp.
Neriene (Linyphia) clathrata Sundevall
Porrhomma terrestris Emerton

Fam. Lycosidae:

Alopecosa (Tarentula) aculeata Clerck
Lycosa frondicola Emerton
Pardosa distincta Blackwell
Pardosa fuscula Thorell
Pardosa groenlandica Thorell

Fam. Lycosidae (con't.):
- *Pardosa moesta* Banks
- *Trochosa terricola* Thorell

Fam. Microphantidae (Erigonidae):

- *Ceraticelus laetus* O.P.-Cambridge
- *Ceraticelus laetibilis* O.P.-Cambridge
- *Diplocephalus cuneatus* Emerton

Fam. Mimetidae:

- *Ero canionis* Chamberlain and Ivie
- *Ero furcata* Villers

Fam. Salticidae:

- *Neon* sp.
- *Phidippus whitmanii* Peckham and Peckham
- *Talavara minuta* Banks

Fam. Theridiidae:

- *Euryopsis argentea* Emerton
- *Theridion* sp.

Fam. Tetragnthidae:

- *Pachygnatha tristriata* C. L. Koch
- *Tetragnatha* sp.

Fam. Thomisidae:

- *Ozyptila conspurcata* Thorell
- *Ozyptila sincera* Kulczynski
- *Ozyptila sincera canadensis* Dondale and Redner
- *Thanatus formicinus* Clerck
- *Thanatus rubicellus* Mello-Leitao
- *Tibellus* sp.
- *Xysticus emertonii* Keyserling
- *Xysticus ferox* Hentz

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* Determinations by Charles D. Dondale, B.R.I., Ottawa, Ontario.

Table 9-3

Species of Araneae Taken in Each Habitat at Fort Whyte, Manitoba

Ridge (26 species):

Agelenopsis actuosa
A. utahana
*Agroeca pratensis**
Drassodes sp.
Zelotes subterraneus
Hahnia cinerea
Neoantistea agilis
Centromerus sylvaticus
Alopecosa aculeata
Lycosa fronidoca
*Pardosa distincta**
P. groenlandica
*P. moesta**
Trochosa terricola
*Ceraticelus laetus**
C. laetabilis
Neon sp.
Talavera minuta
Theridion sp.
Oxyptila sp.
Xysticus sp.*
Xysticus emertoni
Xysticus ferox
Thanatus formicinus
Argenna obesa

Meadow (23 species):

Cicurina robusta
*Agroeca ornata**
Clubiona johnsoni
Zelotes subterraneus
Hahnia cinerea
Neoantistea agilis
N. riparia
Lepthyphantes sp.
Meioneta sp.
*Neriene clathrata**
Macrargus multesimus
Alopecosa aculeata
Pardosa fuscula
*P. moesta**
Ceraticelus laetus
Pachygnatha tristriata
Scotinella pugnata
*Oxyptila conspurcata**
Xysticus sp.
Thanatus rubicellus
Tibellus sp.
Argenna obesa

Woods (25 species):

Agelenopsis potteri
*Agroeca ornata**
*Phrurotimpus borealis**
Castianeira cingulata
Zelotes subterraneus
Neoantistea agilis
N. riparia
*Centromerus sylvaticus**
Neriene clathrata
Meioneta sp.
Porhomma terrestris
Alopecosa aculeata
*Pardosa moesta**

Woods (con't.):

Diplocephalus cuneatus
Ero canionis
E. furcata
Phidippus whitmani
Euryopsis argentea
Tetragnatha sp.
Scotinella pugnata
Oxyptila sincera
O. s. canadensis
Xysticus emertoni
*Ceraticelus laetus**
Trochosa terricola

* common

Table 9-4

List of Species of Winter-Active Spiders Taken at Fort Whyte, Manitoba

Family	Species
Clubionidae	*Agroeca ornata* *A. pratensis* *Phrurotimpus borealis*
Erigonidae	*Ceraticelus laetus*
Linyphiidae	*Centromerus sylvaticus* *Meioneta* sp. *Neriene clathrata*
Lycosidae	*Pardosa distincta* *P. moesta* *Trochosa terricola*
Thomisidae	*Oxyptila conspurcata* *Thanatus formicinus* *Xysticus emertoni*
Hahniidae	*Hahnia cinerea* *Neoantistea riparia*
Agelenidae	*Cicurina robusta*
Theridiidae	*Theridion* sp.
Salticidae	*Neon* sp.
Tetragnathidae	*Tetragnatha* sp.

Table 9-5

List of Species of Spiders Taken Only in Summer at Fort Whyte, Manitoba

Family	Species
Agelenidae	*Agelenopsis actuosa* Gertsch and Ivie
Clubionidae	*Castianeria cingulata* C. L. Koch
Erigonidae	*Diplocephalus cuneatus* Emerton
Gnaphosidae	*Drassodes* sp.
Lycosidae	*Pardosa fuscula* Thorell *Pardosa groenlandica* Thorell
Salticidae	*Talavera minuta* Banks
Theridiidae	*Euryopsis argentea* Emerton
Thomisdae	*Thanatus rubicellus* Mello-Leitao *Xysticus ferox* Hentz

Table 9-6

Immature Clubionids and Lycosids Tested in Cold Rooms (33 Trials, 23 Individuals)

Temperature in °C	Exposure Time	Number of Spiders Tested	Number of Spiders With Normal Activity	Number of Spiders With Loss of Motor Control
3-4°C	5 minutes	23	all	none
-4°C	3 minutes	23	all (slower)	none
-9.5°C	1 minute	23	12	11
-12°C	1 minute	9	3*	6**

* All held one to two weeks at 3° to 4°C.

** Three of these specimens died.

Table 9-7

List of Known Nearctic and Holarctic Species of Spiders Occurring in Southern Manitoba

Species	Reference
NEARCTIC	
Ceraticelus laetabilis	Chamberlain and Ivie 1947
Pardosa groenlandica	Hackman 1954
Xysticus emertonii	Chamberlain and Ivie 1947
Oxyptila conspurcata	Chamberlain and Ivie 1947
Neoantistea riparia	Chamberlain and Ivie 1947
Hahnia cinerea	Chamberlain and Ivie 1947
HOLARCTIC	
Centromerus sylvaticus	Hackman 1954
Macrargus multesimus	Lindroth 1957
Neriene clathrata	Koponen 1975
Trochosa terricola	Koponen 1975
Alopecosa aculeata	Koponen 1975; Hackman 1954
Thanatus formicinus	Koponen 1975; Hackman 1954
Zelotes subterraneus	Hackman 1954

Chapter X

ORDER OPILIONES

I. REVIEW OF LITERATURE

The Opiliones, or phalangids, are nocturnal predators and scavengers, feeding on a variety of species of soil fauna (Todd 1950, Savory 1962, Cloudsley-Thompson 1968, Wallwork 1970). They are most abundant in woodland, occurring in litter and on vegetation (Savory 1966, Wallwork 1970). Williams (1962) found adults active above the ground layer in trees and collected them in pitfall traps in autumn when they descended to mate and oviposit in the soil. Juveniles which had not begun vertical migration were also trapped. They are most abundant in late summer and early autumn. Usually eggs and some newly-hatched young overwinter (Williams 1962, Savory 1966). Schmoller (1970) did not find adults in late summer and early autumn in his traps in Colorado alpine tundra, and hence concluded that they are probably unable to overwinter in that habitat. In subarctic Finnish birch forests (69°N), 97.3% of the catch consisted of phalangids, _Mitopus moric_ Fabricius being common (Koponen 1971). The duration of the life cycle is temperature-dependent, varying from one year for _Homolophus biceps_ Thorell and _Taracus packardi_ Simon in Colorado alpina tundra (Schmoller 1970) to more than one year for _Nemastoma lugubre_ in England (Wallwork 1970).

The activity of phalangids is humidity- and temperature-dependent. Todd (1949) tested four species in temperature gradients in an atmosphere of 100% relative humidity and found that most species survive one hour at -4° to -4.5°C after acclimation at 16.5°C. _Phalangium_ _opilio_ L. was killed after one hour at -9°C, its critical minimal temperature. Todd (ibid.) ascertained that species collected in exposed habitats had greater tolerance at lower temperatures.

Williams (1962) found that activity was humidity-dependent and that nocturnal and winter activity were correlated. At night and in winter, temperature is lower and relative humidity higher. In winter he noted that nocturnal movement was five times greater than movement in the day, indicating that the factors controlling the activity of small invertebrates were present at night and in winter (Williams 1962).

II. RESULTS

The seasonal catch of phalangids is presented in Table 10-1. In the first trapping period, two specimens were collected in the meadow, an adult male _Odiellus_ sp. nr. _pictus_ Wood in mid-October, and a juvenile _Leiobunum_ sp. in mid-June. In the second period, four individuals were collected in the woods, and one from the meadow. Single specimens were collected in the woods at the end of October, in the first week of November, in early May and in late May. The two species trapped are listed in Table 10-2.

No temperatures were available for 1973-1974. For 1974-1975, the recorded soil surface temperature at the end of October was -0.6°C; in the first week in November the temperature varied between 0° and +4°C; in early May it was +2°C.

III. DISCUSSION

The period of vertical migration from trees to the soil surface for adult phalangids occurs in autumn, at which time they usually mate and oviposit. At this time, they are most likely to be collected in pitfall traps. Juveniles are usually taken at other times (Williams 1962, Savory 1966). Three of the seven specimens collected in the present study in southern Manitoba were trapped in this time period, one of which was an adult male. While phalangids are commonly caught in subarctic Finnish birch forests (Koponen 1971), they are rare on the soil surface in southern Manitoba.

Todd (1949) found that the species with which she experimented were able to survive at -4° to -4.5°C for one hour, and furthermore that -9°C was the critical minimal temperature for _P_. _opilio_. _O_. _pictus_ appeared to be active in the temperature range of -0.6° to +4°C in autumn and early winter.

IV. CONCLUSION

Phalangids occur rarely in pitfall traps in southern Manitoba, usually only after they have descended from the trees in autumn and before they ascend them again in spring. They were active in the temperature range of -0.6° to +4°C.

Table 10-1

Numbers of Opiliones Trapped Seasonally at Fort Whyte, Manitoba; 1973 to 1975

Year	Autumn	Winter	Spring	Summer
1973-1974	1*	0	0**	1
1974-1975	1	1	2	1

* Trapping occurred only in the last three weeks of October.

** One collection only.

Table 10-2

Species of Opiliones* from Fort Whyte, Manitoba

Leiobunum sp.
Odiellus sp. nr. *pictus* Wood
Odiellus pictus Wood

* Determinations by: Charles D. Dondale, B. R. I., Ottawa, Ontario.

Chapter XI

ORDER ACARINA

I. REVIEW OF LITERATURE

Acarina, or mites, are especially common in soil, humus and litter of deciduous forests. The suborders Prostigmata, Mesostigmata, Cryptostigmata and Astigmata contain predators, parasites and detritus-feeders. Larger mites, e.g. _Pergamasus_ sp., are usually seen in litter or on the soil surface (Wallwork 1970). They comprise 70 to 80% of the total fauna in mosses, top soils and humus of woods, and up to 95% of the arthropod species in English heathland (Hughes 1959). In southeastern Manitoba, core samples of soil taken from May to December contained 70 species of mites, 59% of which were cryptostigmatids, 27% mesostigmatids, 13% prostigmatids and 1% astigmatids (Oswald and Minty 1970). Firstly, responses to temperature by mites are considered, and secondly, each suborder except the Astigmata will be discussed.

Wallwork (1970) examined mites from Michigan and from Ghana in a temperature gradient that ranged from 4° to 50°C, with constant relative humidity. They were preconditioned for twelve hours at 23°C and 30°C respectively, which were the normal litter temperatures at midday in the hottest season of the year. The tolerance zone for the North American species was narrow (16° to 28°C), and most species avoided temperature conditions outside or near their critical limits, the lower and upper limits being 15° and 30°C for most species. The tolerance zone for the West African species was 18° to 36°C, with lower and upper critical limits of 17° and 37°C respectively. Preference zones seemed to be 25° to 30°C. Wallwork (1960) described in detail the response of mites to cold stupor and immobility.

The threshold temperature for development of the mite, *Panonychus ulmi* Koch, was determined in summer to be 11.7°C (Putman 1970). That was the temperature at which eggs were able to hatch and produce fertile adults. Sømme (1965b) found that eggs of the same species contained sorbitol, which decreased the supercooling points. Stenseth (1965) in Norway recorded cold-hardiness in *Tetranychus urticae* Koch, as shown by larvae and cold-acclimated females which were active at 15°C. He also noted that diapausing females survived cold temperatures better than the supercooled, active females.

Temperature also affects the rate of development; at 20°C *Pergamasus crassipes* L. requires three weeks to develop from egg to adult, four weeks at 15°C, and up to 94 days at 7.3°C (Wallwork 1970). In northwest Iceland where the mean annual temperature is 2.5°C, Cloudsley-Thompson (1948) collected prostigmatids *Erythraeus* sp., *Bdella semiscutata* Thorell, and mesostigmatids *Pergamasus theseus* Berlese and *P. robustus* Oudemans. Gasdorf and Goodnight (1963) noted a possible correlation between the number of mites and temperature and none between the number of animals and soil moisture. A downward movement of mites into humus was observed at the onset of winter, and these litter-dwellers had low thermal preferences (Wallwork 1970).

The Prostigmata are predators and detritus-feeders, usually in soils with high organic content (Wallwork 1970). The order contains numerous families, six of which will be discussed. The Anystidae is a cosmopolitan family that contains species that are predaceous on mites and small insects that occur in leaf litter, on plants, grass and soil (Baker and Wharton 1952, Krantz 1970). *Anandia alticola* Hirst was collected on Mount Everest at 5,000m (Hughes 1959). The Bdellidae is composed of species that are predaceous on spider mites and collembola. Bdellids are found in many moist environments, e.g. moss, lichens, leaf mold and litter (Baker and Wharton 1952, Hughes 1959, Krantz 1970). The Erythraeidae are parasitic in the larval stage on insects and predatory in the nymhpal and adult stages. They occur in foliage, dead leaves or in humus (Baker and Wharton 1952, Schmoller 1969, Krantz 1970). In midsummer they have been found in the high alpine tundra of Colorado (Schmoller 1969) and in northeastern Iceland (Cloudsley-Thompson 1948). The Eupodidae and Rhagidiidae are fast-moving predators found in crevices of damp soil, humus or moss of temperate climates. *Eupodes* spp. and *Rhagidia* spp. are predaceous, and *Linopodes* spp. are fungivorous. The genus *Rhagidia* is holarctic (Baker and Wharton 1952, Hughes

1959, Krantz 1970). The Tetranychidae is composed of species that are phytophagous and ubiquitous. The ubiquitous Trombidiidae are parasitic on insects in the larval stages and predatory in the nymphal and adult stages. They occur in moss, humus and litter (Hughes 1959, Krantz 1970).

The Mesostigmata are free-living predators and detritus-feeders; the predaceous genera Veigaia and Pergamasus feed on collembolans, nematodes, proturans, insect eggs and probably cryptostigmatid mites in woods (Hughes 1959, Wallwork 1970). Two species of Pergamasus were collected in northeastern Iceland (Cloudsley-Thompson 1948). Some members of the families Parasitidae and Laelaptidae practice phoresy, probably on dung insects (Hughes 1959, Krantz 1970).

The Cryptostigmata are detritus-feeders, present in litter, moss, surface vegetation and soil. They require a high relative humidity and prefer decaying leaves (Hughes 1959, Krantz 1970, Wallwork 1970). Many families of this suborder are implicated as tapeworm vectors (Krantz 1970). Peak densities in population occur in the autumn and winter months (Wallwork 1970).

II. RESULTS

Mites were the most abundant winter-active group in both winters, consisting almost exclusively of Prostigmata and of Mesostigmata (Table 11-1). Considerable activity occurred on the soil surface in winter and was greater in the second winter than in the first (3,476 compared to 2,899 individuals). A general increase in numbers of mites occurred during the summer of 1974 and was maintained by favourable weather conditions in autumn, resulting in a larger population than in the first winter. The diversity of families was greatest in autumn, though the number of individuals was not high. (I emphasize that the numbers are relative due to the nature of the field work.) By midwinter the families Eupodidae, Rhagidiidae and Parasitidae were predominant and represented by _Eupodes_ spp., _Linopodes_ spp., _Rhagidia_ spp. and _Pergamasus crassipes_ respectively (Figure 11-1). The family Rhagidiidae was primarily responsible for the large increase in numbers in late February and early March. As the winter progressed, the number of mites declined again, even though the mean daily temperature was rising. The species of Acarina taken at Fort Whyte are given in Table 11-2.

In 1973-1974 autumn activity of mites was most apparent on the ridge, while most activity in the early winter occurred in the woods (Figures 11-2A to C). The peak in numbers which took place in late February-early March was highest in the woods, the habitat with much litter in the ground cover (Table 3-4). Numbers declined rapidly at the end of March and in early April. During autumn 65% of the total acarine activity was due to Prostigmata; in winter prostigmatids constituted 95% of the catch; in spring, 39%; and in summer, 57%.

In 1974-1975 mites were more abundant on the ridge and in the woods in late autumn, but following the establishment of permanent snow cover in mid-December the populations of mites increased on the ridge and in the meadow, but fell in the woods (Figures 11-3A to C). The midwinter peak was not distinct on the ridge, while definite peaks occurred in the woods and meadow, the latter habitat having the highest peak (Figure 11-3C). The species of mites taken in each habitat are presented in Table 11-3. Eighteen species were collected on the ridge, seven in the woods, and eight in the meadow. _Rhadigia_ sp. and _Eupodes_ sp. occurred in all habitats, while bdellids, _Veigaia cerva_ and cryptostigmatids were present on the ridge. _Linopodes_ sp. preferred the litter in the woods and meadow. The autumn prostigmatids comprised 91% of the total catch; in winter, 98%; in spring, 52%; and in summer, 32%.

Virtually no correlation existed between the number of active Acarina in all habitats and T(s) in the first winter (r = -0.06, not significant; Figure 11-4A). A slightly negative and not significant correlation occurred in the second winter (r = -0.21; Figure 11-4B). Even at -8° and -9°C, large numbers of mites were collected in midwinter. Hence the activity of these mites does not appear to be restricted by temperature. No correlations were found between activities of Acarina and Collembola or Araneae.

In 1975, the number of active Acarina was plotted against the temperature difference between T(s) and T(a), and no significant correlation was found between the two (r = -0.02; Figure 11-5). Thus, even large differentials in temperature between T(s) and T(a) do not affect acarine activity.

The soil surface samples taken in March, 1975, determined the relative population densities of all three major suborders in all habitats. On the ridge and in the meadow Mesostigmata were most abundant; in the woods, Prostigmata dominated Density of mites was greatest in the meadow and least dense on the ridge. These results agree well with the numbers taken in traps during the winter (Figure 11-3A to C), and also imply that some activity of mites does occur.

The Cryptostigmata were not collected until April, as were mesostigmatid Gamasellus sp. and the prostigmatids Erythraeus sp., Protereunetes sp. and trombidiid mites (Table 11-2). The other species occurred in autumn, winter and spring. There were no species found exclusively active in winter.

III. DISCUSSION

Dowdy (1965) in Missouri, Mason (1972) in England, and Willard (1973) in Saskatchewan noted an increase in numbers of mites in February or March, followed by a decrease in April. This agrees with my results. Also in late winter as the earth changes its orientation with respect to the sun, the intensity of solar radiation increases markedly from February to March, from 40 to 113 langleys per day (Table

4-3). During the same period, light penetration into snow increases (Näsmark 1964, Geiger 1965). Since many invertebrates are sensitive to changes in light intensity, the increase in light intensity in late winter may explain the dramatic increase in numbers of mites at that time of year. The decrease in numbers in April may be caused by the presence of melt water on the soil and the increase in habitat available to the animals when the snow melts.

Oswald and Minty (1970) sampled southeastern Manitoba forest soils from April to December. They found no population peak for *Rhagidia* spp., and peaks in April and December for *Gamasellus* spp. At Fort Whyte it appears that *Rhagidia* spp. have population peaks in March, and *Gamasellus* sp. possibly in April.

Marshall and Kevan (1964) collected the ubiquitous *Pergamasus longicornis* Berlese, holarctic *Veigaia cerva* Kramer, three species of *Eupodes* and seven of *Rhagidia* in Quebec woodland humus. In southern Manitoba, *P. crassipes* was common, as were *Eupodes* spp. and *Rhagidia* spp., while *V. cerva* was less common. As tetranychids are phytophagous (Krantz 1970), their presence in southern Manitoba only in summer is understandable.

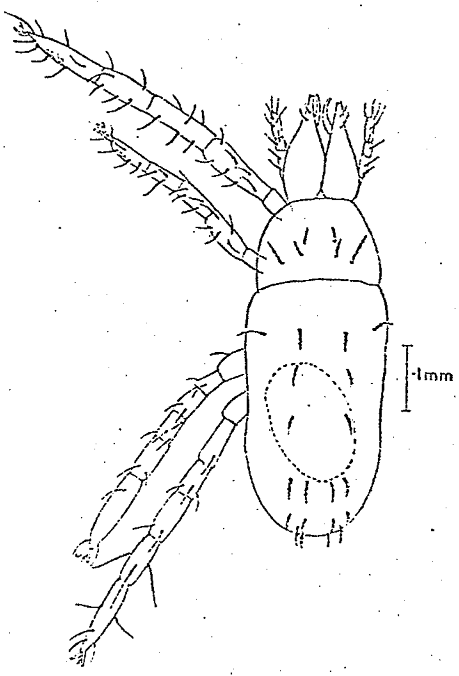
IV. CONCLUSION

Acarina of the Eupodidae, Rhagidiidae and Parasitidae are some of the most abundant winter-active groups, irrespective of temperature. No correlation was found between the number of mites trapped and T(s). There were no species found exclusively in winter. Only _V. cerva_ is holarctic.

