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A POPULATION OF NANORCHESTES ANTARCTICUS
(ACARI: PROSTIGMATA) AT THE VESTFOLD HILLS, ANTARCTICA

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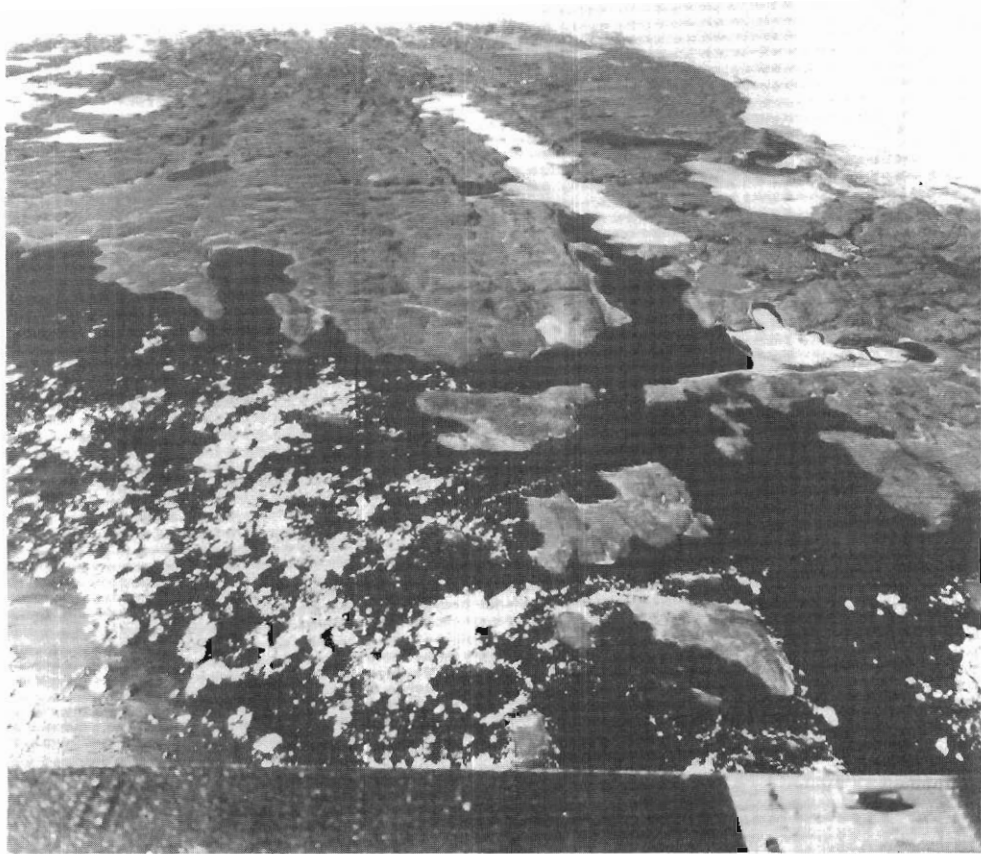


Plate 1. An aerial view of the Vestfold Hills from an altitude of 7,000 m over Prydz Bay.

A POPULATION OF NANORCHESTES ANTARCTICUS
(ACARI: PROSTIGMATA)
AT THE VESTFOLD HILLS, ANTARCTICA

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ABSTRACT

In the Vestfold Hills (68°35'S, 77°58'E), the habitat of *Nanorchestes antarcticus* is soil in areas of seepage produced by snowdrifts that melt from October to January. Water from snowdrifts provides the only significant source of moisture in the habitat each year. The duration and extent of seepage below snowdrifts determines both the distribution and the abundance of mites through mortality from desiccation.

The mites live under rocks at the surface, and in the upper two centimetres of soil, from October to February. They are active only when the temperature of their surroundings exceeds 0°C. From March to September soil temperature does not exceed 0°C, and the mites are inactive at depths between one and five centimetres below the surface. During most of this time the soil contains less than 0.5 per cent of water.

The food of *N. antarcticus* is soil algae. The most commonly occurring species of organisms in the habitat of the mite are producers and decomposers. The mites have no obvious predators or competitors.

Nanorchestes antarcticus is ovo-viviparous and each female produces three or four larvae annually. These larvae are laid progressively from mid-November until the end of January up to four centimetres deep in the soil. Two years are required to complete a life-cycle.

In one population a mean density of $(188.1 \pm 39.5) \times 10^3$ mites/m² was measured over seventy days during mid-summer; but the mites were less than half as abundant in winter. The maximum population density occurred in early December and the minimum density at the end of February. From mid-January to the end of February 1973, approximately seventy per cent of the population died as the habitat became very dry. Annual fluctuations in the abundance of the mite were caused by asymmetry in the availability of water in the habitat during the year.

It was concluded that *N. antarcticus* is as abundant in the Chalikosystem of Antarctica as species of Acari in other terrestrial ecosystems. Nevertheless, at extreme high latitude where the active season is shorter, it is predicted that the abundance and fecundity of *N. antarcticus* will be less, and the length of the life-cycle longer, than that found in the Vestfold Hills.

1. INTRODUCTION

The ecology of soil organisms is often complex because of the large numbers of edaphic taxa and their diverse interactions within soils at a microscopic level. Almost without exception the Acari are the most abundant animals in soil, both in respect of numbers of species and numbers of individuals (Evans et al., 1961). Most ecological investigations of soil mesofauna have been concerned with forest soils in the Northern Hemisphere (Van den Berg and Ryke, 1967), where the organic content of soil is high.

Ice-free land in Antarctica contains two terrestrial ecosystems: the Bryosystem and the Chalikosystem. These contain mineral substrate with and without macrophytes respectively (*sensu* Janetschek, 1963), and support very few species. Soil in both of these ecosystems is almost completely inorganic (Tedrow and Ugolini, 1966); but still the Acari are the dominant group of land animals in terms of the variety of habitats occupied and of the numbers of species and individuals (Gressitt, 1967a).

The study of Antarctic biology in the past has been concerned with the discovery of biota, whereas present emphasis is on ecology (Holdgate, 1970; Gressitt, 1971). Recent ecological studies have attempted to explain the distributions of species in terms of the severe physical conditions prevailing in the Chalikosystem (Pryor, 1962; Gressitt et al., 1964; Wise et al., 1964; Janetschek, 1967; Wise and Spain, 1967). Perhaps this is because the conditions preclude any species of soil microarthropods from living in many parts of this ecosystem. Other work has focussed on single aspects of species ecology (e.g. soil conditions (Spain, 1971), diet (Fitzsimons, 1971a) and thermal behaviour (Fitzsimons, 1971b), to investigate functional relationships within the ecosystem. Few studies on Antarctic mites have included concurrent work on other types of sympatric organisms. Consequently trophic relationships in the Chalikosystem are little known.

Most of this previous work examined how the Chalikosystem functions, but did not provide a reliable quantitative basis on which to compare this terrestrial ecosystem with others. The population ecology of only one species, a collembolan (*Gomphiocephalus hodgsoni*), has been investigated adequately (Peterson, 1971). Preliminary quantitative data suggest that population densities of this species reach 100 individuals per square metre and a biomass of 15 mg/l (Janetschek, 1970). Nevertheless, individuals of this species form dense aggregations within the habitat (Wise and Spain, 1967), and more quantitative information on other species is required to obtain reliable estimates of population densities in the Chalikosystem (Janetschek, 1970).

To quantitatively compare the Chalikosystem with other terrestrial ecosystems, it would be useful to study the population ecology of a species or group of similar species also present in the Bryosystem and other terrestrial ecosystems.

The prostigmatic mite *Nanorchestes antarcticus* (Strandtmann) is considered to be the most widespread species of terrestrial arthropod in Antarctica (Gressitt and Shoup, 1967), and belongs to the Family Nanorchestidae, whose species occur world-wide in soils. They are small, soft-bodied mites, often abundant in soil, but which have been largely ignored, probably because of their size and the many other edaphic species usually present. Little is known about the biology of any of the Nanorchestidae, except *Nanorchestes antarcticus*, which is remarkable only because it occurs principally in remote Antarctica. A knowledge of this species' part in the rudimentary soil ecosystems of Antarctica should increase our understanding of the formation of more complex soils and the part played by similar species of the Acari elsewhere.

Nanorchestes antarcticus is perhaps the most useful species to study in a comparison of the Chalikosystem with other terrestrial soil ecosystems. It is one of the smallest, yet most numerous, mites present, and has the greatest latitudinal, as well as altitudinal range of any other mite in Antarctica (Gressitt and Shoup, 1967). *N. antarcticus* occurs in the Chalikosystem and the associated Bryosystem, and its range extends to 85° 32'S, 153°W, further south than any other known terrestrial arthropod (Wise and Gressitt, 1965).

Nanorchestes antarcticus is also the most suitable Antarctic species in which to investigate the effects of extreme high latitude on the biology of a terrestrial arthropod. In this sense studies on *N. antarcticus* at different latitudes could form a unique set of data as an analogous situation does not exist in the Arctic. The present work, done in the Vestfold Hills (68°35'S, 77°58'E), provides information on the ecology of *N. antarcticus* from only one locality.

The first specimens of *N. antarcticus* to be found at the Vestfold Hills were collected on 30 January 1973 by the author, who was a member of the 1973-74 Australian National Antarctic Research Expedition (ANARE) at Davis station. Thus began a field study of *N. antarcticus* which continued until 27 February 1974. The study was primarily aimed at providing basic quantitative data on the population ecology of *N. antarcticus* at the Vestfold Hills. It was designed to investigate the main requirements for the habitat of *N. antarcticus* and to estimate the absolute abundance of the mite in a population during a period of one year. To investigate the habitat requirements and explain the observed changes in mite abundance it was necessary to study also the physical environment, other species present in the locality, and the food, behaviour and reproduction of the mite.

2. A REVIEW OF THE FAMILY NANORCHESTIDAE

The genera *Nanorchestes* and *Speleorchestes* contain twenty-four described species of prostigmatic mites and belong in the Family Nanorchestidae (Grandjean, 1937) - which originally contained six other genera. Grandjean (1937) considered these genera to be too diverse and presently the family includes only four genera: *Nanorchestes*, *Speleorchestes*, *Caenonychus* and *Oehserchestes* (Baker and Wharton, 1952). *Caenonychus* and *Oehserchestes* each contain only one described species (Thor and Willmann, 1941), neither of which is well known and will not be dealt with further.

The genera *Nanorchestes* and *Speleorchestes* are represented world-wide, and their known distributions probably reflect the distribution of acarological workers. The greatest number of species in both of these genera are found in temperate regions. Nevertheless, unlike *Nanorchestes*, *Speleorchestes* is unknown from the Arctic, Antarctic and Subantarctic regions. *S. formicorum* is the most boreal species known and is found in the nests of *Formica rufa* at Arilks Lage (55°24'N) in Sweden (Tragardh, 1910).

The most recent account of the two genera is given by Theron and Ryke (1969). Species of *Speleorchestes* are elongated and females possess long ovipositors. Species of *Nanorchestes* are rotund and the females have short ovipositors (Grandjean, 1942).

The genera also differ in the nature of the fine striae which cover the cuticles of all the species. In *Speleorchestes* the striae are simple or smooth, but in *Nanorchestes* they are always punctulate, except on the legs, sensory area and gnathosome generally.

The twenty-four described species in *Nanorchestes* and *Speleorchestes* and their type localities are listed in Table 1. Only four, all species of *Nanorchestes*, have been reported from elsewhere. *N. amphibius* occurs in England, Ireland, Germany, France (Schuster, 1958), and Greenland (Macfadyen, 1954), and also has been reported from Macquarie Island (Womersley, 1937); but specimens subsequently collected there are considered to belong to *N. antarcticus* (Watson, 1967). *N. aboriger* occurs in Germany and Norway (Thor and Willman, 1941), Denmark (Haarlof, 1960), Iceland (Lindroth, 1966), and South Australia (Womersley, 1944). *N. collinus* has been reported from the Canadian Arctic (McAlpine, 1964), Swedish Lappland (Willman, 1943) and South Australia (Womersley, 1944). *N. antarcticus* occurs in Antarctica (Strandtmann 1967), on subantarctic islands (Tilbrook, 1967a; Watson, 1967), and in subalpine habitat in Japan (Shiba, 1969).

Some of the earliest known species are insufficiently described. According to Womersley and Strandtmann (1963), it is not possible to differentiate *N. collinus* and *N. aboriger* from *N. antarcticus* using their descriptions alone. This problem may have caused confusion in the identifications of subsequent collections, and could account for the disjunct reports of some species. The monotypic genus *Gainia* (Trouessart, 1914) contains one species *G. nivalis* described from one specimen collected on Peterman Island (60°10'S, 64°10'W), Antarctica. The description strongly resembles that of a species of *Nanorchestes* (Thor and Willman, 1941). Recent work suggests that *Gainia* is a junior synonym of *Nanorchestes*, and the specimens concerned were probably

Genus *Nanorchestes*

<i>amphibi</i>	Topsent and Trouessart 1890; Calvados France
<i>aboriger</i>	Berlese, 1904; Florence Italy
<i>siculus</i>	Berlese, 1910; Palermo, Italy
<i>collinus</i>	Hirst, 1918; Mendip Hills, England
<i>pulvinar</i>	Grandjean, 1942; Perigueux, France
<i>pseudocollinus</i>	Schuster, 1958; Cote des Alberes, France
<i>antarcticus</i>	Strandtmann, 1963; Ross Is. Antarctica
<i>kirsteueri</i>	Schuster, 1965; Al Ghardaga, Egypt
<i>bifurcatus</i>	Strandtmann, 1967; Tottan Hills, Antarctica
<i>africanus</i>	Theron and Ryke, 1969; Potchefstroom, Transvaal
<i>capensis</i>	Theron and Ryke, 1969; Belville, Cape Province
<i>coatesi</i>	Theron and Ryke, 1969; Welkom, Orange Free State
<i>exsertus</i>	Theron and Ryke, 1969; Potchefstroom, Transvaal
<i>globus</i>	Theron and Ryke, 1969; Potchefstroom, Transvaal
<i>pollicaris</i>	Theron and Ryke, 1969; Durban, Natal
<i>usualis</i>	Theron and Ryke, 1969; Potchefstroom, Transvaal

Genus *Speleorchestes*

<i>termitophilus</i>	Tragardh, 1910; Entendweni Bush, Zululand
<i>formicorum</i>	Tragardh, 1910; Arilks Lage, Sweden
<i>poduroides</i>	Hirst, 1917; Malvern Hills, England
<i>ventriosus</i>	Hirst, 1921; Hindhead, Surrey, England
<i>pratensis</i>	Willman, 1936; Breslau, Germany
<i>meyerae</i>	Theron and Ryke 1969; South Africa (many localities)
<i>natulus</i>	Theron and Ryke 1969; Britstown, Cape Province
<i>potchefstroomensis</i>	Theron and Ryke, 1969; Potchefstroom, Transvaal

Table 1. Species of *Nanorchestidae*.

Footnote: R.W. Strandtmann (pers. comm.) is currently describing 13 new species of *Nanorchestes* from polar and sub-polar regions.

the first *N. antarcticus* to be collected (Strandtmann, 1967; Gressitt, 1967b).

A few species are widespread. For example, *N. antarcticus* occurs generally at high latitudes in the Southern Hemisphere, and may not be separable from arctic forms (Strandtmann, 1971). Eventually some of the described species may become synonymous when the original specimens are compared.