Figure 11-1

Prostigmatid mites: (A) *Rhagidia gelida* Thorell female, dorsal view (Hughes 1959), and (B) *Linopodes* sp. (Oregon, U.S.A.) (from Krantz 1970).

A



B

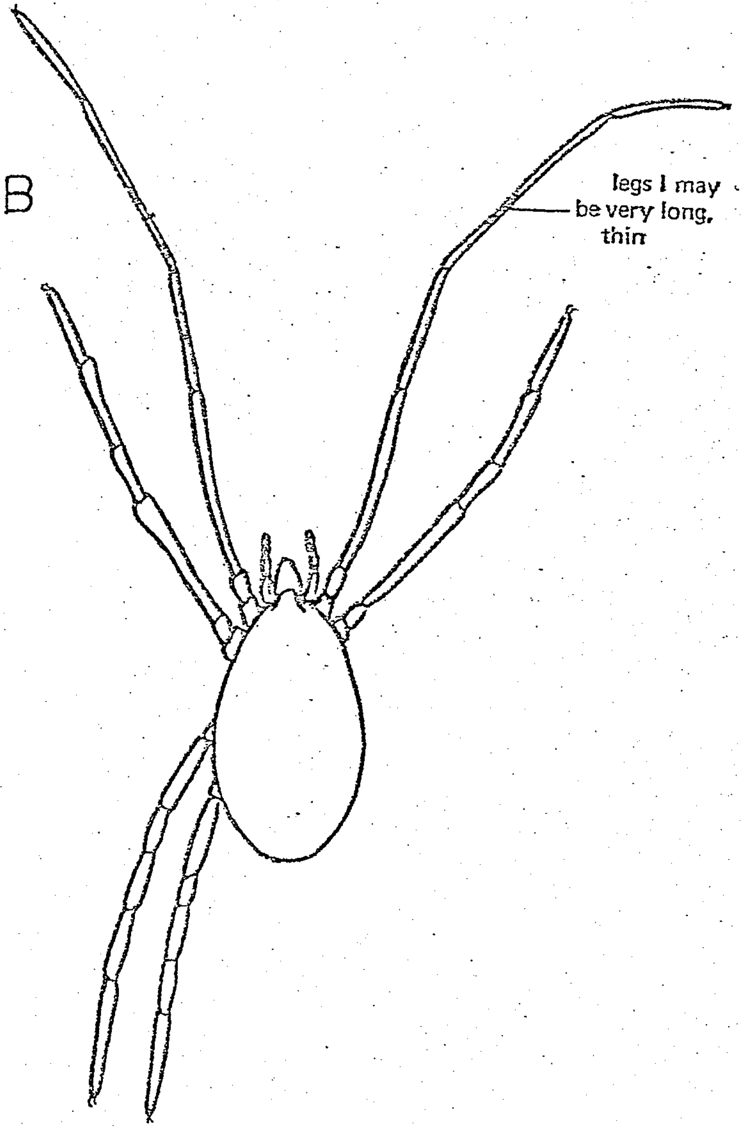
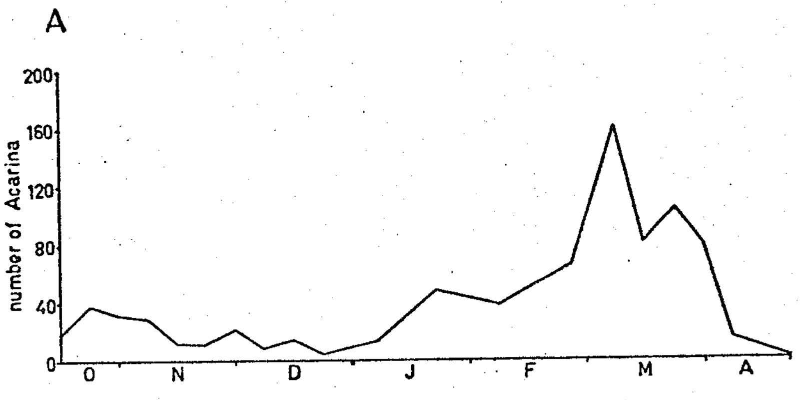
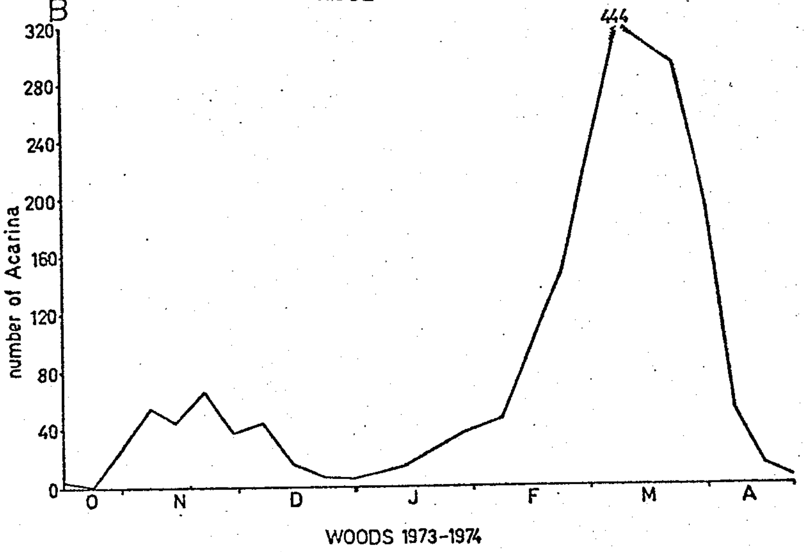

legs I may be very long, thin

Figure 11-2

Number of Acarina taken at each habitat in 1973-1974 (A - ridge; B - woods; C - meadow).


A
number of Acarina
200
160
120
80
40
0
O
N
D
J
F
M
A
RIDGE 1973-1974


B
444
number of Acarina
320
280
240
200
160
120
80
40
0
O
N
D
J
F
M
A
WOODS 1973-1974

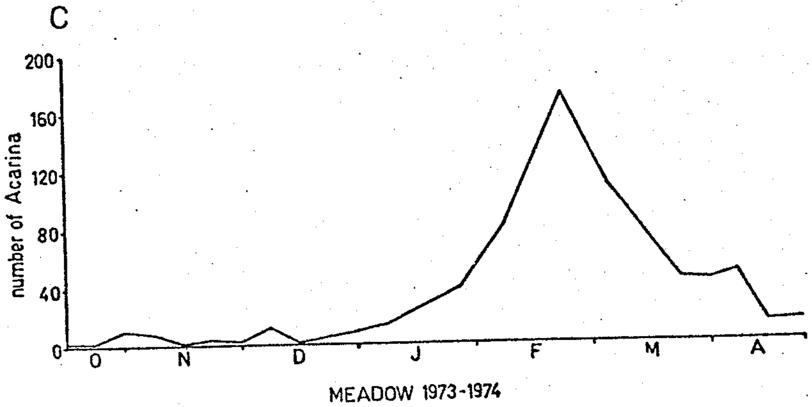
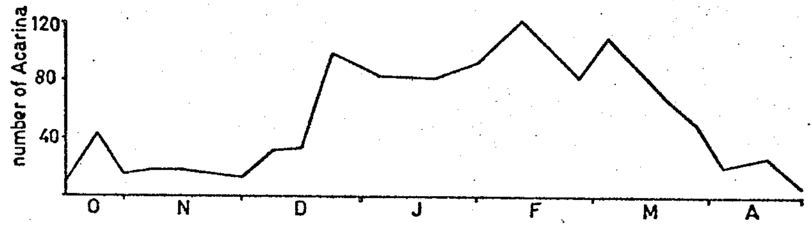

C
number of Acarina
200
160
120
80
40
0
O
N
D
J
F
M
A
MEADOW 1973-1974

Figure 11-3

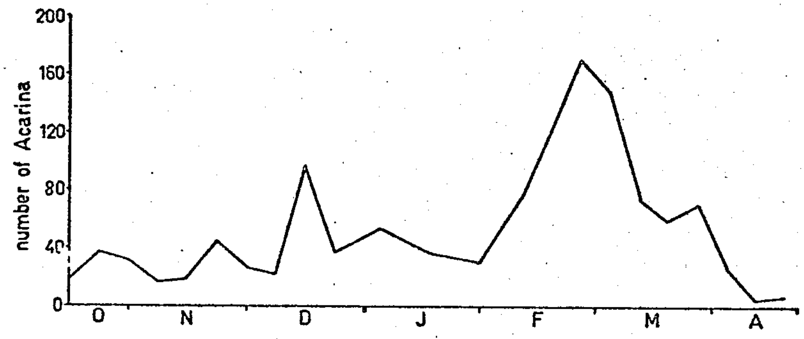
Number of Acarina taken at each habitat in 1974-1975
(A - ridge; B - woods; C - meadow).

A



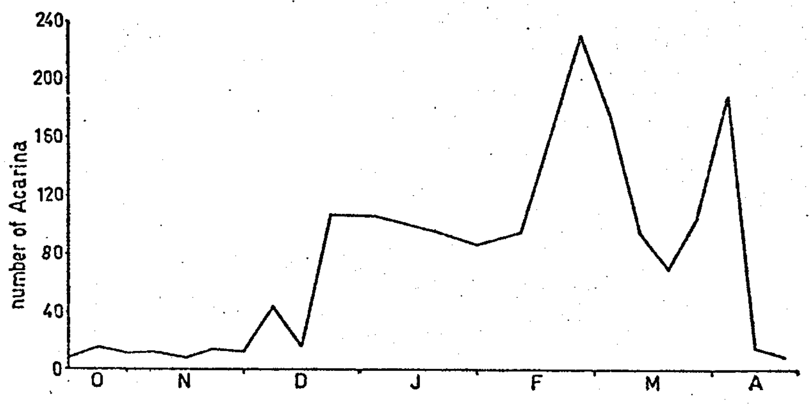
RIDGE 1974-1975

B



WOODS 1974-1975

C

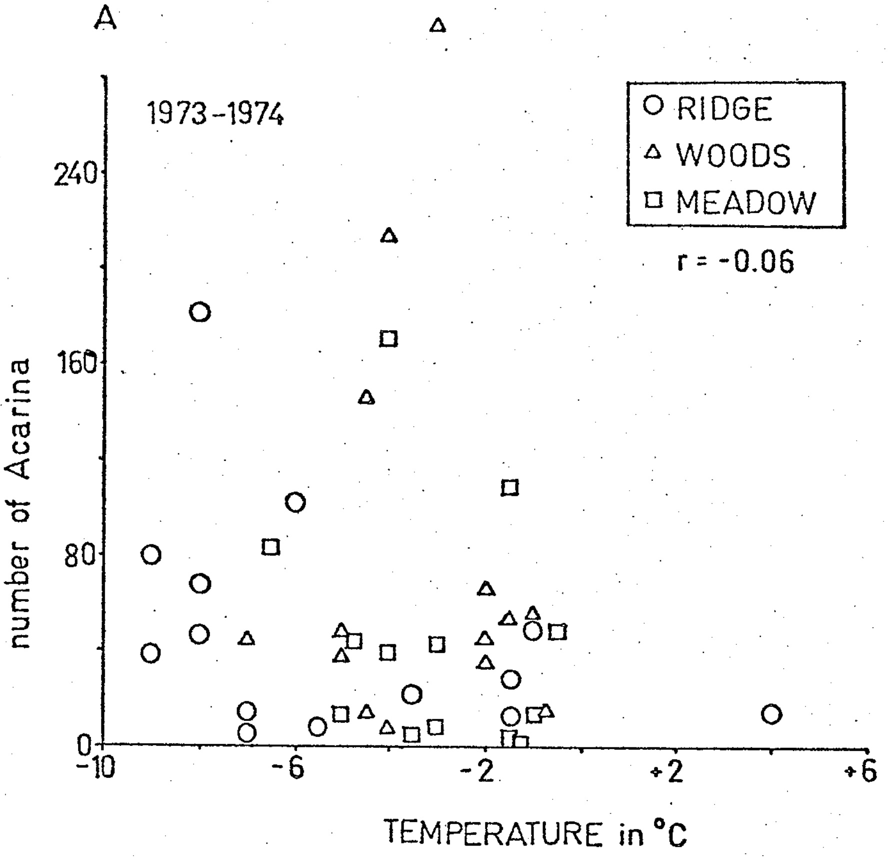


MEADOW 1974-1975

Figure 11-4

Correlations between number of mites trapped and T(s) (A - 1973-1974; B - 1974-1975).

A


1973-1974
○ RIDGE
△ WOODS
□ MEADOW
r = -0.06
number of Acarina
240
160
80
0
-10
-6
-2
+2
+6
TEMPERATURE in °C

B

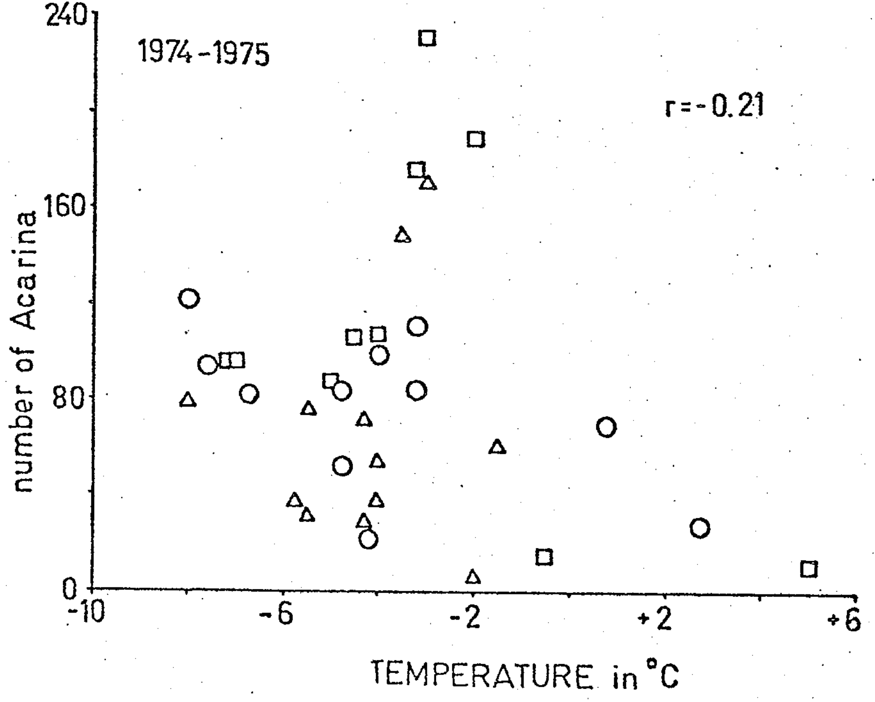

1974-1975
r=-0.21
number of Acarina
240
160
80
0
-10
-6
-2
+2
+6
TEMPERATURE in °C

Figure 11-5

Correlation between number of mites trapped and temperature difference between T(s) and T(a) in 1975.

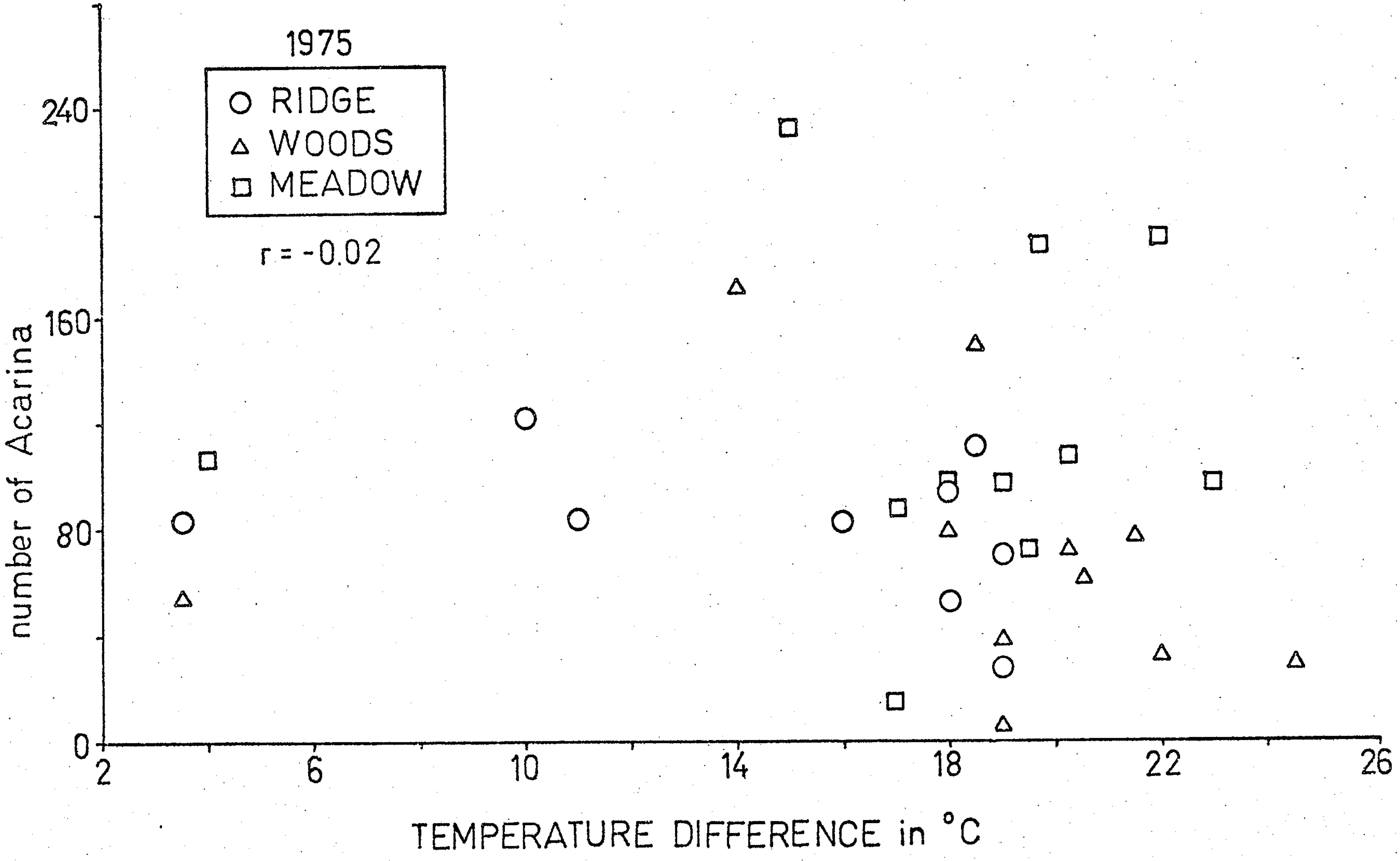

1975
○ RIDGE
△ WOODS
□ MEADOW
r = -0.02
number of Acarina
0
80
160
240
2
6
10
14
18
22
26
TEMPERATURE DIFFERENCE in °C

Table 11-1

Seasonal Activity of Acarina Collected at
Fort Whyte, Manitoba (1973 to 1975)

Year	Autumn	Winter	Spring	Summer
1973-1974				
Prostigmata	86**	2899	11***	193
Mesostigmata*	46**	145	17***	252
1974-1975				
Prostigmata	396	3398	162	352
Mesostigmata*	38	78	151	739

* Includes a few Cryptostigmata.

** Trapping only in the last three weeks of October.

*** One collection only.

Table 11-2

Species of Acarina* Collected at Fort Whyte, Manitoba, from 1973 to 1975

S.O. Prostigmata:

Fam. Anystidae:

Anystis sp.

Fam. Bdellidae:

Bdella sp.
Bdella longicornis Hermann
Bdellodes longirostris Linn.
Biscirus silvaticus Kramer

Fam. Erythraeidae:

Erythraeus sp.

Fam. Eupodidae:

Eupodes sp.
Linopodes sp.
Protereunetes sp.

Fam. Rhagidiidae:

Rhagidia sp.

Fam. Tetranychidae:

Petrobia latens

Fam. Trombidiidae:

Microtrombidium sp.
Podotrombidium sp.

S.O. Mesostigmata (O.Parasitiformes)

Fam. Crytolaelapidae:

Gamasellus sp.

Fam. Laelapidae:

Androlaelaps casalis Berlese

Fam. Parasitidae:

<u>Gamasodes</u> <u>bispinosus</u> Halbert
<u>Parasitus</u> sp. near <u>fimetorum</u> Berlese
<u>Pergamasus</u> <u>crassipes</u> Linn.

Fam. Veigaiidae:

<u>Gorirossia</u> sp.
<u>Veigaia</u> <u>cervus</u> Kramer

S.O. Cryptostigmata:

Fam. Damaeidae:

<u>Epidamaeus</u> sp.

Fam. Liacaridae:

<u>Liacarus</u> sp.

Fam. Metrioppiidae:

<u>Ceratoppia</u> sp.

Fam. Oribatellidae:

<u>Oribatella</u> sp.

Fam. Pelopidae:

one individual

---

* Determinations by E. E. Lindquist, B.R.I., Ottawa, Ontario

Table 11-3

Species of Acarina in Each Habitat at Fort Whyte, Manitoba

Ridge (18 species):

Bdella longicornis
B. sp.
Bdellodes longirostris
Biscirus silvaticus
Erythraeus sp.
Eupodes sp.*
Linopodes sp.*
Protereunetes sp.
Rhagidia sp.
Microtrombidium sp.
Androlaeleaps casalis
Gamasellus sp.
Gamasodes bispinosus
Pergamasus crassipes
Veigaia cerva
Liacarus sp.
Ceratoppia sp.
Oribatella sp.

Woods (7 species):

Anystis sp.
Eupodes sp.
Linopodes sp.
Rhagidia sp.*
Podotrombidium sp.
Pergamasus crassipes
Gorirossia sp.

Meadow (8 species):

Anystis sp.
Erythraeus sp.*
Eupodes sp.
Rhagidia sp.*
Gamasellus sp.
Gamasodes bispinosus
Parasitus spp.
Epidamaeus sp.

---

* common

Table 11-4

Densities of Acarina per m^2 Determined from Snow Samples Collected 17 March, 1975

Suborder	Ridge	Woods	Meadow
Prostigmata	970.1	1238.5	1871.8
Mesostigmata	1266.4	684.8	2258.1
Cryptostigmata	43.0	95.6	374.4

Chapter XII

ORDER COLLEMBOLA

I. REVIEW OF LITERATURE

Next to mites, Collembola rank second in abundance numbers of species of soil invertebrates. Most Collembolans, or springtails, feed on fungal hyphae, soil bacteria, faeces and plant material, while a few are predaceous (Hale 1967, Wallwork 1970). They are distributed from arctic to desert regions and occur in a wide variety of habitats of relatively high humidity, including snow fields. Hence, the term "snow fleas" arose. Population densities may vary from 5,000 to 100,000 animals per m², dependent upon habitat (Kevan 1962, Hale 1967, Healey 1967, Wallwork 1970, Willard 1973). Larger individuals, such as Entomobrya, Orchesella and Tomocerus spp., may be present on the soil surface, while smaller collembolans are in deep litter layers in soil (Kevan 1962, Hale 1967, Wallwork 1970). Predators of springtails include Chilopoda, Carabidae (Bembidion, Pterostichus and Trichocellus spp.), Staphylinidae (Philonthus and Tachinus spp.), Araneae (Centromerus and Trochosa spp.), Parasitidae (P. crassipes and Veigaia sp.), phalangids and pseudoscorpions (Neobisium), all commonly found in deciduous leaf litter (Ernsting and Joosse 1974).

Several researchers examined collembolans in thermal gradients. In subarctic conditions they are active at low temperatures and have no diapause; their swarming on snow was attributed to "active gregariousness" (Hale 1967). *Podura aquatica* L. is cold-resistant and tolerates -6°C for one hour after acclimation to 18°C, with 20% of the individuals jumping, 70% crawling and 9% rigid (Simon 1961). Holmquist (1926) recorded *Entomobrya* spp., *Isotoma* spp., *Neanura muscorum* Templeton and *Tomocerus flavescens* Tullberg normally active under litter and snow in Chicago in winter. In Montana Chapman (1954) noted *Isotoma viridis* Bourlet and five other species of Collembola active on snow in small numbers at temperatures near 0°C in February. In Manitoba, Pruitt (pers. comm.) collected specimens of *Isotoma grandiceps* Reuter and *I. viridis* on snow at temperatures near freezing. The antarctic species, *Isotoma klovstadi*, survived -30°C in experiments, while other species cannot survive -20°C (Wallwork 1970). Many species migrate downwards in winter to avoid temperature extremes, but their distribution appears to be affected by several factors (Wallwork 1970).

In Sweden, north of the arctic circle at 67°C, Agrell (1941) correlated ecological distribution of Collembola and temperature. They are also sensitive to relative humidity (Agrell 1941, Kaczmarek 1963). Cold-resistance experiments established cold stupor at -8°C for *Isotoma olivacea* Tullberg, *Isotoma olivacea violacea* Tullberg, *Hypogastrura armata* Micolet, *I. viridis* and *Lepidocyrtus cyaneus* Tullberg. *I. viridis* and *I. o. violacea* were the most cold-hardy species, active between 0° and -4°C. Isotomidae are the most typical arctic representatives. These collembolans also preferred low light intensities, while surface-dwelling Tomocerus sp., H. armata and Entomobrya nivalis L. were active at all light intensities (Agrell 1941). Wolska (1957) determined the thermal preferendum of Orchesella flavescens Bourlet, collected on melted snow, to be 6° to 12°C. Isotoma saltans Nicolet, also collected active on snow, preferred a temperature range between +5° to -5°C (Wolska 1957).

The length of the life cycle depends upon temperature. Eggs laid in summer develop more rapidly than those laid in winter at 2°C (Hale 1967, Healey 1967, Wallwork 1970), though the growth rate of Onychiurus procampatus Gisin is rapid even at 5°C (Healey 1967). The minimum life cycle takes six weeks and the maximum ten months (Agrell 1941, Hale 1967, Willard 1973). There is no correlation between temperature sensitivity and hatching time (Agrell 1941). The overwintering individuals may live up to one year; and at high altitudes and in arctic and subarctic conditions, there are one to two generations per year, while in temperate conditions there may be three or four (Agrell 1941, Hale 1967). Usually species overwinter as eggs or almost fully-developed or adult specimens. "As a rule, there is...no mortality during the overwintering" (Agrell 1941), when many younger individuals move into the soil. New generations generally appear in the snow-free periods

(Agrell 1941, Healey 1967). Different age groups have different sensitivities to temperature, and increased cold-resistance occurs in early winter (Agrell 1941). In England newly-hatched springtails are present all year, especially between June and October (Healey 1967). Most species breed year-round, excepting the genus Tomocerus which is univoltine (Wallwork 1970).

Population peaks are dependent on locality and length of seasons (Kaczmarek 1963, Hale 1967, Wallwork 1970). In Europe and North America, one peak occurs between February and June, and another between August and December, usually coinciding "with the appearance of the first instar juveniles of the new generation." Declines in population occur in midsummer and midwinter (Wallwork 1970). In Saskatchewan, Willard (1973) found peaks in numbers in November and late March, while in southern England maximum numbers of collembolans occurred in late autumn and early spring (Kaczmarek 1963). However, year-round pitfall trapping by Mason (1972) in England established maximum catches of Collembola in January and February. In Poland maxima in litter were recorded from October to January and in the soil from January to February; an inverse relationship between numbers of collembolans and temperature appeared to exist (Kaczmarek 1963).

Representatives of the families Entomobryidae, Isotomidae, Onychiuridae, Poduridae, and Sminthuridae will be discussed. The entomobryids in the genera Entomobrya, *Orchesella* and *Tomocerus* are large, found on the soil surface and in litter, and feed upon pollen, algae, fungal spores and decaying plant material (Hale 1967, Wallwork 1970). Isotomids are the predominant arctic family (Agrell 1941), and the genera *Isotoma* and *Folsomia* feed on fungal hyphae, faeces, bacteria and decaying plant material, except *I. viridis* which is predaceous (Wallwork 1970). The onychiurid, *Onychiurus* sp., and the podurid, *Hypogastrura* sp., have the same diet as the isotomids and are often found in moss (Wallwork 1970). Many sminthurids are phytophagous and damage crops of economic importance (Borror *et al.* 1976).

II. RESULTS

Collembola were nearly always present in traps, but their numbers were low in extremely cold periods during midwinter. More individuals were active during the first winter than during the second (1,265 versus 564 individuals), and the largest numbers occurred in summer (Table 12-1). More collembolans were trapped in the woods and the meadow than on the ridge. In the first year isotomids predominated in the winter (69% of the total collembolan catch) and sminthurids in the summer (73%); in the second year, isotomids comprised 47% and entomobryids 50% of the catch in winter, and sminthurids predominated in spring and summer (61% and 81% respectively). Podurids were never abundant, and onychiurids were rare. A list of the 27 species taken at Fort

Whyte is presented in Table 12-2. Common winter-active species were *Isotoma subequealis* Folsom-*fennica* Reuter, *Isotoma violacea* Tullberg, *I. viridis* and occasionally *H. armata*.

The general pattern of activity of Collembola in autumn and winter consisted of a peak in late October or early November, a gradual decline until midwinter, followed by a series of peaks starting in early March and continuing into spring. The results for all habitats in 1973-1974 are shown in Figure 12-1. In late December and early January in the woods and in the meadow a small peak occurred, coincident with the marginal rise in T(s) in the meadow from -3.5° to -2.5°C. No temperature rise was detected in the woods (Figures 4-1B and C). On 7 March, 1974, T(s) in the woods and meadow averaged -1.25°C, at a time when an increase in collembolan population occurred.

In 1974-1975 the same pattern of activity was found except for a substantial decrease in the numbers trapped on the ridge (Figure 12-2A) and an increase in the woods (Figure 12-2B). The small peaks in late November, when there was no snow cover, were coincident with soil surface temperature varying between -1° to -3°C. The smaller peak in mid-December was again probably an effect of the warm weather and lack of snow cover in November and early December. In late February another small peak occurred; T(s) had risen from -7.5° to -3°C in all habitats, and the solar light intensity (radiation balance) had increased

(Table 4-3). Peaks of activity were recorded in late March, except on the ridge (Figure 12-2). Obviously several variables are affecting activity, probably temperature, relative humidity and light intensity.

The large increase in numbers each spring was due partially to an increase of early-instar collembolans. It appeared that the rise in T(s) and the increase of radiation under snow may have caused springtails to migrate upwards to the soil surface. Positive correlations between the number of collembolans active and T(s) were found, though the correlation coefficient was larger and significant at the 5% level in 1973-1974 than the non-significant one in 1974-1975 (0.31 versus 0.21 respectively) (Figures 12-3A and B). Using a method described by Walpole (1968), 9% of the variability in numbers was due to T(s) in 1973-1974, and 4% in 1974-1975. Virtually no correlation existed between the number of Collembola active and the temperature difference between T(s) and T(a) (Figure 12-4).

The Collembola species taken in each habitat are presented in Table 12-3. Fifteen species occurred on the ridge, 10 in the woods and 16 in the meadow. *Orchesella ainslei*, *Tomocerus flavescens*, *Isotoma viridis*, and *I. subequealis-fennica* were collected from all habitats, while most sminthurids and *N. muscorum* were taken on the ridge; *I. violacea* in the woods and meadow; and *Entomobrya* spp. in the meadow.

The soil surface samples collected in March, 1975, provided estimates of densities of all families in all habitats (Table 12-4). The entomobryids were most numerous in the woods and next in the meadow; the isotomids in the meadow and then in the woods; and the podurids on the ridge and the meadow. These data imply that the entomobryids are as active during winter as the isotomids, which were 2.5 to 10 times more abundant. In contrast, in 1974-1975 the number of active entomobryids in the winter slightly exceeded that of the isotomids (280:267). Hence, the frequency of activity (Näsmark 1964) of entomobryids appeared to be greater than that of isotomids. The podurids showed little activity in winter.

Ten of the 27 species of Collembola collected at Fort Whyte are known to be holarctic in distribution (Table 12-3). The collection of Neanura muscorum established a first record for Manitoba (Richards, pers. comm.). Two particularly interesting species that probably are holarctic in distribution but were not included in the list because they were previously taken in Europe were: Entomobrya sp. near sibirica-quinquelineata group and Isotoma subequealis-fennica group (Table 12-2). One specimen of this entomobryid was collected in late November, 1973, from the meadow, and constitutes the first occurrence for North America. Isotoma sp. closely resembles subequealis from North America and fennica from Europe; it was the most common winter-active species collected. The only previous record of this species from North America was in Michigan in February; the specimens collected in this study constitute the first record for Canada.

The sminthurids and *Folsomia elongata* MacGillivray were only collected in summer. All other species collected occurred throughout the year.

The following species occurred only once: *Entomobrya* sp. near *sibirica*-*quinquelineata* group in the meadow in November, 1973; *Entomobrya nivalis* L. in the meadow in April, 1974; *Entomobrya gisini* Christiansen in the meadow in January, 1975; *Orchesella cincta* L. var. *vaga* L. in December, 1974; *Isotoma olivacea* and *I. eunotabilis* Folsom from snow samples taken in March, 1975; and *Pseudochorutes* sp. in the meadow in April, 1975.

III. DISCUSSION

The tolerance of -30°C by a collembolan from the Antarctic demonstrated that some species are very cold-resistant (Wallwork 1970). Further evidence for cold-resistance is provided by egg development in other species at 2°C (Hale 1967), locomotory activity at -6°C (Simon 1961), cold stupor at -8°C for several species (Agrell 1941), and the thermal preferendum of +5° to -5°C for *I. saltans* (Wolska 1957). Thus, the results of this study that show activity in the temperature range of -3° to -6°C are not unusual. The correlation coefficient between the number of active collembolans each winter and T(s) was significant the first year and not significant the second, with the latter figure being expected because of the late establishment of permanent snowcover.

Hale (1967), Wallwork (1970), Mason (1972) and Willard (1973) recorded peaks in populations of some species in February and March, which agrees with the data from this study. Since larger specimens are generally found in litter and on the soil surface, and smaller ones in soil crevices (Wallwork 1970), the larger animals occurred more frequently in the trap catches. Agrell (1941) stated that in the overwintering period younger individuals moved into the soil, probably migrating downwards to avoid temperature extremes (Wallwork 1970). It seems clear that in late February and early March as radiation and T(s) increased under the snow, upward migration of these animals occurred, as most of the Collembola caught at those times in southern Manitoba consisted of small, immature specimens.

High densities of collembolans were found in litter and soil in grasslands, but the estimates were determined in summer (Hale 1967, Healey 1967, Wallwork 1970): in winter, maximum densities were in the soil (Kaczmarek 1963). Therefore, the lower densities found in litter and in the top 5cm of soil from Fort Whyte in winter were not unusual. None the less, densities of isotomids and podurids were generally highest in the meadow, while entomobryids had their highest populations in the woods.

Larger specimens of entomobryids are usually found in decaying leaves and litter (Wallwork 1970). In this study

Orchesella ainslei Folsom and *Tomocerus flavescens* were very common in the meadow and slightly less common in the woods; both habitats had much litter. The genus *Tomocerus* is exceptional, because it is univoltine and produces the new generation in spring (Wallwork 1970); mature and nearly mature specimens of *T. flavescens* were taken in winter at Fort Whyte. If more specimens of the *E.* sp. near *sibirica-quinquelineata* group were collected, its status as a new holarctic species would be more clearly defined.

Isotomids were described as the dominant collembolan family in the arctic (Agrell 1941), and some species, such as *I. saltans*, are known as "snow fleas" (Wolska 1957). Three species of *Isotoma*, and *Isotomurus palustris* Muller, that are holarctic in distribution (Table 12-3), were also taken in southern Manitoba. The presence of many winter-active species of the *Isotoma subequealis-fennica* group was most intriguing; no specimens of this species were collected in midsummer. *I. viridis*, a cold-hardy species that is active on snow cover (Agrell 1941, Chapman 1954), was another of the most common winter-active species at Fort Whyte.

Maynard (1951) found the podurid *N. muscorum* associated with rotten logs and decaying leaves of moist soil, while Wallwork (1970) reported its occurrence in deeper soil layers. At Fort Whyte, this species appeared most frequently in the scanty litter on the ridge. *H. armata* is often associated with moist habitats (Maynard 1951); at Fort Whyte it was usually collected in the woods.

Predators of springtails include members of many genera such as Bembidion, Pterostichus (Carabidae), Trichocellus (Staphylinidae), Centromerus, Trochosa (Araneae), Pergamasus, Veigaia (Parasitidae) and Neobisium (Pseudoscorpionida) (Ernsting and Joosse 1974), genera which were represented with Collembola in collections made at Fort Whyte. Thus these predators may feed on the collembolans, which may constitute the base of the food chain under snow, if indeed the predators do feed at low temperatures (see Results, Chapter IX).

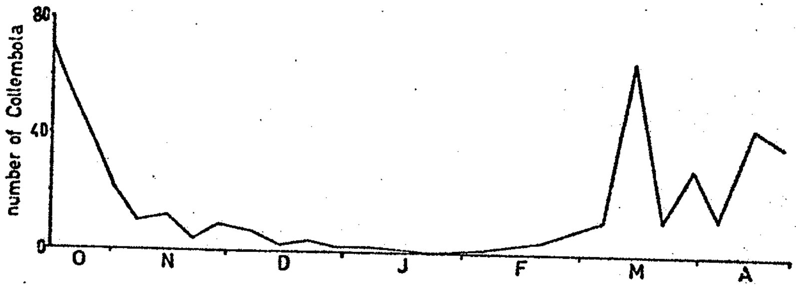
IV. CONCLUSION

In southern Manitoba collembolans were significantly active throughout the year; isotomids and entomobryids were the most numerous of the winter-active species, and sminthurids were the most abundant in summer. Collembolan activity occurred even at -9°C. Isotoma subequealis-fennica group and Entombrya sp. near sibirica-quinquelineata group, E. gisini and O. cincta var. vaga are winter-active species; the first species is the first record for Canada, and the second is the first record for North America. Ten of the 27 species collected in this study have holarctic distributions.

Figure 12-1

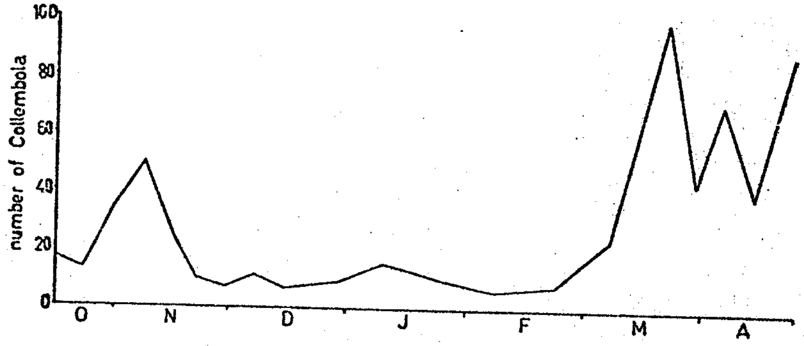
Number of Collembola taken at each habitat in 1973-1974
(A - ridge; B - woods; C - meadow).

A



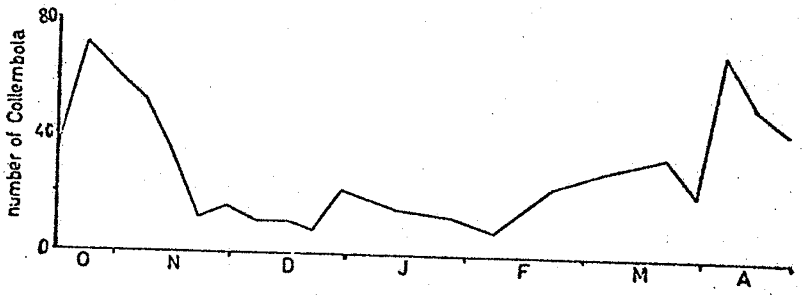
RIDGE 1973-1974

B



WOODS 1973-1974

C



MEADOW 1973-1974

Figure 12-2

Number of Collembola taken at each habitat in 1974-1975
(A - ridge; B - woods; C - meadow).