Undescribed forms belonging to both genera have been reported from New Zealand (Wood, 1964); and undescribed specimens of *Speleorchestes* have been collected in southern Australia (Wood, 1970), southern California, and northern Mexico (Wallwork, 1972b). Two undescribed forms of *Nanorchestes* have been reported from North America prairie (Lussenhop, 1976). Doubtless others will be found and more species described, particularly in temperate soils.

Morphological variation occurs in *N. antarcticus* from different sites in Antarctica; and specimens from the Tottan Hills (74°48'S, 12°10'W) were sufficiently distinct on the basis of size and setation to be assigned to a different species, *N. bifurcatus* (Strandtmann, 1967). Strandtmann (1971) reported a species of *Nanorchestes* occurring in the Arctic to be widespread and possibly conspecific with *N. antarcticus*. Morphological variation occurring in both Arctic and Antarctic forms shows considerable overlap, and more detailed taxonomic work must be carried out before the relative status of each can be resolved (Strandtmann, 1971). *N. antarcticus* is the only morphologically variable species to be reported, probably because relatively few specimens of most other species have been examined to date.

In most early descriptions, and in those based on very few specimens, only one sex, usually the female, was described. Often only a morphological description is given, and no information on instars, reproduction, or other aspects of the species' biology is available. Grandjean (1942) states that three nymphs occur in both genera.

More recently all life stages were described by Theron and Ryke (1969) for *S. meyeræ* and *N. usualis*, and for *N. antarcticus* by Lindsay (1972). Three nymph and one larval stage occur in each of these species. These are all free-living stages and are similar to the adult. From one egg (normal in *N. usualis*) up to seven eggs (*S. meyeræ*) have been found in females.

In *N. antarcticus* the embryo develops into a larva within the female (Lindsay, 1972), and the larva is laid encased in an eggshell (Rounsevell, 1974). Gravid females of *N. antarcticus* usually carry one to four developing eggs (Lindsay, 1972; Rounsevell, 1974). Grandjean (1942) noted that *N. pulvinar* usually carries only one developing egg. This observation is the only indication that other species of the Nanorchestidae may also be oviparous.

Some species of *Speleorchestes* are xerophilic because they occur in arid zones or hot desert microhabitats. In *Acacia karoo* woodland of the semi-arid highveld in South Africa, an unidentified species of *Speleorchestes* was found in dry sandy soil which usually lacks plant cover (Den Heyer and Ryke, 1966). This species was a numerically dominant member of the mite fauna of the soil during periods of drought but declined at times of high rainfall (Den

Heyer and Ryke, 1966). Wallwork (1972b) found that an undescribed species of *Speleorchestes* was characteristic of the driest permanent microhabitat which he studied in the Mojave Desert of southern California. Another undescribed species is the most abundant mite in grassland, steppe and woodland in the arid zone of southern Australia (Wood, 1971).

Species of *Speleorchestes* live in plant litter (Wallwork, 1972a), or in the upper layers of mineral soil containing less than two per cent of organic material (Wood, 1971; Den Heyer and Ryke, 1966) where they appear to be at risk from desiccation (Wood, 1971). The mites are probably able to penetrate deeper into the soil if necessary (Aucamp and Ryke, 1965); but hot desert soils usually cool at night and regular condensation of moisture can occur in the upper three centimetres of soil (Rose, 1968). The condensate should ensure a regular supply of moisture for surface dwelling desert microarthropods (Wood, 1971).

In general it has been found that populations of soil microarthropods diminish during the hottest months of the year (Rapoport and Tschapek, 1967), presumably from desiccation. Den Heyer and Ryke (1966) found that populations of two unidentified species of *Nanorchestes* followed this pattern, but that the opposite occurred in a population of an unidentified species of *Speleorchestes*.

The known habitats of *S. termitophilus* and *S. formicorum* are termite and ant nests (Tragardh, 1910). Tragardh (1910) described two specimens of *S. formicorum* and an unstated number of *S. termitophilus*. Apparently the specimens were obtained only from within the nests, but without further collections it is not possible to ascertain the habitats of such small animals (0.35 mm long).

Speleorchestes meyeræ and *S. potchefstroomensis* occur in pasture and cultivated soils in South Africa (Theron and Ryke, 1969). During most months of the year these species are less abundant than two species of *Nanorchestes* which also occur in these habitats (Loots and Ryke, 1966; Oliver and Ryke, 1965). Unidentified species of *Speleorchestes* and *Nanorchestes* were found in soils from a temperate evergreen forest in South Africa, but they were less abundant than the species from pasture and cultivated soils (Van den Berg and Ryke, 1967).

Species of *Speleorchestes* are rare in Europe; Hirst (1921) found *S. poduroides* and *S. ventriosus* under rocks on hillsides in Worcester and Surrey.

In *Nanorchestes* there are twice as many described species as in *Speleorchestes*. Species of *Nanorchestes* live in a wide range of localities and habitats - from the tropics (Schuster, 1965) to the Arctic (McAlpine, 1964) and the Antarctic (Strandtmann, 1967). *N. antarcticus* occurs as far as 85°32'S and is the southernmost known terrestrial arthropod (Wise and Gressitt, 1965). Nevertheless most species of *Nanorchestes* occur in temperate regions where they are often abundant, but none has been reported from hot deserts.

Three species are confined to the eulittoral zone of rocky coasts where they live in fissures and pores of rocks that support lichen and algae. *N. amphibius* and *N. pseudocollinus* occur along the French Mediterranean coast (Topsent and Trouessart,

1890; Schuster, 1958) and the former also occurs in Greenland (Macfayden 1954), Ireland (Halbert, 1920) and the Isle of Wight (Hirst, 1917). *N. kirstuerei* occurs on the coast of the Red Sea (Schuster, 1965). Other species (e.g. *N. antarcticus* (Watson, 1967) may be found in the littoral zone, but they are not confined to this habitat.

Five species occur in moss, but none exclusively. *N. aboriger* is found in moss and pasture in Yorkshire moorland (Wood, 1967b) and in moss in Germany and Norway (Thor and Willman, 1941). *N. siculus* was collected from moss in Italy (Thor and Willman, 1941). *N. collinus* and *N. antarcticus* have been found in a number of habitats, including moss in the Arctic (Willman, 1943; McAlpine, 1964) and the maritime Antarctic (Tilbrook, 1967a), respectively. The few known specimens of *N. bifurcatus* were found in samples of moss and lichen from Antarctica (Strandtmann, 1967).

N. aboriger is common in sandy soil in England (Evans, 1951) and Denmark (Weiss-Fogh, 1948). In temperate regions other species are also found in soil and under stones (Grandjean, 1942), and in the topsoil of grasslands, pasture and prairie (Olivier and Ryke, 1965; Loots and Ryke, 1966; Wood, 1967b; Lussenhop, 1976). Species of *Nanorchestes* are often among the most abundant mites present in these soils and are not restricted to any particular sites within grassland (Wood, 1967c). In a prairie community two unidentified species of *Nanorchestes* became more abundant after the vegetation was removed by raking or burning (Lussenhop, 1976).

In South Africa species of *Nanorchestes* are most abundant only in moist soils containing less than five per cent organic material (Loots and Ryke, 1967), and do not appear to be associated with any particular macrophytes in grassland (Wood, 1967c).

Nanorchestes antarcticus occurs in the subantarctic, maritime Antarctic and Antarctic regions which are defined by Holdgate (1964). On Macquarie Island *N. antarcticus* lives in a wide variety of habitats including grassland, herbfield, feldmark, and plant litter in terrestrial habitats, and amongst lichen and algae in the littoral zone (Watson, 1967). Tilbrook (1967a) found that *N. antarcticus* was the most abundant mite at all study sites on Bouvet Island.

On the South Sandwich Islands and the Antarctic Peninsula, *N. antarcticus* prefers a barren rocky habitat to bryophytes, but occurs in all types of macrophytic vegetation without showing a preference for any particular type of plant community (Tilbrook, 1967a).