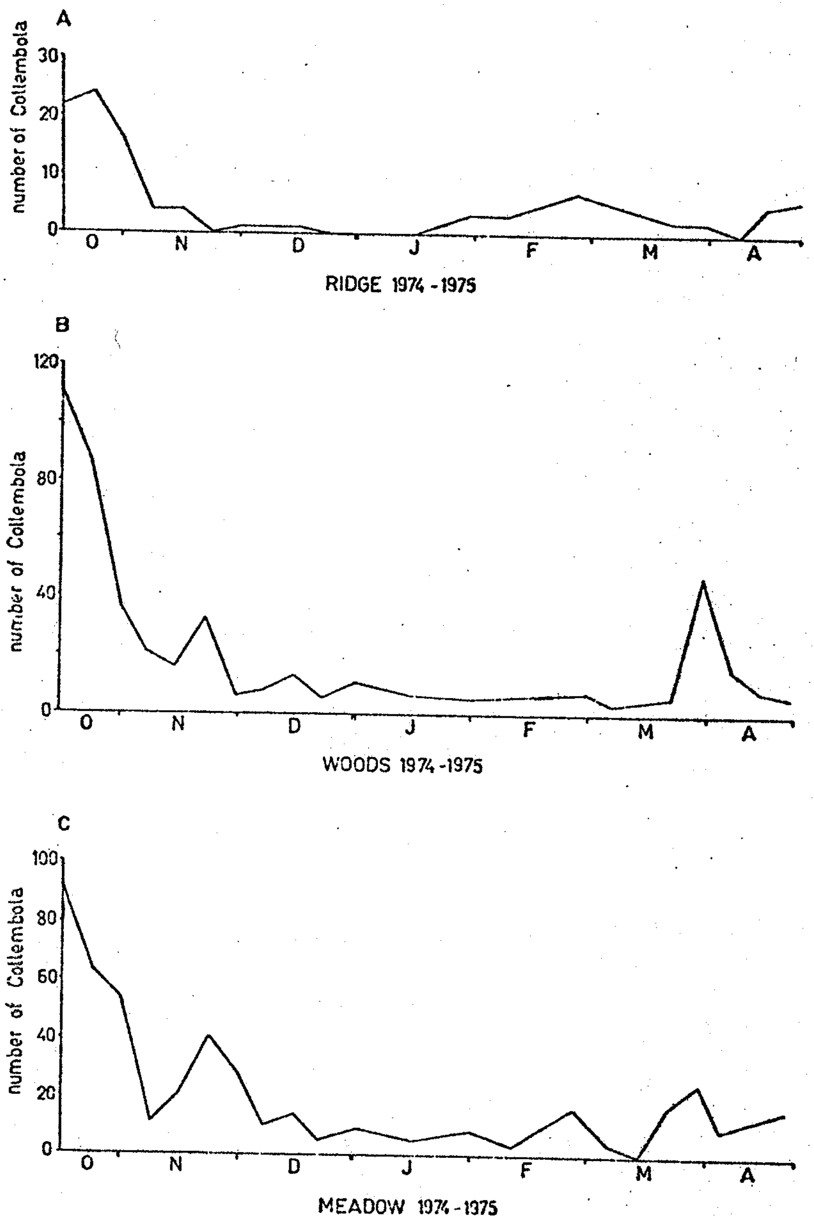
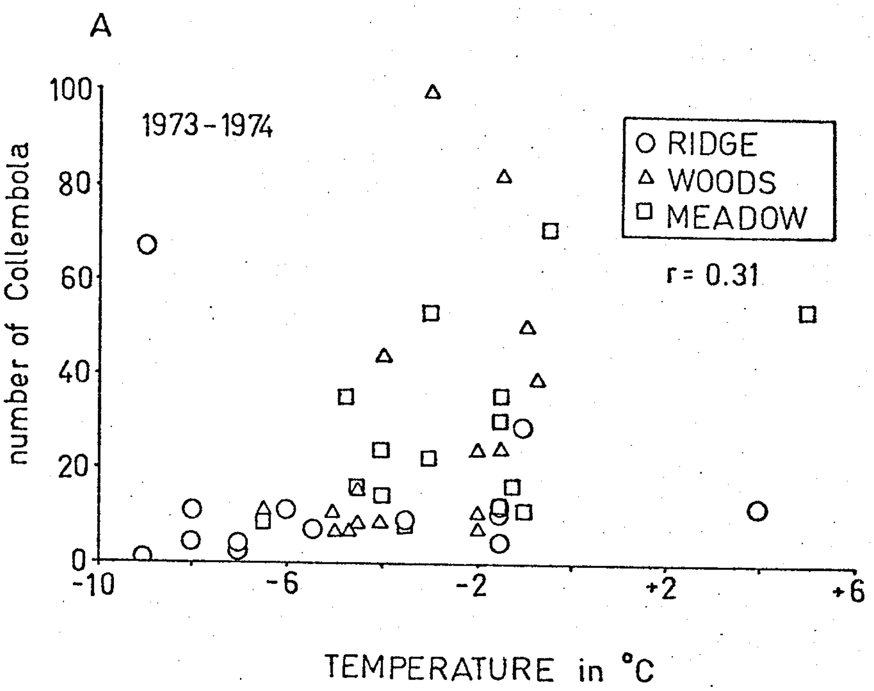

A
number of Collembola
30
20
10
0
O
N
D
J
F
M
A
RIDGE 1974 - 1975
B
number of Collembola
120
80
40
0
O
N
D
J
F
M
A
WOODS 1974 - 1975
C
number of Collembola
100
80
60
40
20
0
O
N
D
J
F
M
A
MEADOW 1974 - 1975

Figure 12-3

Correlations between number of Collembola trapped and T(s) (A - 1973-1974; B - 1974-1975).


A
1973-1974
O RIDGE
Δ WOODS
□ MEADOW
r = 0.31
number of Collembola
0
20
40
60
80
100
-10
-6
-2
+2
+6
TEMPERATURE in °C

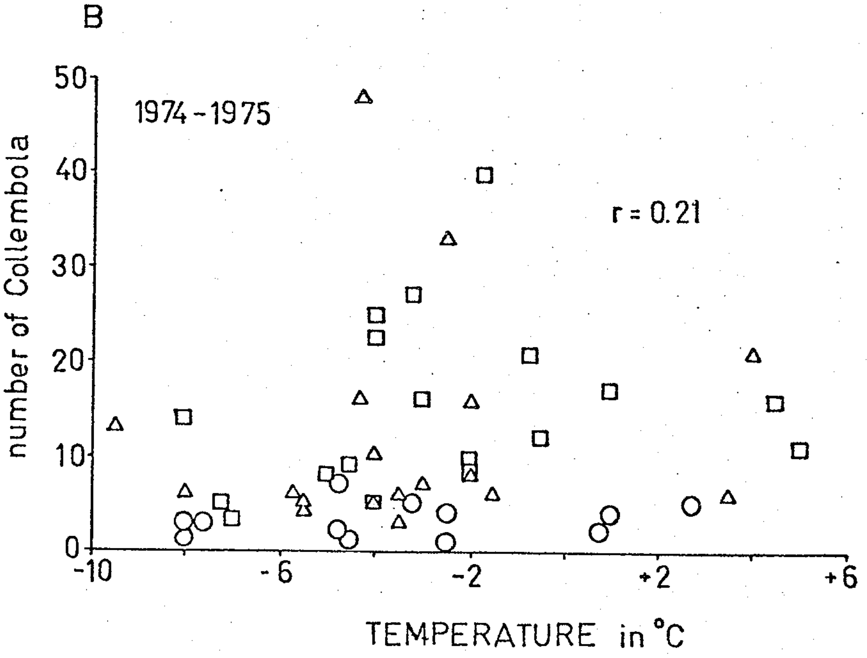

B
1974-1975
r = 0.21
number of Collembola
0
10
20
30
40
50
-10
-6
-2
+2
+6
TEMPERATURE in °C

Figure 12-4

Correlation between number of Collembola trapped and temperature difference between T(s) and T(a) in 1975.

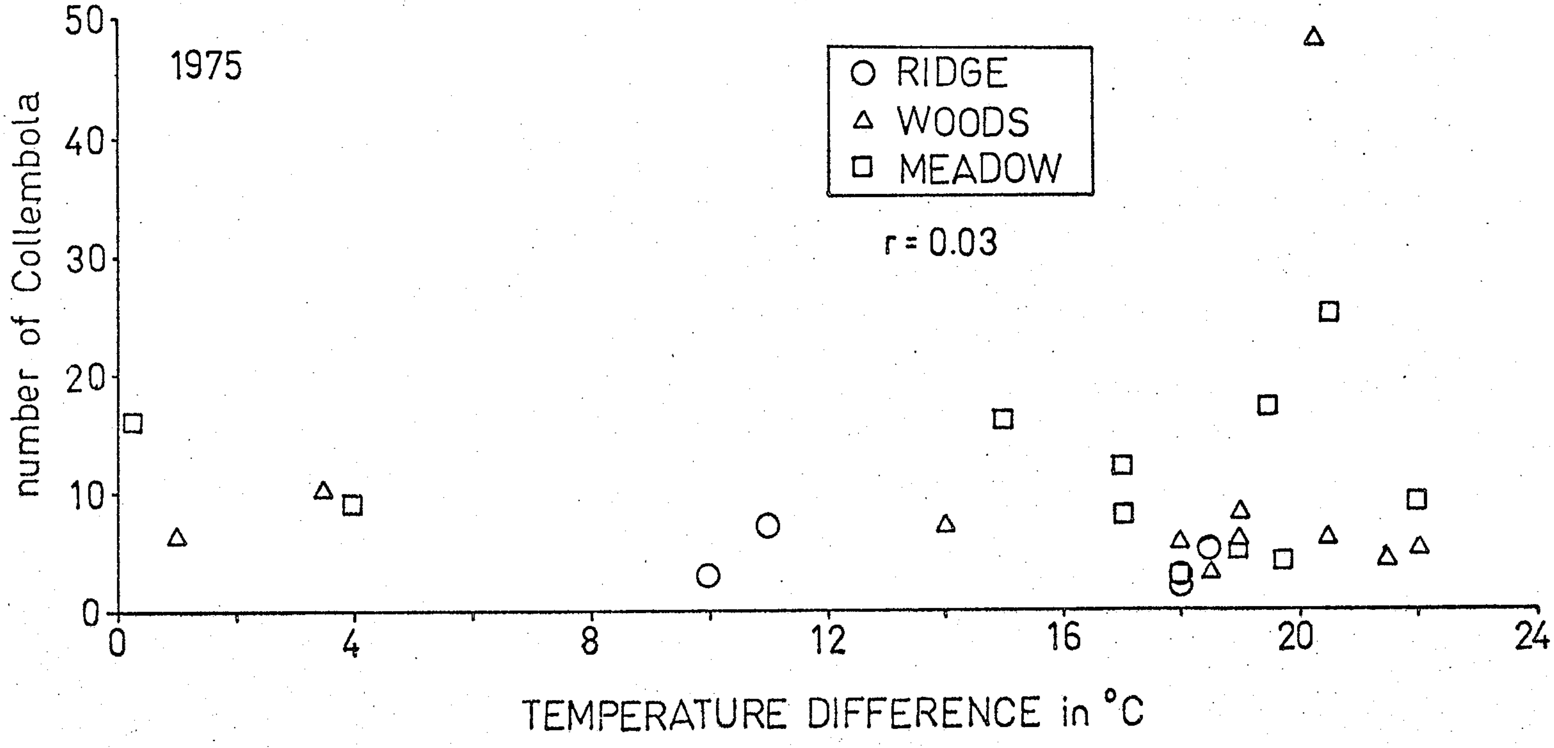

1975
○ RIDGE
△ WOODS
□ MEADOW
r = 0.03
number of Collembola
0
10
20
30
40
50
0
4
8
12
16
20
24
TEMPERATURE DIFFERENCE in °C

Table 12-1

Seasonal Activity of Collembola at Fort Whyte, Manitoba from 1973 to 1975

Date	Autumn	Winter	Spring	Summer
1973-1974	339*	1265	128**	2036
1974-1975	1050	564	1650	4464 approx.

* Trapping only in last three weeks of October.

** One collection only.

Table 12-2

Species of Collembola* Taken at Fort Whyte, Manitoba

S.C. Arthropleona
  Fam. Entomobryidae:

Entomobrya gisini Christiansen
Entomobrya sp.
Entomobrya sp. near *sibirica-quinquelineata* group
Entombrya nivalis L.
Lepidocyrtus cyaneus Tullberg
Orchesella ainslei Folsom
Orchesella cincta L., var. *vaga* L.
Tomocerus flavescens Tullberg

Fam. Isotomidae:

Folsomia elongata MacGillivray
Isotoma eunotabilis Folsom
Isotoma olivacea Tullberg
Isotoma sp. prob. *nigrifrons* Folsom
Isotoma subequealis Folsom-*fennica* Reuter group
Isotoma violacea Tullberg
Isotoma viridis Bourlet
Isotomurus palustris Muller

Fam. Onychiuridae:

Onychiurus sp. poss *subtenius* Folsom

Fam. Poduridae:

Ceratophysella (*Hypogastrura*) *armata* Nicolet
Neanura muscorum Templeton
Pseudachorutes sp.

S.O. Symphypleona
  Fam. Sminthuridae:

Deuterosminthurus repandus Argen
Ptenothrix unicolor Harvey
Sminthurides malmgreni Tullberg
Sminthurinus elegans Fitch
Sminthurinus niger Lubbock
Sminthurinus minutus MacGillivray
Sminthurus medialis Mills

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* Determinations by W. R. Richards, B.R.I., Ottawa, Ontario.

Table 12-3

Species of Collembola Taken in Each Habitat at
Fort Whyte, Manitoba

Ridge (15 species):

- _Lepidocyrtus cyaneus_*
- _Orchesella ainslei_
- _Tomocerus flavescens_
- _Isotoma viridis_*
- _I. subequealis-fennica_
- _Isotomurus palustris_
- _Folsomia elongata_
- _Onychiurus subtenius_
- _Neanura muscorum_*
- _Hypogastrura armata_
- _Deuterosminthurus repandus_
- _Sminthurinus elegans_*
- _S. niger_
- _Sminthurus medialis_*

Woods (10 species):

- _Lepidocyrtus cyaneus_
- _Orchesella ainslei_*
- _Tomocerus flavescens_*
- _Isotoma eunotabilis_
- _I. olivacea_
- _I. subequealis-fennica_*
- _I. violacea_*
- _I. viridis_*
- _Isotomurus palustris_
- _Hypogastrura armata_

Meadow (16 species):

- _Entomobyra_ sp.
- _E._ sp. nr. _sibirica-5-lineata_
- _E. gisini_
- _E. nivalis_
- _Orchesella ainslei_*
- _O. cincta_ var. _vaga_
- _Tomocerus flavescens_*
- _Folsomia elongata_
- _Isotoma olivacea_
- _I. subequealis-fennica_*
- _I. violacea_*
- _I. viridis_*
- _Onychiurus subtenius_
- _Pseudachorutes_ sp.
- _Ptenothrix unicolor_
- _Deuterosminthurus repandus_

* common

Table 12-4

Densities of Collembola per m² Determined from Snow Samples Collected 17 March, 1975

Family	Ridge	Woods	Meadow
Entomobryidae	9.6	83.6	67.7
Isotomidae	109.9	203.1	693.0
Poduridae	57.3	23.9	55.8

Table 12-5

List of Holarctic Collembola Occurring at Fort Whyte, Manitoba

Species	Reference
Entomobryidae:	
Entomobrya nivalis	Agrell 1941, 1963
Lepidocyrtus cyaneus	Agrell 1941
Tomocerus flavescens	Hale 1967
Isotomidae:	
Isotoma violacea	Agrell 1941, 1963
Isotoma viridis	Agrell 1941, 1963
Isotoma olivacea	Agrell 1941, 1963
Isotomurus palustris	Hale 1967
Poduridae:	
Hypogastrura armata	Agrell 1941
Neanura muscorum	Kaczmarek 1963
Sminthuridae:	
Sminthurides malmgreni	Hammer 1954

Chapter XIII

ORDER COLEOPTERA

I. REVIEW OF LITERATURE

Coleoptera are found in many habitats throughout the world and eat a wide variety of foods. Many beetles are of economic importance. The predatory and saprophagous carabids and staphylinids are common on the soil surface (Wallwork 1970). In this chapter, temperature responses, cold-hardiness and population density of coleopterans will be discussed. The major families to be considered are Carabidae and Staphylinidae.

In Sweden, Agrell (1947) tested three species of carabids, *Harpalus pubescens* Mull., *Calathus eratus* Sahlb. and *Pterostichus niger* Schall. from natural habitats for their preferenda in a thermal gradient: the first two species aggregated in the zone from 22° to 25°C while *P. niger* aggregated between 15° and 20°C. He starved some individuals of *H. pubescens* and usually found a rise in their preferenda, probably due to changes of basal metabolic rate and heat production (Agrell 1947).

Heydemann (1956) examined winter activity of staphylinids in agricultural fields for five years, dealing with 26 species. Many of these species were seen only in the cooler months, being cold-resistant and psychrophilic. The temperatures preferred were in the range of 4° to 9°C, with some species active down to -4°C (Heydemann 1956).

In winter Holmquist (1926) collected active larval *Cantharis* sp. near Chicago, while Chapman (1954) found many specimens of two species of staphylinids, *Atheta* spp., actively crawling on snow at 0°C. In Germany and England, cold-resistant cantharids, carabids and staphylinids were active through the year, especially at temperatures near 0°C (Heydemann 1956, Renken 1956, Evans 1967, Mason 1970 and 1972). In fact, cantharid larvae, which abound in winter, are called "Schneewurmen" or "snow worms" (Renken 1956). Wolska (1957) determined that the thermal preferendum for larval *Cantharis* sp. was between 1° and 5°C. Feeding activity by *Pterostichus brevicornis* Kirby on the rotten wood of tree stumps occurred in winter when stump temperatures exceeded -4°C; in warmer months this species had a carnivorous diet (Kaufmann 1971).

Cold-hardiness of coleopterans was investigated by Wolska (1957), Salt (1961), Miller (1969), Baust and Miller (1970, 1972), Kaufmann (1971) and Östbye and Sømme (1972), and since their work was discussed in Chapter II, it will not be discussed further here.

Population density and developmental rate of beetles are also affected by temperature. The "catching facility" of carabids (i.e. numbers caught in pitfall traps) is directly affected by temperature, and differences in density may be related to differences in habitat selection by various age groups (Grüm 1959). The life cycle of *P. brevicornis* in

Alaska requires 14 to 36 months for completion, dependent on the time of oviposition and temperature (Kaufmann 1971). The presence of a thick snow cover, which maintained higher T(s), facilitated activity at T(s) above -4°C (Kaufmann 1971).

The Carabidae have two different types of life histories: (1) those which breed in spring and have overwintering adults, and (2) those which breed in autumn and have overwintering larvae. Genera in the first category include *Abax*, *Agonum*, *Amara*, *Bembidion*, *Calatus*, *Carabus*, *Nebria*, *Notiophilus*, *Pterostichus* and *Quedius* (Larsson 1939, Renken 1956, Williams 1959b, Greenslade 1965, Wallwork 1970, Mason 1972). Seasonal abundance is related to the time of emergence of new adults and weather conditions: warm, moist conditions produce an increase, and hot, dry conditions produce a decrease. Autumn rain and fresh litter give rise to a population increase, while few mobile, hardy adults occur in winter (Wallwork 1970, Mason 1974). Carabids are generally nocturnal predators feeding on annelids, isopods, gastropods, millipedes, mites, spiders, opiliones, small staphylinids and dipterous larvae (Evans 1967, Mason 1972). Scavengers, herbivores and omnivores are usually found in this family (Williams 1959b). Small species feed on smaller arthropods and annelids while larger species feed on larger ones (Wallwork 1970).

Staphylinids were reported as cold-hardy and may constitute one third of the hiemal fauna (Chapman 1954, Heydemann

1956, Renken 1956, Williams 1959b, Greenslade 1965, Wallwork 1970, Mason 1972). Small staphylinids, such as Tachinus, are especially active in the hiemal fauna, and thick snow cover facilitates their activity. In spring as the temperature increases, they are either killed or seek lower temperatures in the soil (Heydemann 1956). Many are coprophagous, others carnivorous (feeding on invertebrates), omnivorous and fungivorous; some feed on economic pests (Mank 1923, Heydemann 1956, Renken 1956, Evans 1967, Mason 1972).

Other families present on the soil surface are cantharids, whose carnivorous larvae are winter-active (Holmquist 1926, Renken 1956, Wolska 1957, Evans 1967), herbivorous elaterids, chrysomelids and silphids (Wallwork 1970). In Germany and England decreasing soil surface temperatures appear to induce surface activity by coleopterans in winter (Heydemann 1956, Williams 1959b).

II. RESULTS

In autumn and early winter Coleoptera were represented mainly by staphylinids and to a lesser extent by carabids. Activity was restricted to early winter almost exclusively, with a slight resumption of activity in late winter as T(s) rose (Table 13-1). More beetles were taken in the woods and the meadow sites than on the ridge. In the first year staphylinids constituted 94% of the autumn, 85% of the winter and 47% of the summer catch of coleoptera; in the second year, 78% of the autumn, 80% of the winter and 51% of the summer catch. A greater proportion of carabids was taken in 1974-1975 (12 to 16%) than in 1973-1974 (5 to 8%). A list of 87 species taken at Fort Whyte is presented in Table 13-2. Common species active at low temperatures were the staphylinids, Aleocharinae (in all habitats), *Atheta* spp. (in the woods), *Falagria dissecta* Er. (in the meadow), *Heterothops fusculus* LeC. (in all habitats), *Hyponygrus* spp. (in the woods and meadow), *Lathrobium* sp. (in the woods), *Philonthus* spp. (in the woods and meadow), *Tachyporus nitudulus* Fab. and *T. rulomus* Blw. (on the ridge and in the meadow), and the carabids, *Bembidion canadianum* Casey, *B. graphicum* Casey (both in the woods), *Pterostichus femoralis* Kirby (in the meadow). Carabids and other coleopterans were rarely active after November.

In the meadow carabids were noted to be abundant in the trap C4, which was on the edge of a small clump of snowberry bushes. In the woods, traps B1 and B2 were in thick brush containing many alders; staphylinids and carabids frequently were collected from these traps. Trap B4 also had a high staphylinid catch while trap B5 had little catch at all. These latter two traps did not appear to be different in microhabitats from those of traps B3 to B8; hence, no explanation of differences can be offered.

In autumn and winter of 1973-1974, the highest numbers of staphylinids were trapped in the meadow and the lowest on the ridge (Figure 13-1). Carabids were taken in all habitats (5%) but were most abundant in the woods and the meadow. Few other families were collected. Activity and diversity of species were greatest in October and in early November, but from mid- to late November both decreased sharply, when T(s) had reached -1.5° to -3.5°C. A few beetles, usually staphylinids, were active in mid- and late winter. In April activity resumed after the T(s) had risen in all habitats, from -4° to -1.5°C in the woods. Thus a temperature of about -1.5°C may be the lower limit for activity.

In 1974-1975 autumnal and early hiemal activity of other families of Coleoptera increased substantially, to form up to 60% of the coleopteran catch on the ridge (Figure 13-2). In the woods 93% of the catch consisted of staphylinids, while in the meadow carabids predominated, forming 65% of the catch. Activity at all habitats declined progressively but continued in the warm days of November and early December. Cessation of activity in mid-December coincided with drops in soil surface temperatures from -2° to -8° and -9.5°C. Some activity, usually of staphylinids, occurred in midwinter in the woods. In late March activity resumed at all sites, coinciding with increases in T(s) from -5.5° to -1.5°C in the woods and from -7.5° to 1°C in the meadow. Again temperatures of approximately -2° to -1.5°C must be the lower limit for coleopteran activity.

In both winters correlation between the number of active beetles and T(s) were not significant (Figure 13-3), as was the correlation between the number of active coleopterans and the temperature difference between T(p) and T(s) (Figure 13-4). Correlations between the number of coleopterans and the number of spiders trapped in 1973-1974 were significant at the 1% level for all habitats, while in 1974-1975 a correlation coefficient significant at the 1% level only occurred in the data from the woods habitat. Hence, variability in beetle activity was not significantly affected by temperature, while variability in beetle and spider activity were closely related; presumably both are affected by the same variables.

The carabid and staphylinid species taken in each habitat are presented in Table 13-3; seven species occurred on the ridge, 25 in the woods and 24 in the meadow. *Tachyporus nitidulus* was collected from all habitats; *Atheta* spp. mostly from the woods; *Agonum* and *Bembidion* spp. from the woods; *Hyponygrus* spp., *Philonthus* and *Pterostichus* spp. mostly from the meadow but occasionally from the woods; *F. dissecta*, *H. fusculus* and *T. chrysomelinus* from the meadow. Lathridiids were confined to the ridge in their distribution.

Laboratory experiments at low temperatures on the carabids *Trichocellus cognatus* and *Bembidion graphicum* collected weekly in November of 1974 showed that all five specimens were active at 3° to 4°C, the temperature at which they were stored (Table 13-4). At -4°C for three minutes, all specimens moved, but more slowly; at -9.5°C for one minute, three *T. cognatus* moved very slowly, but one *B. graphicum* and one *T. cognatus* lost their coordination (motor control). At -12°C for one minute no carabids were active. Thirty-three staphylinids, 32 *Atheta* and one *Lobrathium* sp. were exposed to the same temperatures for the same periods of time and exhibited normal activity at -4°C. However, at -9.5°C, 29 *Atheta* sp. lost motor control and two *Atheta* and one *Lobrathium* remained active. Thus, normal activity is possible at -4°C for specimens collected in November but not at -9.5°C, whereas most animals, excluding *T. cognatus*, *Atheta* and *Lobrathium* spp., are inactive. At -12°C mortality occurs within one or two minutes.

The species of carabids active at low temperatures at Fort Whyte were: *P. femoralis*, *Acupalpus canadensis*, *B. canadianum* and *B. graphicum*. *T. cognatus* also exhibited activity at low temperatures. Staphylinids found active at low temperatures were: Aleocharinae, *Atheta* spp., *F. dissecta*, *H. fusciceps*, *Lathrobium armatum*, *Lobrathium* sp., *Philonthus* sp. and *T. nitidulus*.

Soil surface samples collected in March, 1975, contained four families on the ridge, five in the woods, and three in the meadow (Table 13-5). The density of carabids in the snow samples was greatest on the ridge, in contrast to the small numbers found in the traps; that of chrysomelids was greatest in the woods, again contrasted with virtually none found in the traps; and that of staphylinids was greatest in the meadow. One specimen of the carabid *B. quadrimacula-*

tum, was collected on the ridge; another, A. canadensis, in the woods; and one B. graphicum and one Tachinus sp. collected from the meadow.

Seven of the 87 species of coleopterans are known to have holarctic distributions (Table 13-6).

Generally, almost all species of carabids and staphylinids were collected in October and/or November; only Agonum retractum LeC. was taken solely in summer. Most members of the families represented in the collections were not active on the soil surface in the warmer months. Curculionids, dytiscid larvae, elaterids and leiodids were restricted in their activity to the summer.

III. DISCUSSION

Activity by cantharids and staphylinids was observed at temperatures near 0°C (Holmquist 1926, Chapman 1954, Heydemann 1956, Renken 1956, Wolska 1957, Mason 1972), and these families also exhibited activity in October and November at Fort Whyte when temperatures were about 0°C. The staphylinids were rarely seen in summer, as they apparently moved into moist, soil crevices ; the pattern of activity described by Heydemann (1956) in Germany was also observed in Manitoba, in which maximal activity on the soil surface occurred in October and November. Heydemann (1956) found that the activity of hiemal staphylinids was inhibited at -4°C and lower; in southern Manitoba some members of this family were capable of movement at this temperature in the laboratory, but in the field they were inhibited at -2°C. Carabids exposed to low temperatures in the laboratory were active at -9.5°C for up to one minute. Some beetles become active in decreasing, or at lower, temperatures. *Tachinus* and other small staphylinids were most numerous in the hiemal fauna in Germany (Heydemann 1956); in southern Manitoba *Atheta* spp. and other small species were abundant in October and November. Also the genera of carabids and staphylinids which were winter-active in Europe (Renken 1956) were also winter-active at Fort Whyte.

Generally cantharids, carabids and staphylinids are predaceous (Evans 1967, Mason 1972), and the subnivean environment offers this group a sufficient diet of a few active, and many hibernating, invertebrates as prey, or of rotting vegetation or fungal hyphae. Many carabids and staphylinids are associated with litter, which provides them with moist, cool surroundings and adequate food (Vlijm *et al.* 1968, Mason 1972); in this study *Agonum*, *Atheta* and *Bembidion* spp. were found in the thick litter of the woods, and *Pterostichus* spp., *F. dissecta*, *H. fusculus* and *T. chrysomelinus* were usually associated with the thick litter in the meadow.

Spring-breeding carabids overwinter as adults, while autumn-breeding species overwinter as larvae (Larsson 1939, Greenslade 1965, Murdoch 1967, Wallwork 1970, Mason 1972). Almost all carabids taken in October and November at Fort Whyte were adults, with the exception of a few pterostichini larvae. Thus, it can be concluded that nearly all species taken at Fort Whyte are spring-breeders, the exception being some *Pterostichus* spp. In northeastern Europe, more adults overwinter than in northwestern Europe (Greenslade 1965). The high proportion of overwintering adults in Manitoba is comparable to the situation in northeastern Europe, suggesting that species of carabids that overwinter as adults are selected for in a colder climate.

IV. CONCLUSION

In southern Manitoba coleopteran activity was mainly represented by carabids and staphylinids in October and November, at temperatures down to -2°C. A few individuals were active in winter but rarely below -4°C, though cold room experiments indicated that staphylinids were capable of activity at -4°C and carabids at -9.5°C for short periods. *Atheta* spp., *F. dissecta*, *H. fusculus*, *Hyponygrus* spp., *Philonthus* spp. and *T. nitidulus* represented those staphylinids commonly active, while *B. canadianum*, *B. graphicum*, *P. femoralis* and *T. cognatus* represented the carabids. Seven of the 87 species collected in this study have holarctic distributions.

Figure 13-1

Number of Coleoptera collected in three habitats in 1973-1974 (A - ridge; B - woods; C - meadow).

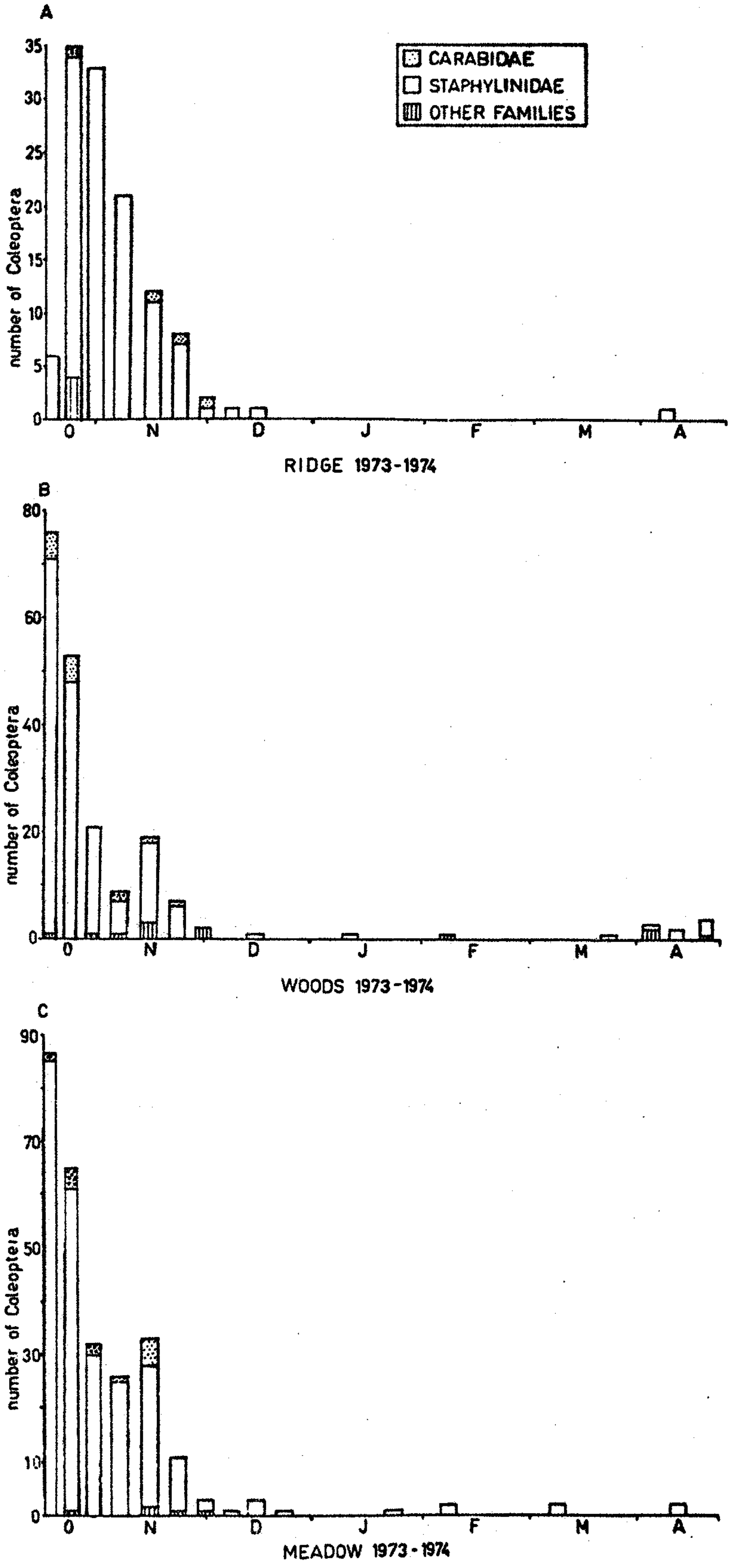

A
CARABIDAE
STAPHYLINIDAE
OTHER FAMILIES
number of Coleoptera
35
30
25
20
15
10
5
0
O
N
D
J
F
M
A
RIDGE 1973-1974
B
number of Coleoptera
80
60
40
20
0
O
N
D
J
F
M
A
WOODS 1973-1974
C
number of Coleoptera
90
70
50
30
10
0
O
N
D
J
F
M
A
MEADOW 1973-1974

Figure 13-2

Number of Coleoptera collected in three habitats in 1974-1975 (A - ridge; B - woods; C - meadow).

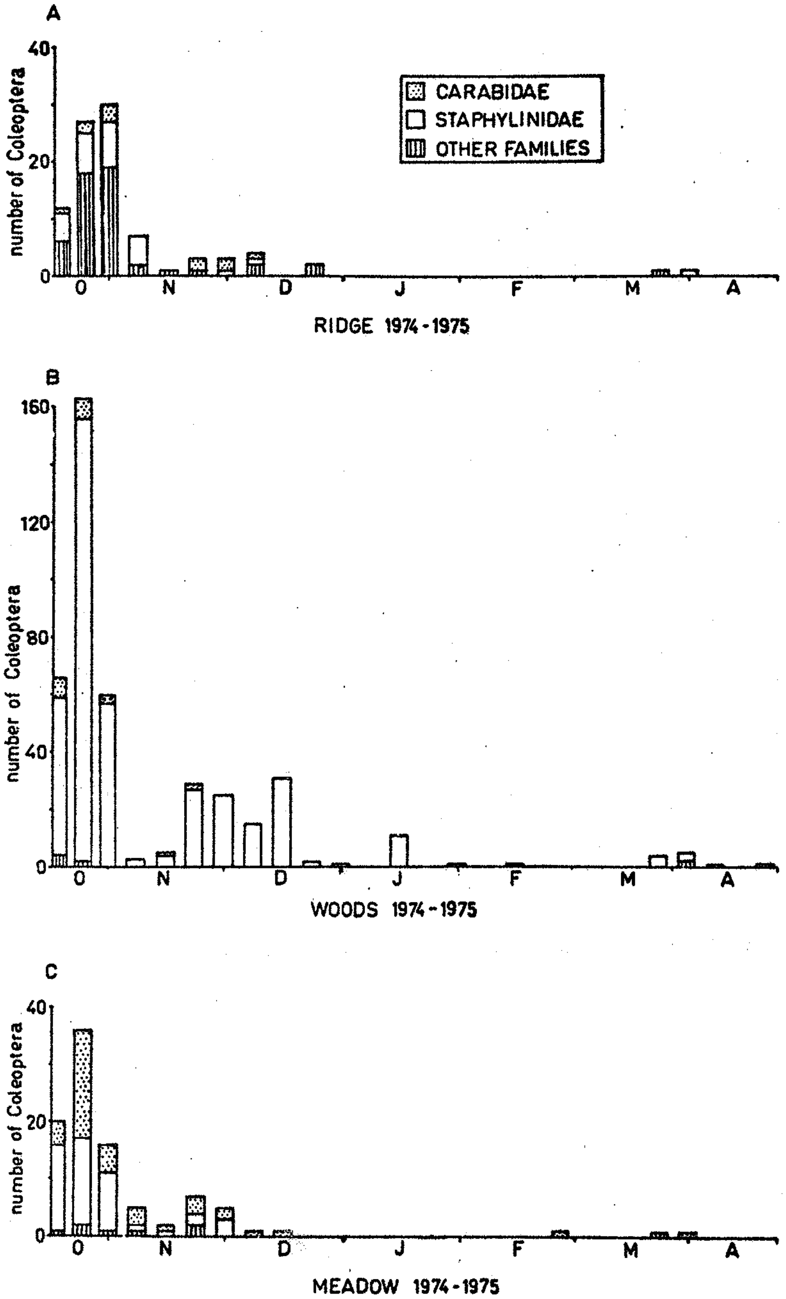
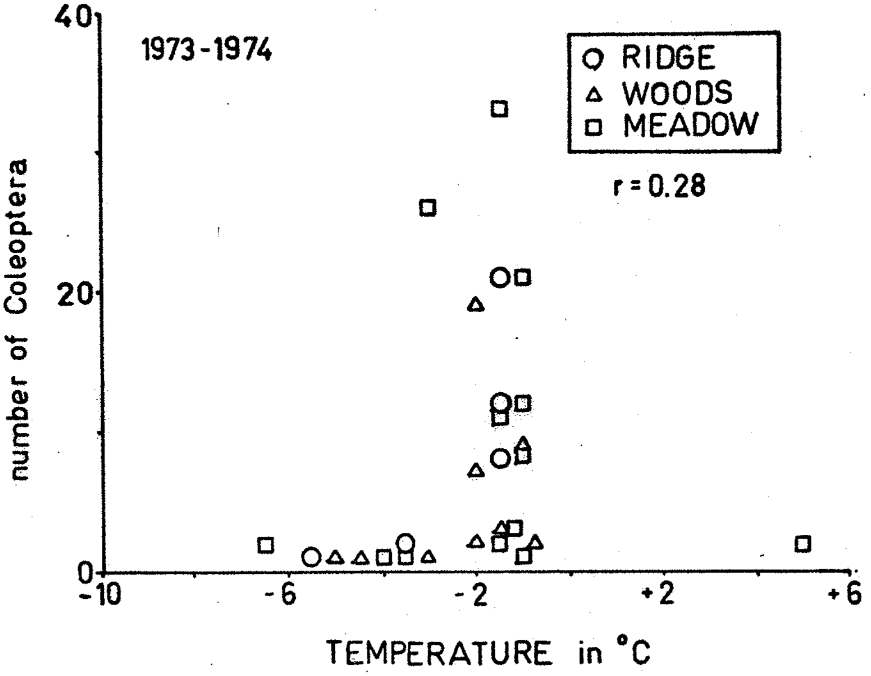

A
40
20
0
number of Coleoptera
▨ CARABIDAE
☐ STAPHYLINIDAE
▥ OTHER FAMILIES
O
N
D
J
F
M
A
RIDGE 1974-1975
B
160
120
80
40
0
number of Coleoptera
O
N
D
J
F
M
A
WOODS 1974-1975
C
40
20
0
number of Coleoptera
O
N
D
J
F
M
A
MEADOW 1974-1975

Figure 13-3

Relationship between the number of Coleoptera collected and T(s) (A - 1973-1974; B - 1974-1975).

A


1973-1974
RIDGE
WOODS
MEADOW
r = 0.28
number of Coleoptera
40
20
0
-10
-6
-2
+2
+6
TEMPERATURE in °C

B

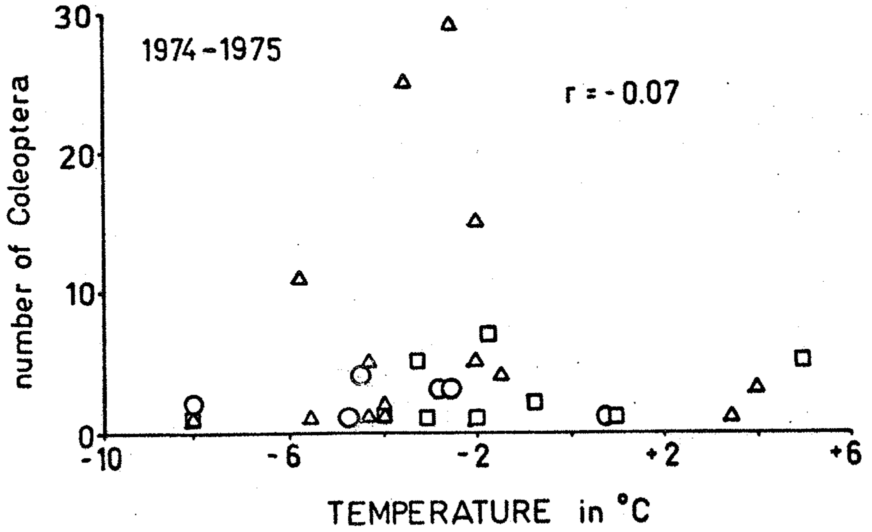

1974-1975
r = -0.07
number of Coleoptera
30
20
10
0
-10
-6
-2
+2
+6
TEMPERATURE in °C

Figure 13-4

Relationship between the number of Coleoptera collected in 1975 and the temperature difference between T(s) and T(a).