In the Bryosystem and the Chalikosystem of the Antarctic Peninsula *N. antarcticus* is abundant under rocks near melting snow (Strong, 1967; Gressitt, 1967b). At high latitudes in the Antarctic, *N. antarcticus* is confined to areas of soil moistened by meltwater seepage (Gressitt et al., 1963; Wise et al., 1964; Janetschek, 1967). The greatest numbers of *N. antarcticus* occur in the Chalikosystem (Janetschek, 1967; Gressitt and Shoup, 1967); and the densest populations occur in sand under rocks (Gressitt et al., 1963; Rounsevell, 1974). *N. antarcticus* is widespread in the Chalikosystem, and is only absent from penguin rookeries and permanently dry substrates (Gressitt and Shoup, 1967).

Soils of the maritime Antarctic are generally moist and contain less than one per cent of organic material, except where peat is formed (Ugolini, 1970). Antarctic soils are dry, contain less organic material, and display the characteristics of desert soils (Ugolini, 1970). Ice-free land in Antarctica can be regarded as a cold desert.

In the different climatic regions discussed above, the commonest microhabitats of species of *Speleorchestes* and *Nanorchestes* are plant litter or topsoil in woodland, grassland or desert. In these microhabitats, macrophytes are sparse or absent, and the soil is porous and contains little organic material. Moreover, species of *Speleorchestes* occur in hot deserts, and species of *Nanorchestes* in cold deserts; but the reverse situation has not been found.

Except for *N. antarcticus*, the food of species of *Speleorchestes* and *Nanorchestes* is not known. Fitzsimons (1971a) found that *N. antarcticus* eats green algae, blue-green algae and diatoms; and that the diets of the mites depend largely upon the types of algae available. Although soil fungi occurred at all the study sites, *N. antarcticus*, unlike two other species of microarthropods present, did not contain fungal hyphae or viable fungal spores (Fitzsimons, 1971a).

Loots and Ryke (1967) suggested that species of *Nanorchestes* may eat protozoa and bacteria. Hirst (1917) collected specimens of *N. amphibius* containing "brown material" from the seashore, and Womersley (1944) collected specimens of *N. collinus* and *N. aboriger* containing "dark green material" from moss. The coloured matter in these mites may have been plant material, possibly algae.

Krantz (1969) considered that species of *Speleorchestes* were fungivorous because some were found in insect nests (Tragardh, 1910). Wallwork (1972a) considered an undescribed species of *Speleorchestes* to be a predator. Species of *Nanorchestes* also have been considered as predators (Baker and Wharton, 1952). Grandjean (1939) originally suggested that species of *Speleorchestes* and *Nanorchestes* are predatory by inference from their morphology, but no first-hand observations of predation are known.

Scarcely any information is available on mites which graze soil algae (Lund, 1967). *N. antarcticus* is the only prostigmatic mite listed by Harding and Stuttard (1974) that is known to graze on soil algae. It is possible that many species of *Speleorchestes* and *Nanorchestes* eat algae, and this may explain why these species live in some mineral soils that do not support macrophytes. Soil algae growing in the top layer of porous soil would be accessible to small soil-dwelling mites. Thus it would be unnecessary for the mites to leave the soil and risk desiccation except when conditions above the soil were favourable.

All species of *Speleorchestes* and *Nanorchestes* are saltatorial (Grandjean, 1942), and therefore can move quickly over the surface of soil if necessary. Highly mobile species of *Speleorchestes* occur in dry litter on mineral soil in the Mojave Desert (Wallwork 1972a), in California; and near Alice Springs (P.J.M. Greenslade, pers. comm.) in central Australia. In these

localities high mobility may be required in these mites to permit nomadic movements. This mobility would allow the mites to exploit new microhabitats as water is relocated in the soil diurnally and seasonally.

N. antarcticus is saltatorial, but slow-moving (Cressitt and Shoup, 1967) and is less active than species of *Speleorchestes*. This species hibernates at one centimetre or more below the surface of the soil during the Antarctic winter, and thus avoids the extreme minima of temperature and relative humidity of the surface layer (Rounsevell, 1974). All the water available in the habitat of this mite comes from snowdrifts that melt during the thaw (Rounsevell, 1974), thus a supply of water to the habitat is spatiotemporally predictable and the mites are not required to actively seek moist soil.

Species of *Speleorchestes* are 0.25 mm to 0.35 mm long, elongated, and have soft cuticles folded regularly in simple furrows, or striae (Theron and Ryke, 1969). Long genital and propodosomal tracheae occur in some species of *Speleorchestes* (Grandjean, 1939). Species of *Nanorchestes* are 0.15 mm to 0.35 mm long, globular, and have soft cuticles with striae, but the striae carry regularly-spaced punctulations (Theron and Ryke, 1969). Tracheae have not been found in any species of *Nanorchestes* (Grandjean, 1939). The habitat of *N. antarcticus* is saturated with water during the thaw (Rounsevell, 1974). Presumably when *N. antarcticus* is submerged in water, oxygen can diffuse through the cuticle at a rate sufficient to meet metabolic demands of the adult and embryos in females. A layer of air over the surface of the cuticle is necessary for cuticular respiration in water (Hinton, 1969). The punctulations on the cuticular striae of species of *Nanorchestes* may maintain a layer of air for cuticular respiration in water in the same manner as the micro-papillae on the cuticle of *Peripatosis moseleyi* make the surface of this animal hydro-negative (Robson, 1964). Species of *Speleorchestes* which depend on tracheal respiration would suffocate in water after a short period of time, as would any mite with normal spiracles for atmospheric respiration (Hinton, 1971).

Without the ability to survive a long period of submergence in water, it is unlikely that species of *Speleorchestes* would occur in a cold desert. Correspondingly species of *Nanorchestes* are unlikely to occur in a hot desert without greater mobility.

3. THE VESTFOLD HILLS

The Vestfold Hills are ice-free and occupy about 500 square kilometres at the eastern side of Prydz Bay on the coast of Princess Elizabeth Land between latitudes 68° 22'S and 68° 40'S and longitudes 77° 49'E and 78° 33'E. This tract of rock and water is triangular in shape and bounded by the sea to the north-west, the continental ice plateau to the east, and the Sørsdal Glacier to the south. The country is low-lying and hilly, deeply indented by sea-inlets and fringed by numerous islands up to five kilometres offshore (Plate 1). The hills and ridges rise to 158 m above sea level and are separated by narrow valleys filled by many lakes and tarns. Most of the lakes and tarns contain fresh water. The whole region was once glaciated, but from about 6,000 years ago (Gill, 1955) the lowland valleys which formed the bed of the sea have risen isostatically, trapping seawater in their deepest parts as lakes which are now hypersaline through evaporation (McLeod, 1963a).

A history of expeditions to the area is given by Law (1959). The Australian station, Davis, was established on the coast of the Vestfold Hills in 1957, and apart from temporary closure during 1965-68, has been in continuous operation.

Physical descriptions of the Vestfold Hills are given by Law (1959) and McLeod (1963a), and the geology of the region is described by Crohn (1959) and McLeod (1963b). The bedrock is metamorphic and composed of a variety of gneisses intruded by swarms of dolerite dykes. Valley floors and lowland slopes are covered by morainic debris ranging in particle size from large boulders to sand and silt. The rock debris is similar in composition to the underlying bedrock. Fine shallow substrate accumulates on the surface of the ground in less-exposed situations as wind-blown sand and small amounts of alluvium. Most of this substrate is ahumic, lacking plant cover, and does not have the structure of a soil. Almost all of the region can be described as Chalikosystem (*sensu* Janetschek, 1963). Seventeen species of lichens (Johnstone et al., 1973) and two species of mosses, *Bryum antarcticum* (Filson, 1966) and *Tortula andersoni* (R. Seppelt, pers. comm.) occur, but only in limited areas. These areas can be described as Bryosystem (*sensu* Janetschek, 1963).