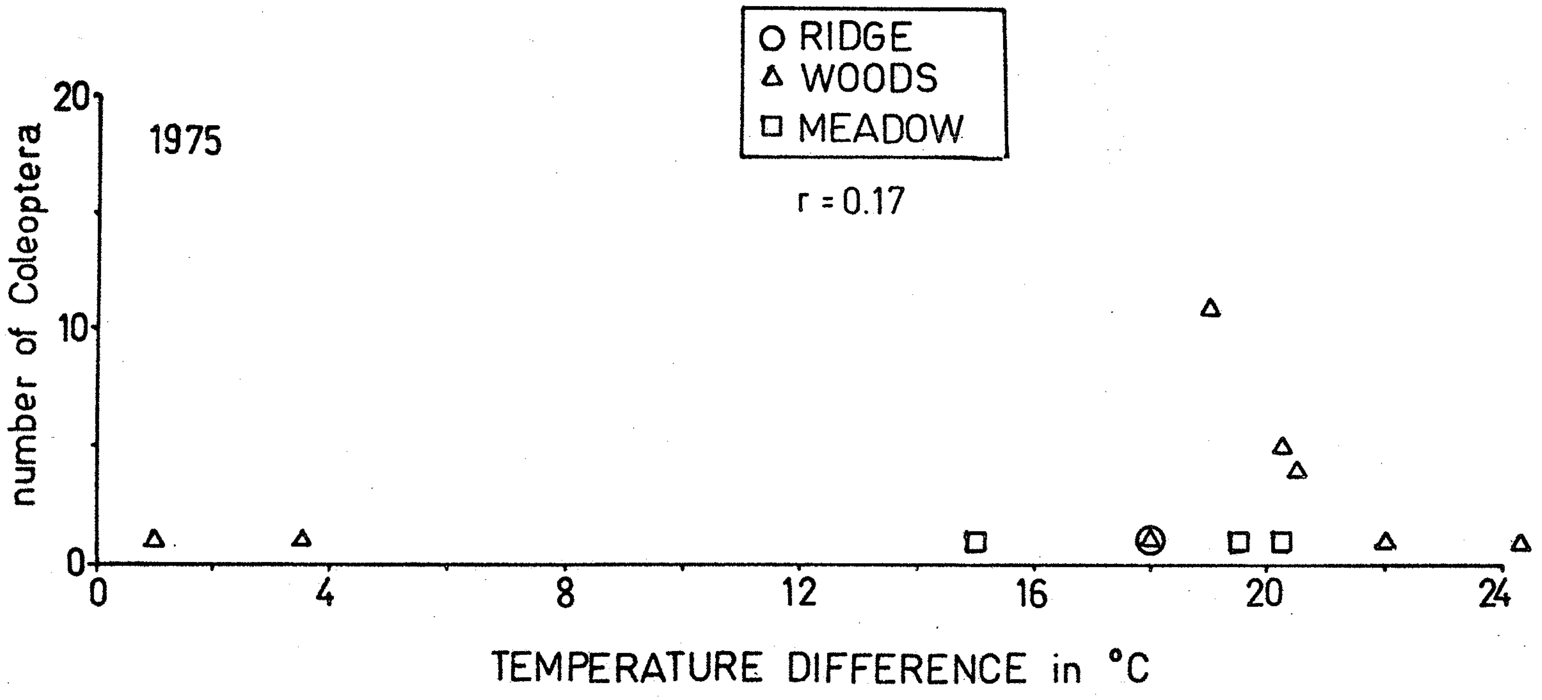

O RIDGE
Δ WOODS
□ MEADOW
r = 0.17
1975
number of Coleoptera
20
10
0
0
4
8
12
16
20
24
TEMPERATURE DIFFERENCE in °C

Table 13-1

Numbers of Coleoptera Active Seasonally at Fort Whyte, Manitoba (1973 to 1975)

Date	Autumn	Winter	Spring	Summer
1973-1974				
Carabids	19*	13	0**	12
Staphylinids	379*	145	3**	25
Others	7*	12	1**	16
1974-1975				
Carabids	70	20	11	7
Staphylinids	417	137	33	56
Others	47	15	23	46

* Trapping occurred only in the last three weeks of October.

** One collection only.

Table 13-2

Species of Coleoptera* Taken at Fort Whyte, Manitoba

Fam. Anthicidae:
  a few individuals

Fam. Cantharidae:
  Cantharis sp.
  Cantharis sp. prob. *rufa* L.

Fam. Carabidae**
  Acupalpus canadensis Casey
  Agonum puncticeps Casey
  Agonum retractum LeC.
  Badister neopulchellus Lindroth
  Bembidion canadianum Casey
  Bembidion graphicum Casey
  Bembidion quadrimaculatum L.
  Bembidion transparens Gebl.
  Bembidion versicolor LeC.
  Bradycellus congener LeC.
  Bradycellus lecontei Csiki
  Calathus ingratus Dejean
  Chlaenius pensylvanicus Say
  Pterostichus caudicalis Dejean
  Pterostichus femoralis Kirby
  Pterostichus luctuosus Dejean
  Pterostichus lucublandus Say
  Pterostichus pensylvanicus LeC
  Pterostichus patrielis Dejean
  Stenolophus comma Fabricius
  Trichocellus cognatus Gyllenhal

Fam. Chrysomelidae:
  Alticinae
  Altica sp.
  Graphops sp. prob. *marcassitus* Cr.

Fam. Cryptophagidae:
  Anchicera sp.

Fam. Curculionidae:
  Sitona cylindricollis Fehr.
  Sitona hispidulus F.

Fam. Dytiscidae:
  Laccophilus sp. (larvae)

Fam. Heteroceridae:
  Dampfius sp. prob. *undatus* Melsh.

Fam. Hydrophilidae:
Enochrus hamiltoni Horn
Orchthebius sp.

Fam. Lathridiidae:
Cartodere constricta Gyll.
Corticaria sp. (larvae)
Melanophthalma sp.

Fam. Leiodidae:
Colenis impunctata LeC.
Leiodes spp. 1 and 2

Fam. Nitidulidae:
Omosita colon L.

Fam. Pselaphidae:
several specimens

Fam. Staphylinidae:
Acidota subcarinata Er.
Aleocharinae
Anotylus suspectus Casey
Atheta sp.
Bolitobius cingulatus Mann.
Bolitobius intrusus Horn
Cyphon variabilis Thunberg
Falagria dissecta Er.
Heterothops fusculus LeConte
Hyponygrus sp. 1
Hyponygrus sp. 2
Hyponygrus fusciceps LeC.
Hyponygrus hamatus Say
Lathrobium armatum Say
Lathrobium niger LeC.
Lathrobium nigrum LeC.
Lobrathium sp.
Mycetoporus sp.
Olophrum consimile Gyll.
Orus (Pycnorus) dentiger LeC.
Oxytelus sp.
Philonthus sp. 1 to 4
Philonthus n. sp.
Philonthus fulvipes Fab.
Philonthus instabilis Horn
Philonthus occidentalis Horn
Philonthus schwarzi Horn
Philonthus varians Paykyll
Quedius caseyi caseyi Scheerp.
Quedius sublimbatius Makl.
Silusa sp.
Stenus sp.
Tachinus scrutator Gemin. and Harold
Tachyporus sp. 1 to 3

Fam. Staphylinidae (con't.):
Tachyporus n. sp.
Tachyporus acaudus Say
Tachyporus chrysomelinus L.
Tachyporus jocusus Say
Tachyporus rulomus Blw.
Tachyporus tamacus Blw.

Fam. Tenebrionidae:
several specimens

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* Determinations by: E. C. Becker, D. E. Bright, J. M. Campbell and A. Smetana, B.R.I., Ottawa, Ontario.

** Determinations by: G. E. Ball, Department of Entomology, University of Alberta, Edmonton, Alberta.

Table 13-3

Carabid and Staphylinid Species in Each Habitat at Fort Whyte, Manitoba

Ridge (7 species):

- *Bembidion quadrimaculatum*
- *B. versicolor*
- *Chlaenius pensylvanicus*
- *Trichocellus cognatus*
- Aleocharinae
- *Philonthus varians*
- *Tachyporus nitudulus**

Woods (25 species):

- *Acupalpus canadensis*
- *Agonum puncticeps*
- *A. retractum*
- *Badister neopulchellus*
- *Bembidion canadianum*
- *B. graphicum*
- *B. quadrimaculatum*
- *B. transparens*
- *B. versicolor*
- *Calathus ingratus*
- *Pterostichus caudicalis*
- *P. luctuosus*
- *P. pensylvanicus*
- *Stenolophus comma*
- *Atheta* sp.*
- *Bolitobius intrusus*
- *Cyphon variabilis*
- *Heterothops fusculus*
- *Hyponygrus* spp.*
- *Philonthus instabilis*
- *P. occidentalis*
- *P. schwarzi*
- *Quedius caseyi caseyi*
- *Tachyporus* spp.*
- *T. nitidulus*

Meadow (24 species):

- *Bembidion canadianum*
- *B. graphicum*
- *Bradycellus congener*
- *B. lecontei*
- *Pterostichus caudicalis*
- *P. femoralis*
- *P. lucublandus*
- *P. pensylvanicus**
- *P. patuelis*
- *Trichocellus cognatus**
- Aleocharinae
- *Falagria dissecta**
- *Atheta* sp.*
- *Heterothops fusculus**
- *Hyponygrus* spp.*
- *Mycetoporus* sp.
- *Orus dentiger*
- *Philonthus instabilis*
- *P. occidentalis*
- *P. varians*
- *Silusa* sp.
- *Tachinsu scrutator*
- *Tachyporus chrysomelinus*
- *T. nitidulus*

* common

Table 13-4

Coleoptera Used in Cold Room Experiments in November, 1974;
(A) Carabids: 10 trials, 5 individuals; and
(B) Staphylinids: 35 trials, 33 individuals

Temperature in °C	Exposure Time	Number of Beetles Used	Number of Beetles With Normal Activity	Number of Beetles With Loss of Motor Control
3° - 4°C	5 minutes	(A) 5	5	0
		(B) 33	33	0
-4°C	3 minutes	(A) 5	5	0
		(B) 33	32	1
-9.5°C	1 minute	(A) 5	3	2
		(B) 32	3	29
-12°C	1 minute	(A) 2	0	2
		(B) 2	0	2

Table 13-5

Densities of Coleopterans per m^2 Determined from Snow Samples Collected 17 March, 1975

Family	Ridge	Woods	Meadow
Carabidae	9.6	8.0	4.0
Chrysomelidae	38.2	75.7	---
Elateridae	---	4.0	---
Lathridiidae	14.3	---	---
Staphylinidae	---	15.9	47.8
Others	14.3	8.0	4.0

Table 13-6

Coleoptera with Holarctic Distributions that were Taken at Fort Whyte, Manitoba (1973 to 1975)

Species	Reference
Carabidae:	
Bembidion quadrimaculatum	Lindroth 1957
Bembidion transparens	Lindroth 1957
Trichocellus cognatus	Lindroth 1957
Curculionidae:	
Sitona cylindricollis	Lindroth 1957
Sitona hispidulus	Lindroth 1957
Staphylinidae:	
Olophrum consimile	Kauri *et al*. 1974?
Tachyporus chrysomelinus	Mason 1972

Chapter XIV

ORDERS DIPTERA AND HYMENOPTERA

I. REVIEW OF LITERATURE

A. Diptera

Diptera are abundant in many habitats. Some members of this order are associated with snow in Europe and North America, especially the tipulid genus *Chionea*, while culicids, chironomids and simulids are numerous in arctic regions. Activity at low temperatures will be considered in this chapter.

Classical studies on winter-active dipterans were done on *Chionea* spp. (Tipulidae) and *Trichocera* spp. (Trichoceridae) (Wojtusiak 1951, Chapman 1954, Dahl 1969, Hågvar 1971). Other winter-active families are Anthomyiidae, Chironomidae, Mycetophilidae, Phoridae, Sciaridae and Sphaeroceridae (Holmquist 1926, Renken 1956, Hågvar and Östbye 19733).

In western Montana Chapman (1954) noted four species of *Chionea* active on the snow surface at about 0°C. This genus is associated with forested, windless areas , was active down to -5.6°C, and exhibited no movement at -7.2°C. In similar conditions in Norway, *Chionea araneoides* Dalm. was found moving continuously on the snow surface in the temperature range of 0° to -6°C. Its supercooling point was determined to be -7.5°C, and this species obviously must be acclimated to be active down to -6°C (Hågvar 1971). In Poland the thermal preferenda for two species of Chionea was between -1° and -5.5°C; these species were collected on snow at temperatures near 0°C on windless days from October to March (Wojtusiak 1951).

Four species of chironomids collected from the snow surface from December to April in southern Norway exhibited thermal preferenda in the ranges of 0° to -2°C. Diamesa permacer Walk. was active at -4.5°C (Hågvar and Östbye 1973). Holmquist (1926) collected Mycetophila punctata Meig. in winter from the subnivean space.

Renken (1956) collected cold-resistant anthomyiids, phorids, sciarids and sphaerocerids in winter. In Sweden four species of trichocerids exhibited low critical temperatures between -1.5° to -5°C. Larvae of Trichocera saltator Harr. were still mobile at -3°C, and those of another species at -6°C; these larvae tolerated partial freezing while adults did not. None the less, low temperatures were associated with low levels of activity (Dahl 1969). In addition, the cecidomyid, Anocha sp. poss. new, has been collected from the snow surface in the boreal regions of Manitoba (Pruitt, pers. comm.).

B. Hymenoptera

Winter activity of hymenopterans was noted by Renken (1956) at temperatures near 0°C, especially of diapriids, formicids (ants) and the braconid, Blacus ruficornis; he found some ceraphronids in the soil and ichneumonids under bark also. Near Chicago, U.S.A., Holmquist (1926) noted ichneumonids active in early November, and ants and larval ichneumonids on the soil surface later in the winter.

Mellanby (1940) examined low temperature activity in the ant, Formica rufa, which was active at 6°C or higher and showed cold stupor at a temperature of 1°C in Finnish Lapland. Cold-hardiness in Bracon cephi, Cephus cinctus and ants was discussed previously in Chapter II (Salt 1950, 1959; Ohymama and Asahina 1972).

Predation by wasps in the families Chalcididae, Ichneumonidae, Scelionidae and Sphecidae occurs on spiders or on egg sacs of spiders (Kessler 1971, Norton 1973), while parasitism by species in the families Ichneumonidae and Braconidae occurs on a wide variety of hosts, including cyclorrhaphous dipterans and aphids (Muesebeck et al. 1951, Matthews 1974). In addition ceraphronids and diapriids parasitize coniopterygians and dipterans; mymarids are internal parasites in eggs of homopterans and of coleopterans; and scelionids develop in such hosts as lepidopterans, hemipterans, orthopterans, dipterans, spiders, coleopterans and neuopterans (Muesebeck et al. 1951). Ants usually prey upon homopterans and dipterans, especially larval cecidomyids, dolichopodids and sciarids (Petal et al. 1971).

II. RESULTS

A. Diptera

The numbers and diversity of species of flies were greatest in October, but both steadily decreased throughout November (Table 14-1). In winter dipterans displayed virtually no activity, but in late April and May activity was resumed. The most representative species of this order were: Suilla longipennis Loew., Mycetophila spp., Megaselia spp., Leptocera spp. and Bradysia spp. All species taken at Fort Whyte are represented in Table 14-2.

In October, 1973, numbers of dipterans were greatest in the woods and least on the ridge (57 vs. 14 individuals on 17 October, 1973). Activity ceased on the ridge and in the meadow by the end of November, while some activity occurred until late December in the woods. In October, the dipteran catch on the ridge was 38% mycetophilids, in the woods, 49% anthomyiids, and in the meadow, 22% phorids. The one specimen taken in the woods in the spring of 1974 was a phorid; the specimens taken in the summer represented families not collected in winter. The individuals taken from the subnivean space were collected at T(s) of -1.5°C on the ridge, -4°C in the woods and -1.25°C in the meadow.

In 1974 - 1975, a similar pattern was seen, though early winter activity was greater than the previous year in all habitats. The dipteran catch in autumn was 19% phorids; the winter catch, 26% mycetophilids; and the spring catch, 36%

phorids. Most of the summer catch was from families that did not form the major component of the winter catch. In winter, activity was recorded at T(s) of -3.2°C on the ridge, -3.5°C in the woods and -3°C in the meadow. Hence, -3.5°C appears to be a lower limit for activity.

No correlations between dipteran activity and T(s) were possible since recordings of temperature were not available until after the cessation of activity of most of this order. Correlations between dipteran and hymenopteran activity were calculated for each year. In 1973 - 1974 the correlation coefficient was not significant ($P > 0.05$), while in 1974 - 1975, it was significant at the 1% level ($r = 0.64$).

One mycetophilid, _Mycetophila fungorum_ Laffoon, was tested in cold room experiments in November, 1974. The specimen was active down to -9.5°C, but lost its motor control at -12°C.

Snow samples collected in March, 1975, contained mostly larval stages of Diptera: none were taken from the ridge, 12 animals/m^2 were estimated in the woods, and 143/m^2 in the meadow. Hence, the meadow was most densely populated with dipterans. One genus from the meadow was identified as _Corynoptera_ sp.

Of the 34 species collected, eight were taken only in summer which were in the families Cecidomyidae, Chironomidae and Dolichopodidae. Most of the other species were taken in October, of which a few were active into the winter period.

B. Hymenoptera

This order followed the same general pattern of activity as the dipterans. The majority of wasps trapped were small in size and were usually species known to be parasitic on the families of dipterans and coleopterans that were also collected. Generally, hymenopterans were more restricted in activity than dipterans. The numbers trapped each year are recorded in Table 14-1. Probably the high numbers recorded in 1974 - 1975 are a reflection of the warm autumnal period and of the readily available prey. The species taken are tabulated in Table 14-3. The main representatives of the order were: *Ceraphron* spp., *Dendrocerus* spp., *Belyta* spp., *Scelio* spp. and *Trimorus* spp.

In 1973-1974 little activity occurred in October and November except on the ridge, where 57% of the hymenopteran catch was braconids. A sudden drop in activity occurred in late October, which continued until activity eventually ceased at the end of November. Three individuals were taken in winter, at a T(s) of -1.5°C. In spring almost no activity was exhibited, whereas in summer 81% of the soil surface activity was due to ants.

In 1974-1975 the same pattern was seen again, except for high numbers on the ridge. In autumn the ridge had 152 active individuals, and the woods and meadow both had 48, 19% of which were ants. In winter fifteen specimens were collected from the ridge and seven from the woods, when T(s) ranged from -2.5° to -5.5°C. In the spring of 1975 ants comprised 63% of the total hymenopteran catch, the highest proportion of which came from the meadow. In summer, 44% of the catch was ants.

Soil surface samples taken in March, 1975, revealed no hymenopterans on the ridge (hence, they must be active in early winter and overwinter elsewhere); 24 animals/m² were found in the woods, including some scelionids, Idris sp., and a ceraphronid, Aphanogmus sp. B.; and 20 animals/m² in the meadow including Idris sp. and the scelionid, Baeus sp.

A total of forty-four species were taken at Fort Whyte, seven of which were taken only in summer (from the braconids, cynipids, eucoilids and scelionids), and two of which were collected in winter only. The latter two species, an ichneumonid, Diadromes pentellae Ashm., and a diapriid, Zygota sp., could be labelled winter-active. All other species were taken mostly in autumn, except for the ants. Determinations past the generic level were often not possible, since many groups have not been studied intensively (Ivanochko, pers. comm.).

Myrmica lobicornis has a holarctic distribution (Lindroth 1957).

III. DISCUSSION

A. Diptera

The dipterans, Chionea and Trichocera spp., were active at low temperatures (Wojtusiak 1951, Chapman 1954, Dahl

1969, Hågvar 1971), as were cold-resistant anthomyiids, mycetophilids, phorids, sciarids and sphaerocerids (Holmquist 1926, Renken 1956). These families were active in autumn at Fort Whyte. Chapman (1954) recorded activity for _Chionea_ sp. at -5.6°C, and Hågvar (1971) at -6°C, while in southern Manitoba _Mycetophila fungorum_ was still active at -9.5°C.

The large numbers and great species diversity in autumn and subsequent declines in both into November imply migration from other layers to the soil surface in autumn, in search of overwintering quarters.

B. _Hymenoptera_

Renken (1956) recorded activity of braconids, diapriids and ants at low temperatures (i.e. near 0°C), while Holmquist (1926) found active ichneumonids in November. These groups were also active in October and November at Fort Whyte.

Predation by wasps occurs on many species of hosts (Muesebeck _et al_. 1951, Kessler 1971, Norton 1973, Matthews 1974), most of which were present on the soil surface in October and November at Fort Whyte. Hence, it may be assumed that the wasps were in search of hosts. The correlations between dipteran and hymenopteran activity were significant on the ridge in 1973-1974 ($P < 0.01$) and at all habitats in 1974-1975 ($P < 0.01$), indicating that predation may be partially responsible for the relationship. More than 40% of the activity of hymenopterans is related to that of dipterans in 1973-1974 (r = 0.66), (Walpole 1968), and since many of the wasps are parasitic on families of the Diptera that were collected, parasitism is a possible explanation for the high degree of correlation.

Ants are numerous in fields and are reported to reduce the numbers of invertebrates in summer (Petal _et_ _al_. 1971). In southern Manitoba ants represented 81% of the hymenopteran summer catch in 1974 and 44% in 1975. The greatest summer activity of this family occurred on the ridge and in the meadow.

IV. CONCLUSION

Most activity of dipterans on the soil surface was seen in October and November. Virtually no activity occurred in winter but there was a resumption of activity in late spring. Hymenopterans were especially active in summer, and their activity in autumn and early winter was closely correlated with that of dipterans. Both orders were restricted in movement at low temperatures of -3.5°C and -5.5°C respectively, with the exception of the activity shown by _Mycetophila_ _fungorum_ at -9.5°C. _Suilla_ _longipennis_, _Mycetophila_ spp., _Megaselia_ spp., _Bradysia_ spp. and _Leptocera_ spp. represented the majority of dipterans active at low temperatures, while _Ceraphron_ spp., _Dendrocerus_ spp., _Belyta_ spp., _Scelio_ and _Trimorus_ spp. represented the greatest proportion of the hymenopterans.

Myrmica lobicornis has a holarctic distribution.

Table 14-1

Numbers of Diptera and Hymenoptera Active Seasonally at Fort Whyte, Manitoba

Date	Autumn	Winter	Spring	Summer
1973 - 1974				
Diptera	138*	14	1**	83
Hymeno.	38*	4	1**	288
1974 - 1975				
Diptera	113	18	31	122
Hymeno.	248	23	76	338

* Collections only in last three weeks of October.

** One collection only.

Table 14-2

Species of Diptera* Taken at Fort Whyte, Manitoba from 1973 to 1975

Fam. Anthomyiidae

Suilla longipennis Loew.

Fam. Calliphoridae

a few larvae

Fam. Cecidomyiidae

Anaerte sp.(?)
Rhabdophaga sp.

Fam. Chloropidae

Conioscinella sp.
Eribolus nanius Zett.
Oscinella incerta Becker
O. umbrosa Loew.
Thaumatomyia sp.