The biology of the region is described by Johnstone et al. (1973). Two species of terrestrial Acari (*Tydeus erebus* and *Nanorchestes antarcticus*) occur. Both are prostigmatic mites. Local information about these species is given by Rounsevell (1974 and 1977).

Climatic data for the Vestfold Hills was obtained from weather observations made at Davis station by the Commonwealth Bureau of Meteorology. Philpott (1967) contains data drawn from the years 1957 to 1963. The data for subsequent years have been collated by Antarctic Division biologists (Burton and Campbell, 1980), and are summarized in Figures 1 to 6.

The climate is cold, dry and windy. Mean daily temperatures rise to just above freezing point in January but are between -15°C and -20°C from May to September (Figure 1). The extreme

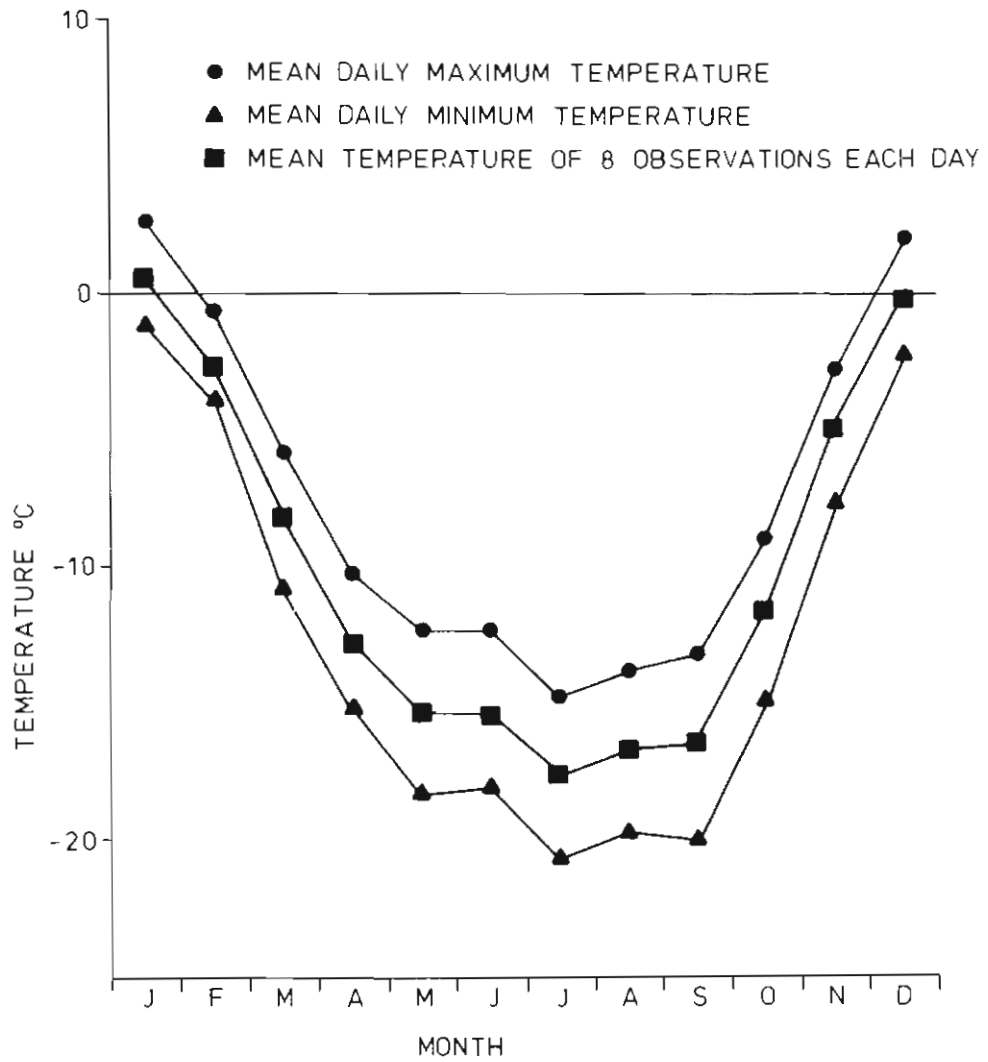


Figure 1. Temperatures at Davis station from 1957 to 1974 (years 1965 to 1968 not recorded).

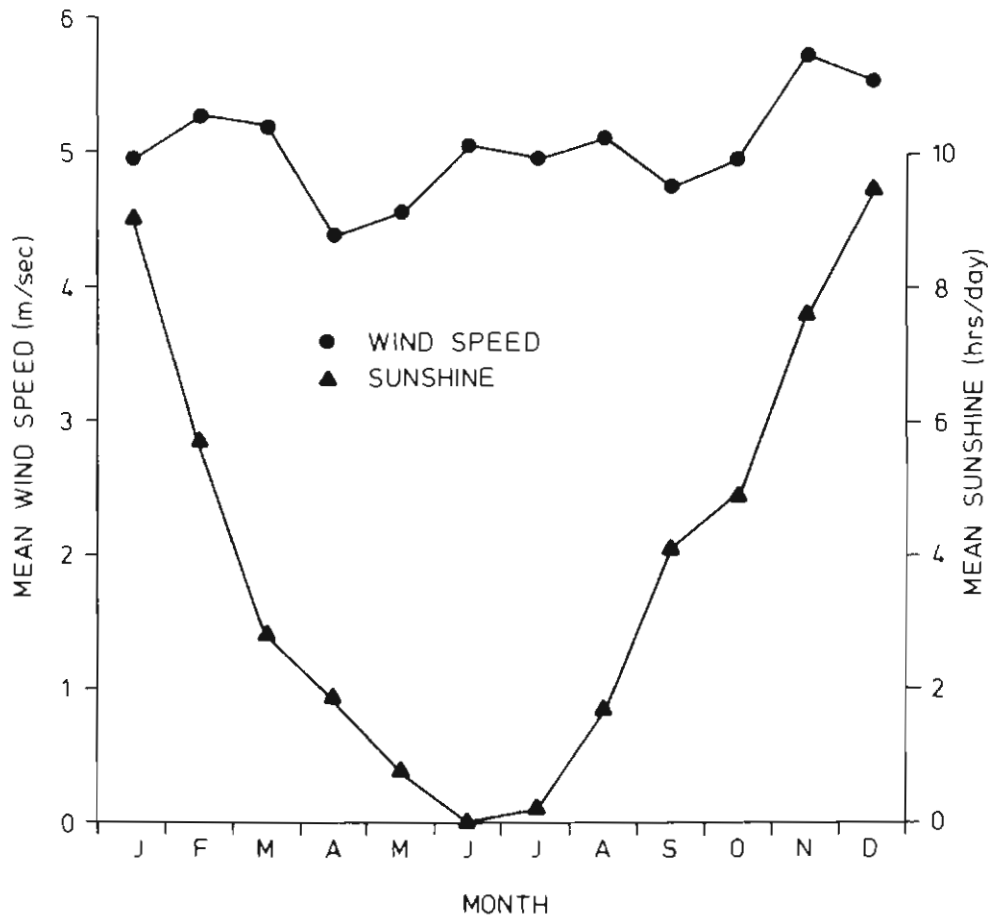


Figure 2. Mean monthly windspeed and sunshine at Davis station from 1957 to 1975 (years 1965 to 1968 not recorded).

maximum temperature, recorded in January 1974, was $+12.4^{\circ}\text{C}$, and the extreme minimum temperature, recorded in July 1973, was -32.0°C .

Mean daily temperature reflects the extreme cycle of solar radiation at Davis station, $68^{\circ}34'\text{S}$ (Figure 2). Summer radiation produces the high mean daily temperatures, whereas, in winter synoptic depressions (Streten, 1962) are thermally dominant. The depressions are accompanied by rising temperatures and short-lived blizzard winds. Blizzards occur most frequently in the winter months (Figure 3). At Davis these winds cause the major axis of the wind direction in June to be ESE (Figure 4).

Mean monthly wind speeds at Davis (Figure 2) are low compared with many other Antarctic stations (Streten, 1968), and are unaffected by the daily katabatic winds flowing from the ice plateau (Lied, 1964). Figure 5 shows that strong winds (more than 34 knots) have a frequency of occurrence of less than four per cent, compared with ten per cent for calms. Calms are defined as less than one knot. The major wind direction in January is NNE (Figure 4). In each month following January the major wind direction shifts successively towards ESE and in each month

following June it shifts back again. In summary, Davis station has frequent calm days, few days of strong winds (which usually occur in winter), and the wind is remarkably unidirectional about a compass axis following a yearly cycle.

The occurrences of drifting snow (Figure 6) are greatest in winter when the strongest winds occur. The winds blow the snow into deep drifts on the lee sides of hills and boulders. In summer the snowdrifts melt and supply most of the moisture which enters the substrate. Falling snow occurs most often in March (Figure 6), but is rarely a source of moisture for the land surface because it soon blows away after reaching the ground. Land not receiving meltwater remains very dry all year round.

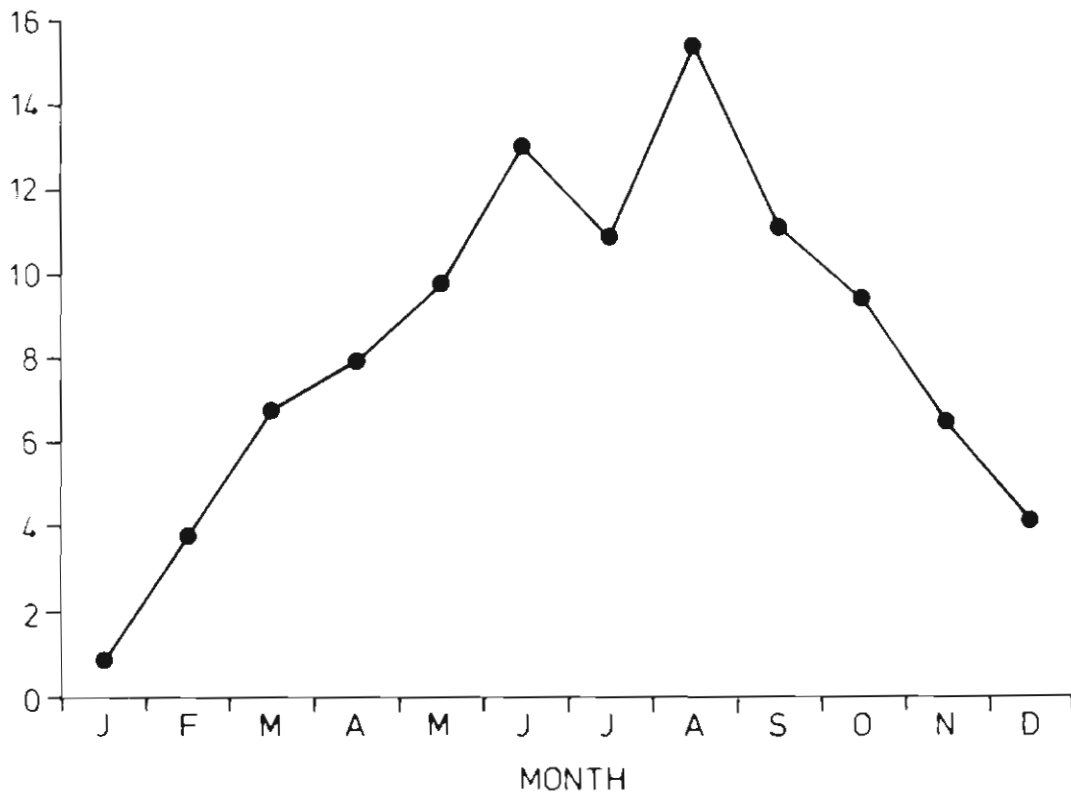


Figure 3. Mean monthly observations of strong winds (> 34 knots) at Davis station from 1957 to 1974 (years 1965 to 1968 not recorded).

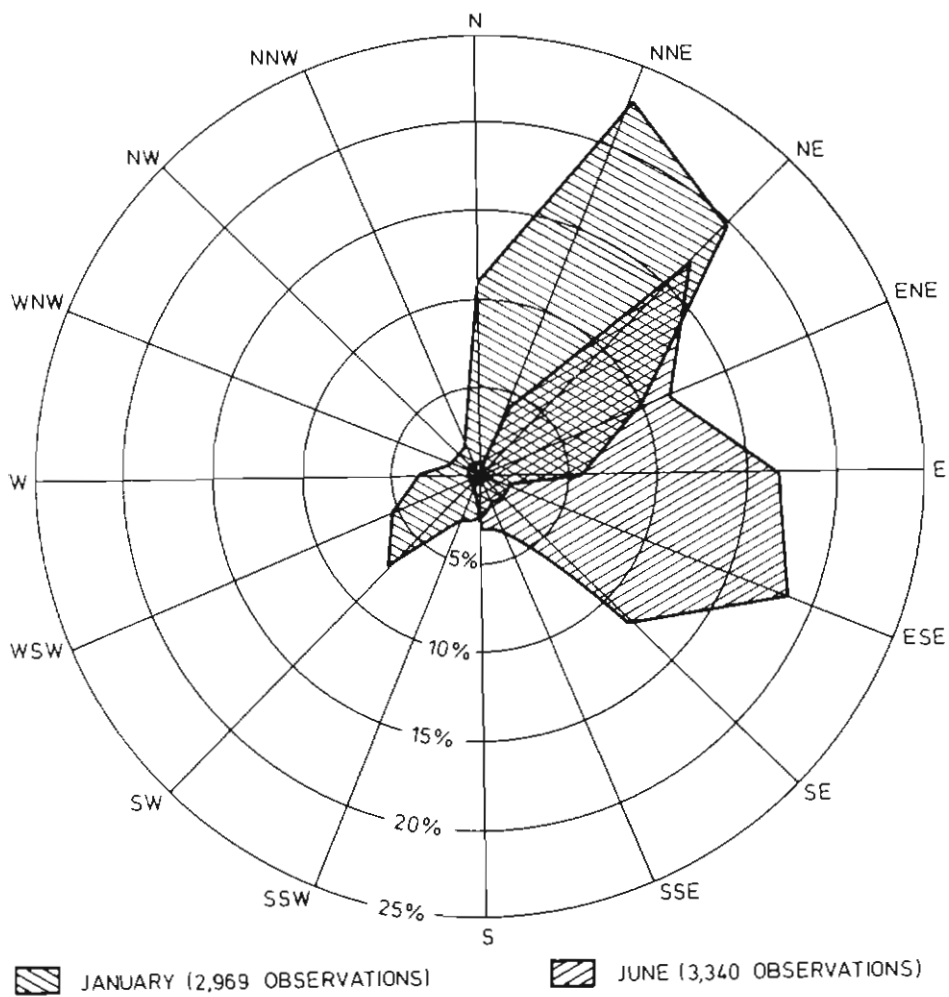


Figure 4. Wind direction at Davis station.
 (Figures are percentage of observations
 with wind in chosen direction. All
 times of day and all years combined
 from 1957 to 1974. Years 1965 to 1968
 not recorded).