Fam. Chironomidae

Chironomus sp.
Coryneura sp.
Harnischia grp.
Monopelopia sp. poss. *boliekae* Beck and Beck
Paraphaenocladius sp.
Pseudosmittia sp.(?)

Fam. Dolichopodidae

Micromorphus sp.

Fam. Dryomyzidae

Dryomyza sp.

Fam. Ephydridae

Coenia curvicauda Mg.

Fam. Mycetophilidae

Exechia sp.
Mycetophila fisherae Laffoon
M. fungorum Deg.
Orfelia sp.

Fam. Phoridae

Diplonerva funebris Mg.
Megaselia (*Aphiochaeta*) sp.
Puliciphora suavis Borg.

Fam. Psychodidae

Psychoda sp.

Fam. Sciaridae

Bradysia sp.
Corynoptera(?) sp.
Scatopsciara sp.

Fam. Sphaeroceridae

Leptocera n. sp.
Leptocera (*Pterogramma* or *Rachispoda*) *limosa* Villen-Duda
Sphaerocera micropyga Duda

Fam. Stratiomyidae

Neophacygaster sp.

Fam. Trichoceridae

Trichocera sp.

---

* Determinations by B. Cooper, L. Forster, J. F. McAlpine, D. R. Oliver, B. V. Peterson, H. J. Teskey and J. R. Vockerboth, B.R.I., Ottawa, Ontario.

Table 14-3

Species of Hymenoptera* Taken at Fort Whyte, Manitoba from 1973 to 1975

Fam. Braconidae

- *Aphidius* sp.
- *Blacus* sp.
- *Orgilus consuetus* Mues.
- *Synaldis* sp.

Fam. Ceraphronidae

- *Aphanogmus* sp. A and B
- *Ceraphron* sp.A
- *Conostigmus* sp.
- *Dendrocerus* sp. A

Fam. Cynipidae

- *Xystoteras* sp.

Fam. Diapriidae

- *Basalys* sp.
- *Belyta* sp. A and B
- *Opazcn* sp.
- *Psilus* sp.
- *Trichopria* sp.
- *Zygota* sp.

Fam. Eucoilidae

- *Pilinothrix* sp.

Fam. Eulophidae

- *Tetrastichus oecanthivorus compar* Gahan

Fam. Formicidae**

- *Campanotus noveboracensis* Fitch
- *Lasius pallitarsus (sitkaensis)* Provencher
- *Leptothorax muscorum* Hylander
- *Myrmica lobicornis fracticornis* Emery
- *Tapinoma sessile* Say

Fam. Ichneumonidae

- *Atractodes* sp.
- *Diadromas pentellae* Ashm.
- *Helictes* sp.
- *Ichneumon* sp.
- *Megastylus* sp.
- *Melanichneumon* sp.
- *Orthocentrus* sp.
- *Phygadeuon* sp.
- *Stenomarcus* sp.

Fam. Mymaridae

- *Gonatocerus* sp.

Fam. Scelionidae

- *Baeus* sp.
- *Gryon misellus* Haliday
- *G. myrmecophilus* Ashmead
- *Holoteleia bicolor* Harrington
- *Idris* sp.
- *Scelio singularis* Muesebeck
- *S. striativentris* Kieffer
- *Trimorus* sp. A and B

Fam. Sphecidae

- *Aclista* sp.

---

* Determinations by: H. E. Bisdee, M. Ivanochko, L. Masner, W. R. M. Mason and C. M. Yoshimoto, B.R.I., Ottawa, Ontario.

** Determinations by: G. L. Ayre, Canada Agriculture Research Station, 195 Dafoe Road, Winnipeg, Manitoba R3T-2M9.

Chapter XV

OTHER INSECT ORDERS

I. REVIEW OF LITERATURE

The orders Hemiptera, Homoptera, Lepidoptera, Neuorptera, Orthoptera and Thysanoptera will be considered. In the Chicago area Holmquist (1926) found many insects active in early November, including nabids, arctiids, acridids and gryllids. He also found cicadellids normally active in winter, and larval Apantesis virgo L. which were capable of movement in winter.

Chapman (1954) collected active female geometrid moths, Operophtera sp., from the snow surface, and Renken (1956) recorded nabids as winter-active. The latter author stated that phytophagous species were rarely winter-active; most of the species that he found in winter were predatory. Glycerol was found in the cold-hardy slug caterpillar, Monema flavescens (Asahina 1966).

II. RESULTS

The number of representatives of each order found active seasonally are presented in Table 15-1. Data on Neuroptera, Orthoptera and Thysanoptera were sparse and therefore were combined. Most activity in these orders was shown by orthopterans. Generally, the homopterans were active on the soil surface in the greatest numbers in all seasons; cicadellid nymphs were most numerous in winter, and other orders were restricted to the summer and autumn seasons. Forty-two species were collected in these orders of minor importance (Table 15-2). The ridge site usually had the greatest numbers of all orders, except for homopterans which were most active in the woods in winter. Orthopterans were abundant on the ridge in October.

The pattern of a sharp decline in numbers in late autumn, almost no activity in winter, and resumption of activity in late spring and summer was general for these orders. The trap catches in both years were similar, except for an increase in catch in the autumn of 1974 - 1975; hence, the results of both years will be discussed concurrently.

Nabis alternatus Parsh. was collected in October and N. roseipennis Reuter in November when the T(s) was about -5°C. The tingid, Corythucha sp. prob. coryli, was taken in October and November. Aphids, e.g. Amphorophora sp. poss., were collected in October, December, January and February at T(s) of -3.5°, -2°, -4° and -5°C respectively. Cicadellid nymphs were taken occasionally throughout the winter, especially in the woods, at T(s) in the range of -1.5° to -7°C. A lepidopterous larva was collected from the meadow in early April, 1974, at T(s) of -0.5°C. In late November, 1974, a thysanopteran was taken in the meadow when the soil surface temperature had fallen to -7.2°C from

-4.5°C.

Experiments at low temperatures in the laboratory on a lygaeid, *Eremocoris ferus* Say, collected in late November, 1974, showed this hemipteran to be active at -4°C but was unable to maintain coordination after one minute at -9.5°C and died.

Winter activity in these orders was exhibited mostly by cicadellid nymphs, e.g. *Aceratagallia* sp., taken in January, and occasionally by aphids (e.g. *Amphorophora* sp.), nabids (*Nabis* spp.) and lygaeids (*E. ferus*).

Soil surface samples collected in March, 1975, established that many thysanopterans were present under snow but were inactive. On the ridge a population density of 894 thrips/m² was estimated; in the woods 64/m²; and in the meadow 255/m². Both *Frankliniella tritici* Fitch and *Nesothrips bicolor* Heeger were collected from snow samples in the meadow, as were hemipterans *Corimelaena pulicaria* Germer and *Ischnodemus brevicornis* Parsh. The lygaeid *Sphragisticus nebulosus* Fallen and an immature pseudococcid were collected in the woods.

III. DISCUSSION

The records of activity at low temperatures of cicadellids, nabids, arctiids, acridids and gryllids (Holmquist 1926, Renken 1956) are supported by data on activity in the same families in southern Manitoba in October and November, especially by Cicadellidae, which can be classified as winter-active in this region. The activity of predatory species in winter months (Renken 1956) was generally true at Fort Whyte, except for the cicadellids.

Aphids were thought to migrate in autumn to overwintering sites where they remain immobile throughout the winter; e.g. in autumn *Rhopalosiphum padi* L. moves to *Prunus* sp., on which it overwinters (Robinson, pers. comm.). One specimen of *R. padi* taken from the ridge in late October was presumably searching for *Prunus* spp., though it was caught late in the season. *Amphorophora* sp. usually occurs on shrubs such as *Rubes* spp. and does not feed on grasses (Robinson, pers. comm.); however, in December one individual was collected from the meadow, at the end of the transect with bushes in the vicinity.

Geometrid moths were collected from the snow surface in Montana by Chapman (1954); in southern Manitoba active adult lepidopterans were not found in the winter months, though some had been collected in October. Generally, at Fort Whyte this order was restricted in activity to temperatures at or greater than 0°C.

In late November when there was little snow and the soil surface temperature was -4.5°C, a thysanopteran was collected. Its activity may have been facilitated by the radiant energy from the sun. Though numerous in snow samples collected in the open and grassy areas of the ridge and meadow, thrips were generally not active at low temperatures.

IV. CONCLUSION

The orders Hemiptera, Homoptera, Lepidoptera, Neuroptera, Orthoptera and Thysanoptera occurred in autumn but rarely exhibited activity at temperatures below 0°C, with the exception of a few cicadellid nymphs that were collected at T(s) ranging from -1.5° to -4.5°C. The minimum temperature at which activity was recorded for Lepidoptera was close to 0°C; for thysanopterans,-4.5°C; and for aphids, -5°C. The lygaeid, *Eremocoris ferus*, exhibited normal activity at -4°C but was killed after one minute at -9.5°C.

Table 15-1

Seasonal Activity of Other Insect Families Collected at Fort Whyte, Manitoba

Date	Autumn	Winter	Spring	Summer
1973 - 1974				
Hemiptera	6*	2	2**	6
Homoptera	2*	8	3**	123
Lepidop.	1	1	0**	24
Others	0*	0	0**	35
1974 - 1975				
Hemiptera	10	4	1	6
Homptera	110	19	66	122
Lepidop.	19	0	3	28
Others	48	7	9	88

* Collections only in last three weeks of October.

** One collection only.

Table 15-2

List of Species of Hemiptera, Homoptera, Lepidoptera, Neuroptera, Orthoptera, and Thysanoptera*
at Fort Whyte, Manitoba from 1973 to 1975

ORDER HEMIPTERA

- Fam. Corimelanidae
  - *Corimelaena pulicaria* Germar

- Fam. Lygaeidae
  - *Eremocoris ferus* Say
  - *Ischnodemus brevicornis* Parsh.
  - *Scolopostethus thomsoni* Reuter
  - *Sphragisticus nebulosus* Fallen

- Fam. Nabidae
  - *Nabis alternatus* Parsh.
  - *Nabis roseipennis* Reuter

- Fam.Tingidae
  - *Corythucha* sp. prob. *coryli*
  - *Corythucha marmota* Uhler

ORDER HOMOPTERA

- Fam. Aphidae**
  - *Amphorophora* sp. poss.
  - *Aspidaphium utahensis* Smith and Knowlton
  - *Aulacorthum* sp. prob.
  - *Capitophorus elaeagni* del Guercio
  - *Rhopalosiphum* sp. prob. *fitchi* Sand.
  - *R. padi* L.
  - *R. poae* Gillette

- Fam. Cicadellidae
  - *Aceratagallia* sp.
  - *Cuerna septentrionalis* Walker
  - *Draeculacephala antica* Walker
  - *Metapterus* sp.

- Fam. Cixiidae
  - *Cixius misellus* Van D.

- Fam. Delphacidae
  - *Macrotomella* sp.

ORDER LEPIDOPTERA

Fam. Arctiidae
  Apantesis _virgo_ L.

Fam. Noctuidae
  larvae prob. Amphipyrinae
  Heliothis sp. poss.
  Homorthodes _furfurata_ Grt. poss.
  Orthodes _crenulata_ Butl. poss.
  Polia sp. prob.

Fam. Pyralidae
  Alsophila _pometaria_ Harr.
  Crambus sp. prob.
  Synclita _obliteralis_ Walker

Fam. Olethreutidae
  possibly a few larvae

Fam. Oecophoridae
  Agonopterix sp. prob.

ORDER NEUROPTERA

Fam. Coniopterygidae
  Hemorobriidae

ORDER ORTHOPTERA***

Fam. Acridiidae
  Chorthippus _curtipennis_ _curtipennis_ Harris

Fam. Gryllidae
  Allonemobius _allardi_ Alexander and Thomas

ORDER THYSANOPTERA

Frankliniella _tritici_ Fitch
Nesothrips (_Bolothrips_) _bicolor_ Heeger
Sericothrips _cingulatus_ Hinds

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* Determinations by D. Brown and K. G. A. Hamilton (Hemiptera); K. G. A. Hamilton (Homoptera); S. Allyson, K. B. Bolte, A. Mutuura, and E. G. Munroe (Lepidoptera); B. A. Parks (Neuroptera) ; and W. R. Richards (Thysanoptera), B.R.I., Ottawa, Ontario.

** Determinations by A. G. Robinson, Department of Entomology, University of Manitoba.

*** Determinations by J. McFarlane, Department of Entomology, University of Manitoba.

Chapter XVI

SEASONAL ACTIVITY OF THE SUBNIVEAN FAMILIES

I. REVIEW OF LITERATURE

Temperature has a profound effect upon all ectotherms. These groups will be discussed phylogenetically.

The activity of oligochaetes is positively correlated with temperature (Satchell 1967), while sudden drops in temperature and cool weather induce activity in gastropods (Dainton 1954, Rising and Armitage 1969) and in Chilopodes (Cloudsley-Thompson 1951, 1968). Pseudoscorpions exhibit little activity in North American winters (Nelson 1973), while in Europe they remain active throughout the cold season (Weygoldt 1969).

Certain families of spiders are winter-active and cold-resistant, e.g. clubionids, linyphiids and lycosids (Wolska 1957, Williams 1962, Buche 1966, Kronestedt 1968, Kirchner and Kestler 1969, Hågvar 1973). Breymeyer (1966) and Uetz (1975) found numbers of spiders decreased from July to a low in November and February, and increased in April. In Europe mites were recorded as cold-hardy (Sømme 1965b, Stenseth 1965), and in North America this group is active in March (Dowdy 1965, Willard 1973). Some species of phalangids can survive exposure to -4.5°C, but do not exhibit much activity at these low temperatures (Todd 1949).

Collembola are cold-hardy, active at low temperatures and have been collected from the snow surface in the northern hemisphere (Holmquist 1926, Agrell 1941, Chapman 1954, Wolska 1957, Simon 1961, Kaczmarck 1963). Coleoptera are also active at low temperatures in winter (Holmquist 1926, Chapman 1954, Heydemann 1956, Renken 1956, Williams 1959b, Wolska 1957, Greenslade 1965, Mason 1972 and 1974), and are a well-known cold-hardy group (Salt 1961, Baust and Miller 1971 and 1972, Kaufmann 1971). Diptera contain a few winter-active families which have been collected on snow (Holmquist 1926, Wojtusiak 1951, Chapman 1954, Renken 1956, Dahl 1969, Hågvar 1971, Hågvar and Östbye 1973). Low temperature activity was recorded in hymenopterans (Holmquist 1926, Mellanby 1940, Renken 1956), as was cold-hardiness (Salt 1950, 1959; Ohymama and Asahina 1972).

II. RESULTS

The numbers of families collected from October to April of each trapping period are presented in Figures 16-1 and 16-2. This pattern was well exemplified in all major groups, excepting Acarina and Collembola. The families most frequently collected in winter were Eupodidae, Rhagididae, Clubionidae, Erigonidae, Lycosidae, Entomobryidae, Isotomidae and Staphylinidae.

In 1973-1974, the number of families exhibiting activity gradually decreased in autumn, followed by small peaks in early to mid-November, to a low in the period from December to February when three to five families were active. In

March activity by other families resumed, and gradually increased from April onwards. In October more families were active on the ridge than in the woods and meadow (Figure 16-1).

In the autumn of 1974, the number of families exceeded that of the previous year, due to the prolonged warm autumn and late establishment of permanent snow cover (Chapter IV). A sharper decline in numbers occured by the end of November, when soil surface temperatures were approximately -8°C (Figure 16-2). The last peak of the year occurred just prior to permanent snow cover in mid-December, and from that time on numbers gradually decreased to three to five families per habitat, followed by a slight increase in March and a definite rise in April. An exception was no catch on the ridge in mid-April, when local conditions flooded and froze all the traps. The fluctuations in numbers of families in the meadow from February to spring may have been due to coincident sudden changes of T(s).

The numbers of families collected was correlated against T(s), and the correlations were found to not be significant in both years (Figure 16-3). For individual habitats, the correlation coefficient was significant only on the ridge ($r = 0.78$; $P < 0.01$) and in the woods in 1973-1974 ($r = 0.53$; $P < 0.05$). The correlation between the numbers of families and the temperature difference between T(s) and T(a) was also not significant (Figure 16-4).

III. DISCUSSION

The decreases in temperature which occur in autumn induce activity in slugs, snails and centipedes (Dainton 1954, Rising and Armitage 1969, Cloudsley-Thompson 1951 and 1968), as the high humidity does for oligochaetes (Satchell 1967). At Fort Whyte these orders were most abundant in October, when temperatures were decreasing and relative humidity was high.

Activity of spiders, mites and collembolans in winter was noted by many authors, with clubionids, linyphiids, lycosids and isotomids predominating (Wolska 1957, Williams 1962, Buche 1966, Kronestedt 1968, Hågvar 1973, Dowdy 1965, Willard 1963; Holmquist 1926, Agrell 1941, Chapman 1954, Wolska 1957, Simon 1961, Kaczmarek 1963). In southern Manitoba the orders represented by the same families provided the largest number of winter-active families. In Poland and in Delaware, the density of spiders was high in July and low from November to February, with a rise in April (Breymeyer 1966, Uetz 1975). In southern Manitoba, the number of spiders was decreased from October to midwinter and gradually increased from April after the snow melted (Chapter IX).

Winter activity by coleopterans was studied by Heydemann (1956) and Renken (1956), who noted staphylinids and cantharids were especially active. At Fort Whyte staphylinids were very abundant in October and November, but temperatures less than -4°C appeared to restrict their activity. Cantharids were occasionally taken in the same months. Dipterans of the families Mycetophilidae, Sciaridae, Tipulidae and Trichoceridae were recorded as winter-active (Wojtusiak 1951, Chapman 1954, Renken 1956, Dahl 1969, Hågvar 1971), and all these families, excepting tipulids, were taken at low temperatures at Fort Whyte. Low temperature activity by hymenopterans has been recorded (Holmquist 1926, Mellanby 1940, Renken 1956), but in southern Manitoba this order ceased to be active after mid-November.

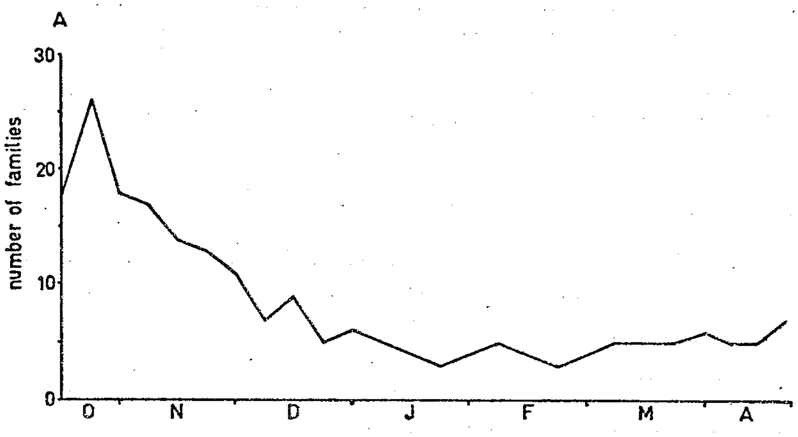
The correlation between numbers of families and T(s) demonstrated that temperature plays a minor role with respect to cessation of activity in autumn by most families, except on the ridge and in the woods in 1973-1974. Other variables, such as photoperiod, intensity of solar radiation, litter depth, relative humidity and availability of food, must affect the families to a greater extent than changes of temperature. Also the lack of significant correlation between numbers of families and temperature difference between T(s) and T(a) indicates that the temperature difference does not substantially affect activity, especially in the cases of mites and collembolans.

IV. CONCLUSION

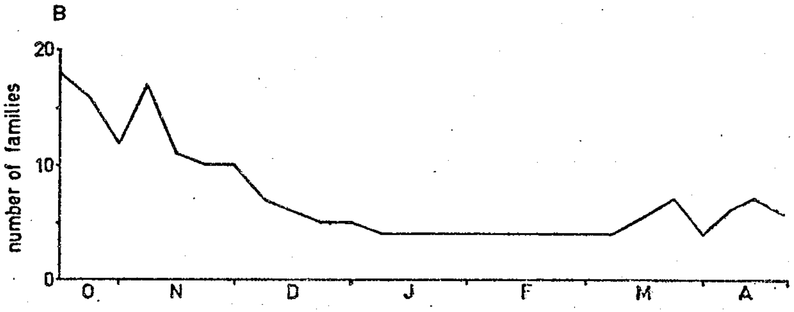
The number of families exhibiting activity was highest in autumn, declined gradually to three or four active families in mid-winter and slowly increased in April towards the summer maximum each year. The number of active families was not significantly correlated with T(s) in either trapping period, nor with the temperature difference between T(s) and T(a) in 1975. Hence, other variables must have a greater effect on numbers of families to cause the autumnal decrease.