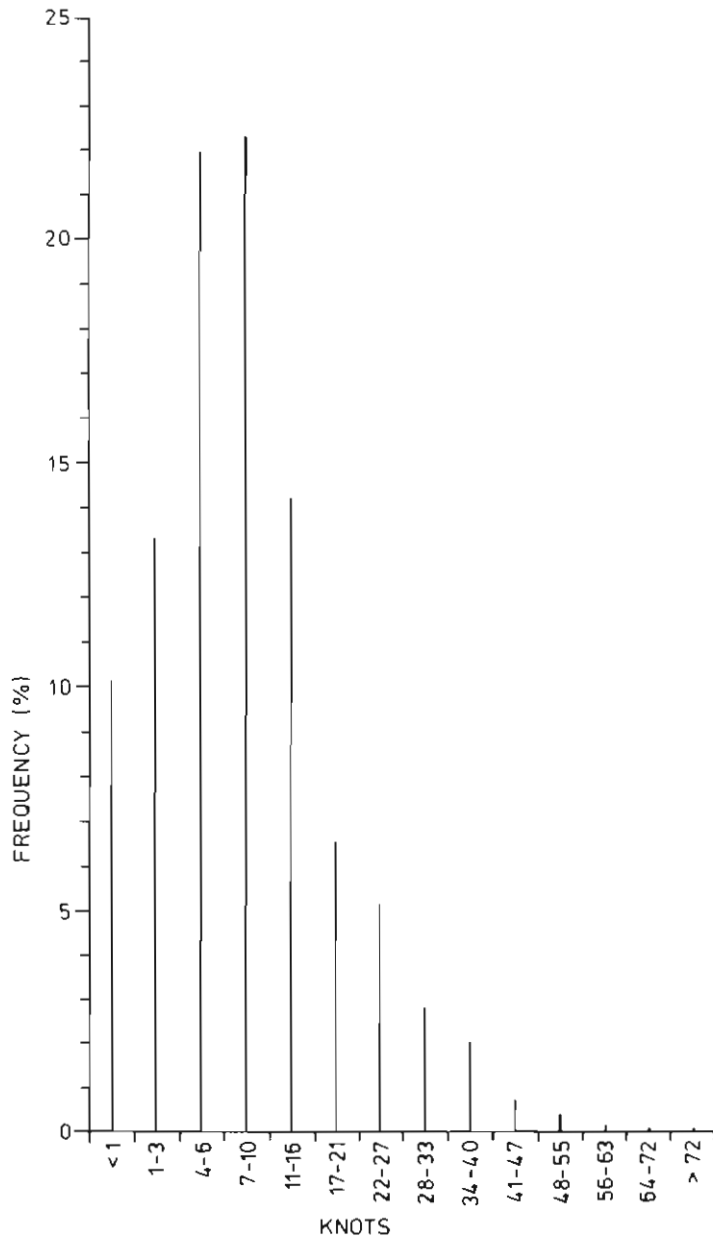


Figure 5. Wind strength at Davis station. (Wind strength is measured as a percentage of observations in each Beaufort wind scale category, whose dimensions are given in Knots. All times of day and all years combined from 1957 to 1974. Years 1965 to 1968 not recorded).

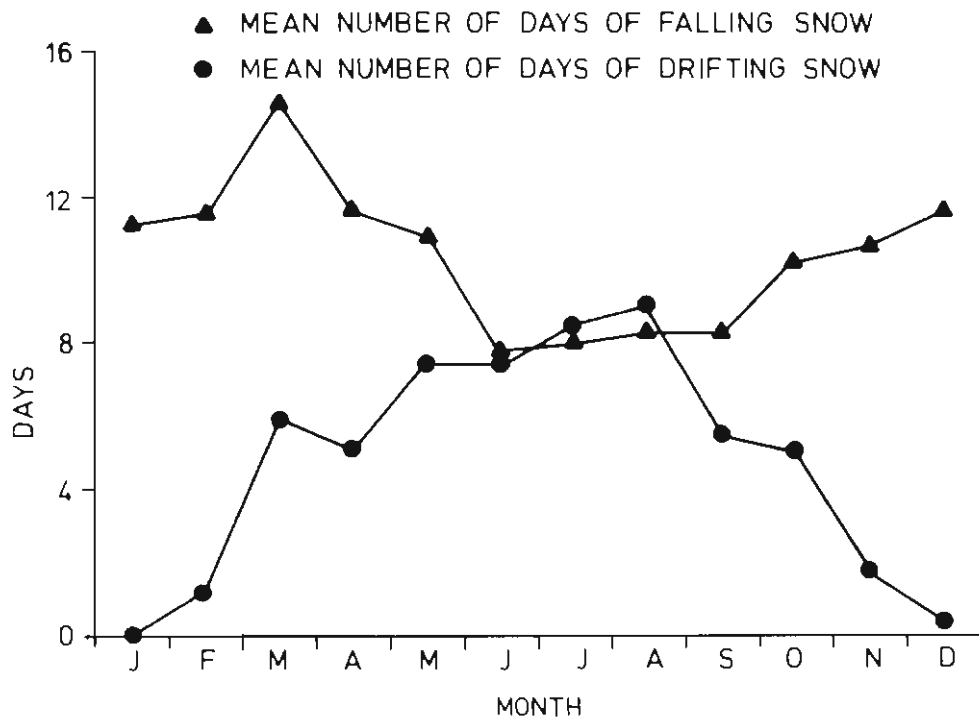


Figure 6. Days of falling and drifting snow at Davis station from 1957 to 1974. (Years 1965 to 1968 not recorded).

4. METHODS AND MATERIALS

4.1 INTRODUCTION

The author left Melbourne on 9 December 1972 to conduct a survey of terrestrial life at the Vestfold Hills. Until that time biologists had made only brief visits to the region in summer. As in most of Greater Antarctica at the time, very few species of organisms were known to inhabit the Chalikosystem at the Vestfold Hills. One species of soil mite, *Tydeus erebus*, was known from a collection made at a single locality in the Vestfold Hills by Dr D.J. Lugg in 1963.

Prior to embarkation preparations were made to conduct a broad survey of terrestrial habitats in an attempt to sample the fullest possible range of organisms which might be found. It was also planned to conduct more specific studies to describe the habitats and the ecology of some of the organisms that were found. A range of suitable methods, equipment and reference material was chosen for the program, and transported to Davis. The station had no facilities for this work except living accommodation. In January 1973 the author, assisted by other members of the expedition, erected a 2 m x 2.4 m x 3 m prefabricated laboratory and fitted it with basic equipment.

Nanorchestes antarcticus was first discovered at the Vestfold Hills during the early stages of the terrestrial survey. From that time the present study was planned in detail using the methods and equipment described below. *N. antarcticus* was deliberately chosen for study because it is the most widespread of Antarctic species of Acari. Available methods and equipment were used, but alternatives were sought for equipment not available. The accurate identification of lifestages of *N. antarcticus* and the identification of other small species of organisms was not attempted in the absence of phase-contrast microscopy at Davis. Moreover, the reference material necessary to identify many species was not available without a reference library. This type of work could only be done after returning to Australia.

4.2 LOCATION AND DESCRIPTION OF STUDY SITES

Nanorchestes antarcticus was discovered in the Vestfold Hills on 30 January 1973, and two main study sites were chosen in the following month. At this time of year the sea was unfrozen, the land was free of snow, and all the snowdrifts from the previous winter had ablated. Offshore islands were precluded as suitable sites for the study of populations of *N. antarcticus* because access was difficult in summer.