Figure 16-1

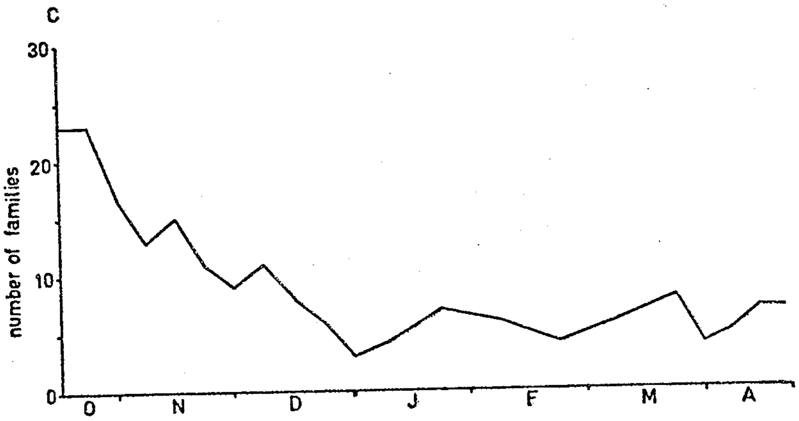
The number of families taken seasonally from all habitats at Fort Whyte, Manitoba in 1973-1974 (A - ridge, B - woods, C - meadow).



RIDGE 1973-1974



WOODS 1973-1974

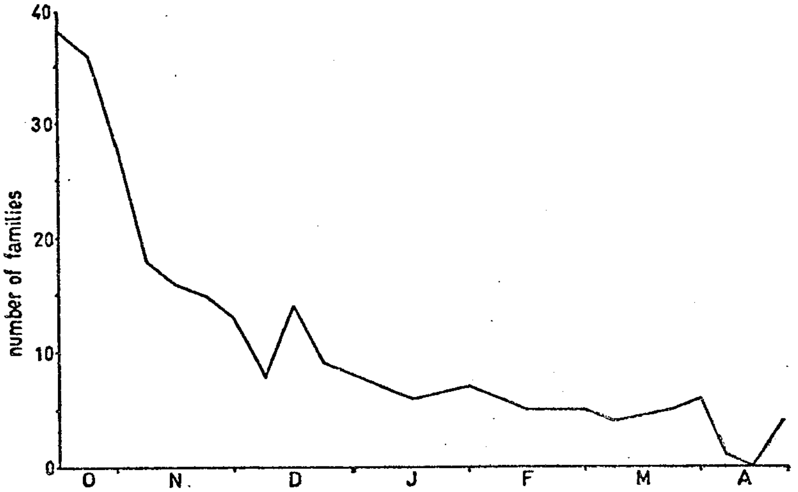


MEADOW 1973-1974

Figure 16-2

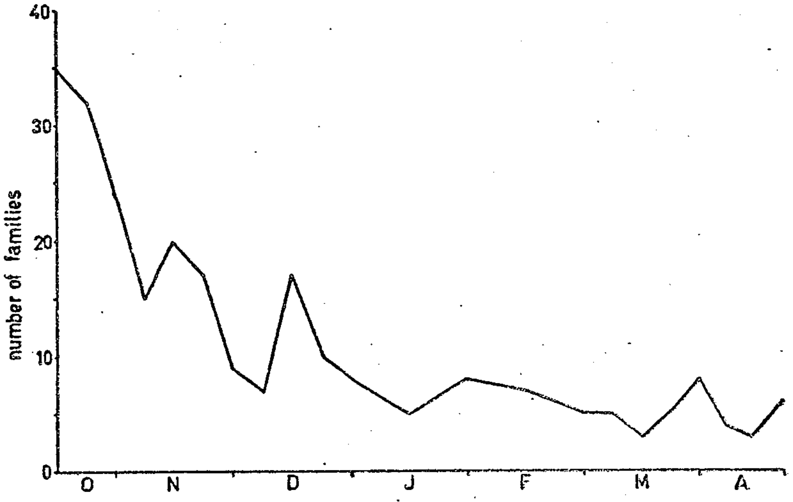
The number of families taken seasonally from all habitats at Fort Whyte, Manitoba in 1974-1975 (A - ridge, B - woods, C - meadow).

A



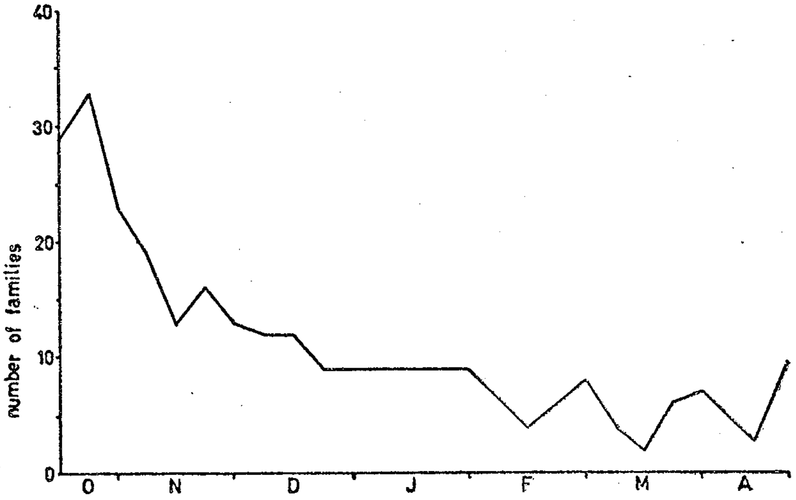
RIDGE 1974-1975

B



WOODS 1974-1975

C

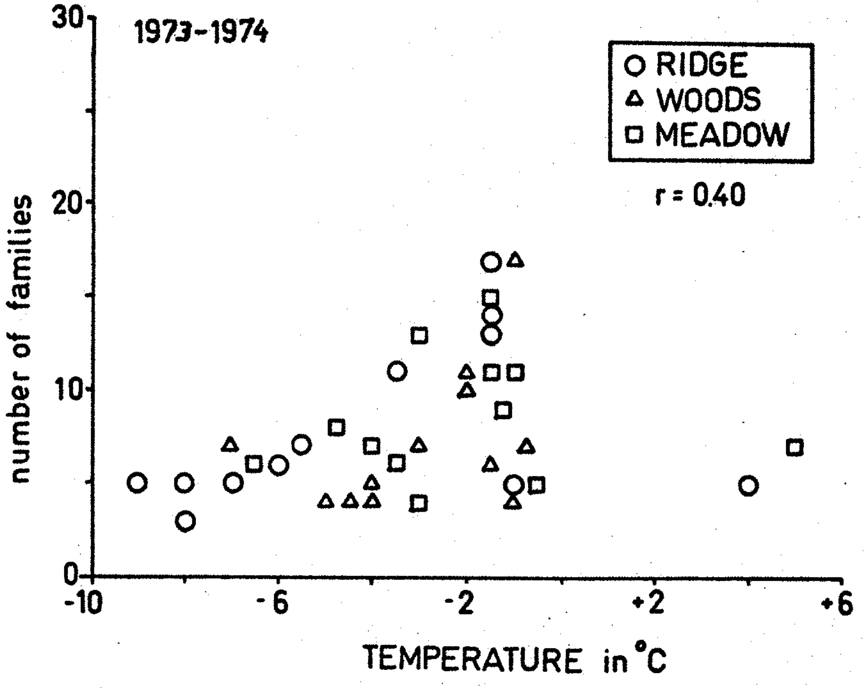


MEADOW 1974-1975

Figure 16-3

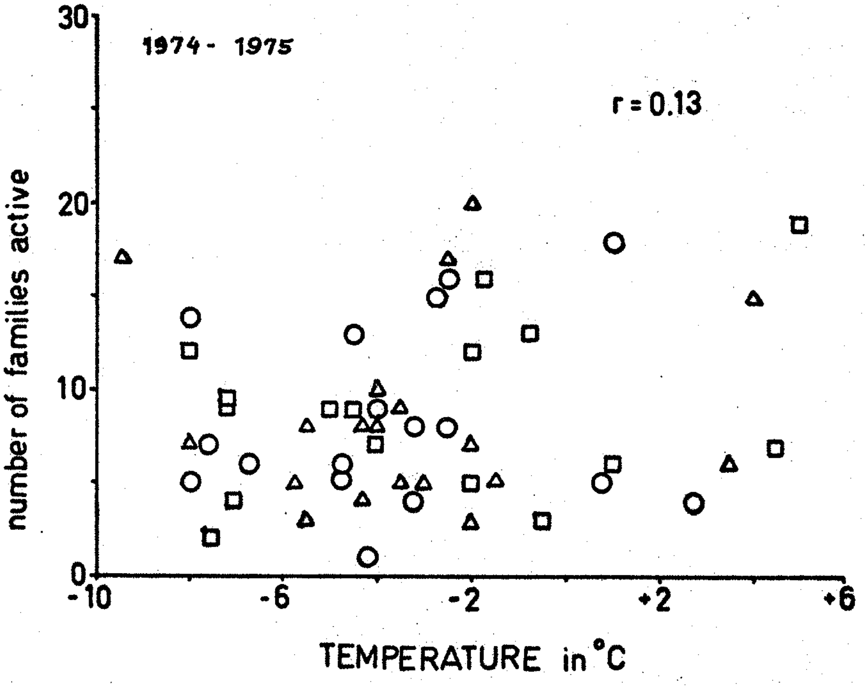
The relationship between the number of families and T(s) at Fort Whyte, Manitoba (A - 1973-1974, B - 1974-1975).

A



30
20
10
0
1973-1974
○ RIDGE
△ WOODS
□ MEADOW
r = 0.40
number of families
-10
-6
-2
+2
+6
TEMPERATURE in °C

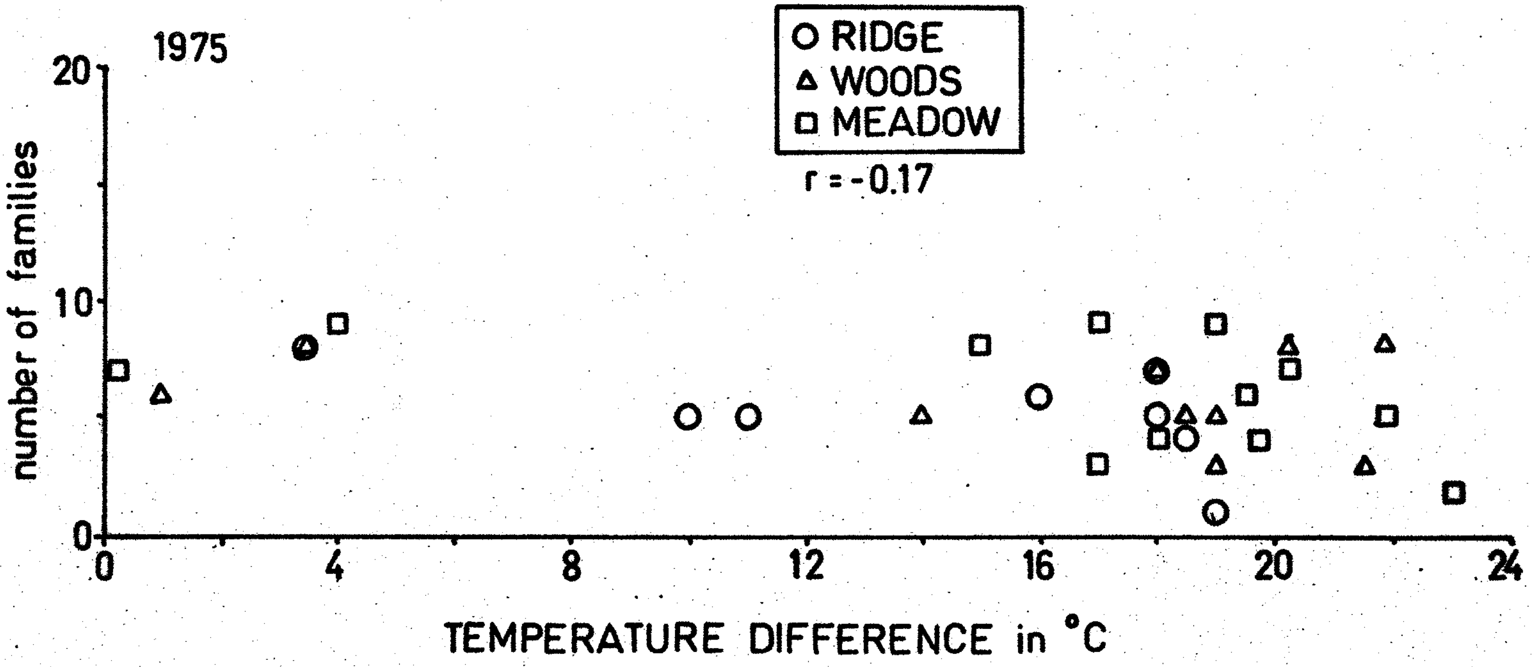
B



30
20
10
0
1974 - 1975
r = 0.13
number of families active
-10
-6
-2
+2
+6
TEMPERATURE in °C

Figure 16-4

The relationship between the number of families and the temperature difference between t(s) and T(a) in 1975.


1975
○ RIDGE
△ WOODS
□ MEADOW
r = -0.17
number of families
20
10
0
0
4
8
12
16
20
24
TEMPERATURE DIFFERENCE in °C

Chapter XVII

SUMMARY, DISCUSSION AND CONCLUSION

I. SUMMARY AND DISCUSSION

The conditions under snow allow some invertebrates to remain active throughout the winter. Density of the snow cover affects its insulating properties: snow of low density provides greater insulation than that of high density. Subsequently, the subnivean temperature (T(s)) fluctuates more in late winter as snow density increases due to metamorphism. Increased density also allows long wavelength light to penetrate further into the snow cover in late winter. Thickness of snow cover must be a minimum of 20cm to provide protection against the ambient air temperature (T(a)); in southern Manitoba the fluctuations of T(a) have a greater effect upon T(s) than snow thickness, with a lag effect of two to five days. The amount of insulation obtained from snow cover is indicated by the temperature profile within the snow.

The snow conditions in southern Manitoba necessitated the use of cylinders in the second winter to prevent soft, friable snow from falling into traps, a problem which probably is never or rarely encountered in Fenno-Scandanavia where the method of using the ring and lid with pitfall traps was developed. The cylinders prevented a large increase in density above the trap sites and therefore maintained insulation in the snow cover similar to that in undisturbed snow.

The number of active families declined from a high of 30 to 40 in the autumn to three or four in the winter, rose to six or seven in the spring and then to the highest level in summer. The number of families active was not correlated with T(s) or with the temperature difference between T(p) and T(a). Hence other factors are mainly responsible for the autumnal decrease in numbers. In Europe the snow depths are generally less and T(s) higher, providing less severe conditions than those in Manitoba. At Fort Whyte, T(s) in winter averaged about -3° to -6°C, while in Sweden it has been recorded as 0° to -2°C.

Lumbricids, gastropods and centipedes were not winter-active, since their activity was restricted by low temperatures. The threshold temperature for activity by lumbricids was about 5° to 7°C in autumn and about 2° to 4°C in spring; by gastropods, near 0°C in autumn; and by centipedes, about -1.5°C in autumn. The gastropods were active when temperature was decreasing to 0°C. Summer and winter collections contained the same species. Four of the eleven species had holarctic distributions.

Pseudoscorpions and phalangids were rare. The former order had peak numbers in November and December in the meadow, at temperatures between -1° and -4°C. Phalangids on the soil surface in autumn were probably migrating to overwintering quarters and were mobile in the temperature range of -0.6°C to 4°C. None of the four species collected had holarctic distributions.

Spiders contain five families which have winter-active species: Clubionidae, Erigonidae, Linyphiidae, Lycosidae and Thomisidae. Of the 49 species taken, nineteen were winter-active (38.8%). Species diversity was high in autumn, low in winter and generally increased in spring to a summer maximum. An analysis of the advantages and disadvantages of the use of pitfall traps to catch spiders was given in Chapter IX.

In the first winter the decrease of T(s) in mid-December limited activity of all families except erigonids and lycosids. Numbers active and T(s) were positively correlated. In the second winter periods with the late appearance of snow cover, clubionids were also winter-active. Negative correlations between numbers trapped and the temperature difference between T(s) and T(a) occurred. As T(s) gradually increased late in each winter, activity resumed very slowly. All species, except Centromerus sylvaticus, had more than one age class present in the overwintering period. Most of the autumn and winter fauna were also collected in summer also, thus, no exclusively "winter species" were found. Cold room experiments on juveniles of Pardosa sp. and Agroeca sp. indicated that normal activity was possible for a short period of time at -9.5°C and -12°C. Seven of the 49 species had holarctic distributions.

Mites were the most numerous winter-active group, especially the families Eupodidae, Rhagidiidae and Parasitidae. Their activity was not correlated with T(s). There were no exclusively winter species, but four species were winter-active. Only one of the 26 species had a holarctic distribution.

Collembolans were another abundant winter-active order; isotomids and entomobryids were taken even at -9°C. In summer sminthurids were most numerous. Isotoma subequealis-fennica group represented a first record for Canada, and Entomobrya sp. near sibirica-quinquelineata group represented a first record for North America. These species and six others were winter-active. Ten of the 27 species had holarctic distributions.

Carabids and staphylinids comprised those families of coleopterans most active down to -2°C in October and November. They were rarely mobile below -4°C, a temperature at which staphylinids were normally active in cold room experiments. Many other families were active in summer. Seven of the 87 species had holarctic distributions.

Dipteran activity was seen on the soil surface in October and November, with almost no activity in winter and early spring. In late spring and into summer, activity by flies resumed. Hymenopterans, especially ants, were active in summer, but in autumn and early winter their activity (i.e. of parasitic wasps) was closely correlated with that of dipterans, many families of which are known hosts for these wasps, and therefore suggesting parasitism. Both orders were restricted in activity at low temperatures of -3.5° and -5.5°C respectively. An exception is Mycetophila fungorum which was active at -9.5°C in cold room experiments. Eleven species were taken at low temperatures. One of the 78 species had a holarctic distribution.

The orders Hemiptera, Homoptera, Lepidoptera, Neuroptera, Orthoptera and Thysanoptera exhibited activity in autumn when temperatures approached 0°C, except for a few cicadellid nymphs collected in the temperature range of -1.5° to -4.5°C. Aphids and a few thrips were active at about the same low temperatures. In a cold room experiment, the lygaeid Eremocoris ferus exhibited normal activity at -4°C. Six of the 42 species were active at low temperatures. There were no species that had a holarctic distribution.

Most of the winter-active species were predatory, except the collembolans and some mites. Hence these predators may feed on other arthropods in the subnivean space, whether they are active or hibernating. Collembolans may form the basis of a food chain under the snow; possibly dipteran larvae and pupae are parasitized by wasps active at the same time. Most species were inactive below -2°C. Relatively few species of the total yearly catch were winter-active (61 species or 19%). Some of these species were active at low temperatures in Manitoba (i.e. -2°C); in other locations with more moderate climates, these species would probably be called winter-active and therefore are classified here as winter-active.

Comparison of winter and summer faunas at Fort Whyte showed that almost all species taken in winter were also collected in warmer months. The greatest number of species was collected in summer, and some species were taken only then. In summer the number of individuals per species which were active on the soil surface was not as high as in the autumn. It may be assumed that in summer a variety of niches are available in three dimensions while in autumn those niches are being abandoned as invertebrates seek their overwintering quarters in the litter or in the soil. Species diversity for most groups was high in autumn, low in winter and gradually rose in spring to a summer maximum. In winter the number of individuals was as high as 40 per trap at times, though species diversity was low. The few cold-hardy species were very numerous, especially mites and collembolans in February and March.

Two species of spiders, four of coleopterans, one dipteran and one hemipteran were tested in cold room experiments. The spiders were most cold-resistant (tolerant of -12°C), followed by the dipteran and some carabids (tolerating -9.5°C). Staphylinids and the hemipteran demonstrated normal activity at -4°C.

Thirty-seven of the identified 320 species collected, or 11.6%, have holarctic distributions. It was initially assumed that winter-active species would have holarctic distributions. Though many of the winter-active genera are holarctic, the assumption was not true in general.

II. CONCLUSION

The conditions in the subnivean space under snow cover allow some invertebrates to be active throughout the hiemal period. In southern Manitoba 320 species were trapped over a 23-month period, 19% of which were winter-active or active at low temperatures, and 11.6% of which had holarctic distributions. The orders that exhibited activity frequently in winter were Acarina, Collembola, Araneae and Coleoptera, and activity was seen less frequently in other orders.

In the first trapping period, snow conditions were close to normal. In the second, permanent snow cover arrived about six weeks later than usual, and a much higher proportion of invertebrates were active prior to that time than in the previous year. A change in collection methods from digging out lids of traps to the use of cylinders to retain snow undisturbed above the trap may have accounted for some of the difference in catch which ensued in the second hiemal period.

The number of individuals active on the soil surface and the species diversity were greatest in autumn, probably attributable to migration from other vegetation layers to overwintering sites. Both were low in winter and gradually increased in spring to a summer maximum. This pattern was general for most orders: exceptions were the mites and collembolans which had population peaks occurring in

February and March, at low T(s). This may be due to increased light penetration into the metamorphosed snow, and the activity on the soil surface would be the resultant effect of photoperiod and not of temperature. The activity of these two groups was not correlated with T(s) as the activity of many of the other orders was.

The winter and summer fauna of southern Manitoba did not vary greatly; more species were active in summer, especially phytophagous ones.

A few spiders, beetles, a fly and a bug were tested in cold room experiments of short duration. The spiders tolerated -12°C, the fly and carabids -9.5°C, and all others were normally active at -4°C. In the field some of these families did not exhibit activity at such low temperatures.

Only 11.6% of the total number of species collected at Fort Whyte have holarctic distributions, and few of these species that were winter-active in Fenno-Scandanavia were winter-active in North America. However, the genera which are winter-active in Europe were usually winter-active in southern Manitoba.

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