One study area, Site A (Figure 7), was only twenty metres west of Davis station on the sloping foreshore separating the station from the sea. The sea was fifty metres away (Plate 2). The location of the site (Plate 3) was marked by pegs and occupied an area of approximately fifty square metres of fine substrate between large boulders. This site was presumed to include

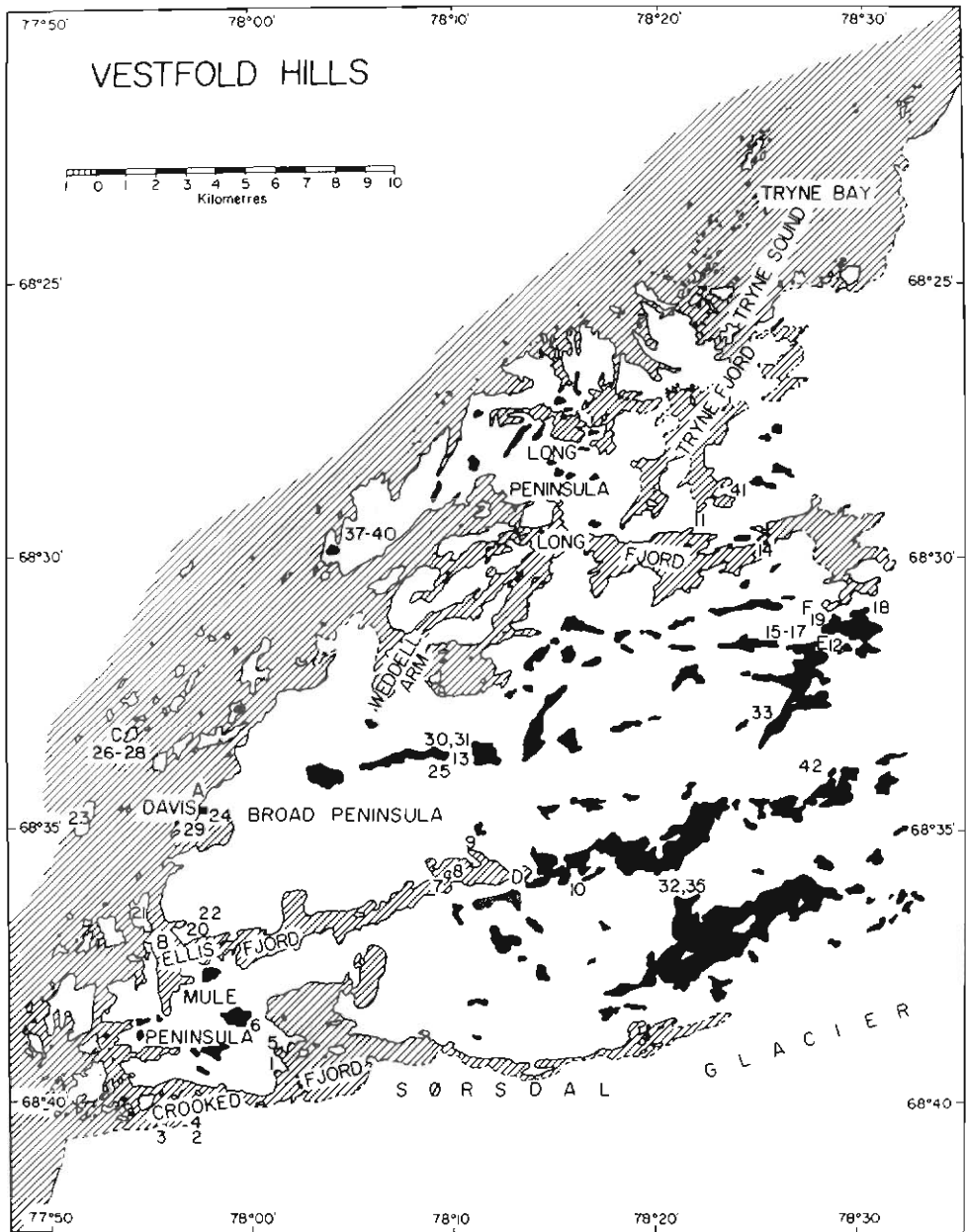


Figure 7. The locations of sites sampled at the Vestfold Hills. Fresh and saline lakes shown in black.



Plate 2. The location of Site A (arrowed) under snow on the foreshore at Davis station in August 1973.



Plate 3. Site A (upper foreground) in March 1973.

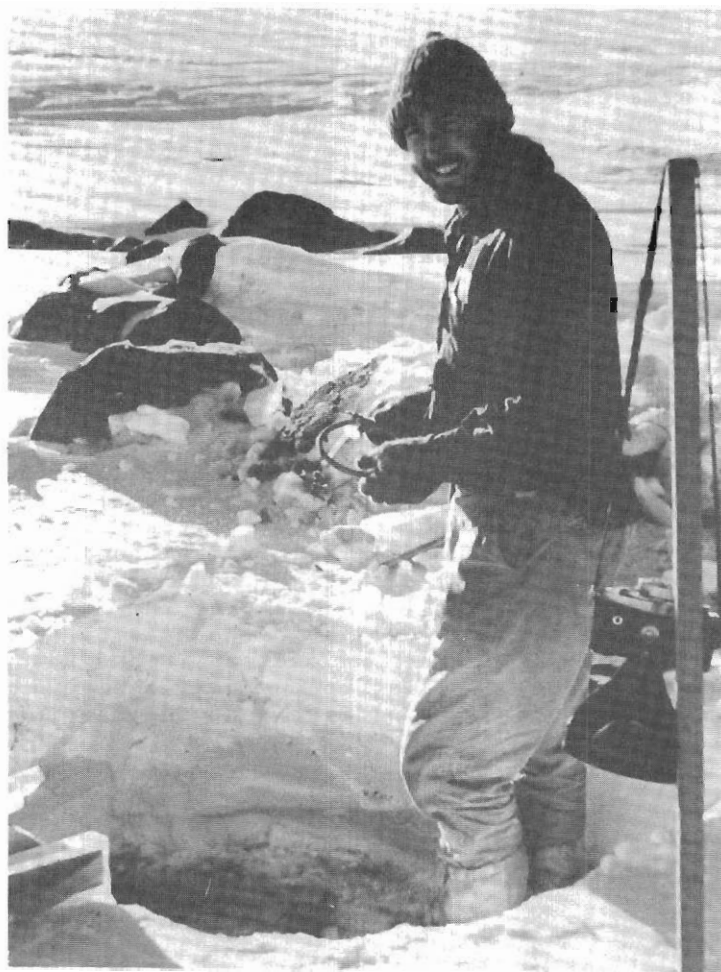


Plate 4. Sampling at Site A through a fifty centimetre deep snowdrift in July 1973.

sufficient mites to provide specimens for laboratory studies throughout 1973. Site A was convenient but also necessary for access to more distant sites was only by foot over rocky terrain on land, or by vehicle on sea ice. Travel on sea ice was safe only from April to October when the surface of the sea was frozen solid.

Site A was considered to be too small to sustain a year-round programme of population sampling on a large scale. It also lay in the lee of station buildings, where the prevailing north-easterly winds had deposited fine splinters of wood and other organic detritus for some years and these had become mixed into the substrate. In the winter of 1973 a snowdrift fifty centimetres deep formed over Site A (Plate 4) and remained throughout most of the thaw. This rendered the area unsuitable for extensive sampling.

A larger study area (Site B), also on a sloping foreshore with a south-west aspect (Plate 5), was chosen on the mainland

coast 4.5 km south of Davis at the mouth of Ellis Fjord. Site B covered an area of 500m² and was exposed so that snowdrifts did not form on it during winter (Plate 6). The site was flat, but sloped gently seaward, and contained a fine heterogeneous substrate mixed with rocks. The majority of rocks at Site B were less than ten centimetres in diameter and lay on the substrate, although boulders embedded in the substrate were common (Plate 7). A twenty-six metre traverse was permanently established across the full width of the site at an angle of 90° to the seaward slope and marked by pegs (Plate 8). Site B was the main sampling location chosen for the study of the associated mite population, and access to it was possible all year round except in extreme weather.

In addition to studies at Sites A and B, the microbiology of forty-four other sites was investigated in the Vestfold Hills during 1973. The locations of all these sites, including Sites A and B, are shown in Figure 7. Multiple samples of substrate were collected from Sites A to F during 1973. Sites C to F were chosen to represent a range of common microbiological habitats. Site C was in a Cape Petrel (*Daption capense*) breeding colony on Bluff Island. Site D was ten kilometres inland at the margin of a large meltwater stream that flowed into the head of Ellis Fjord each summer. Site E was fifteen kilometres inland below a Snow Petrel (*Fagodroma nivea*) breeding colony near the head of Long Fjord. Site F was 500 m north of Site E at the margin of a non-draining meltwater tarn.



Plate 5. Site B on the foreshore at the mouth of Ellis Fjord in April 1973.

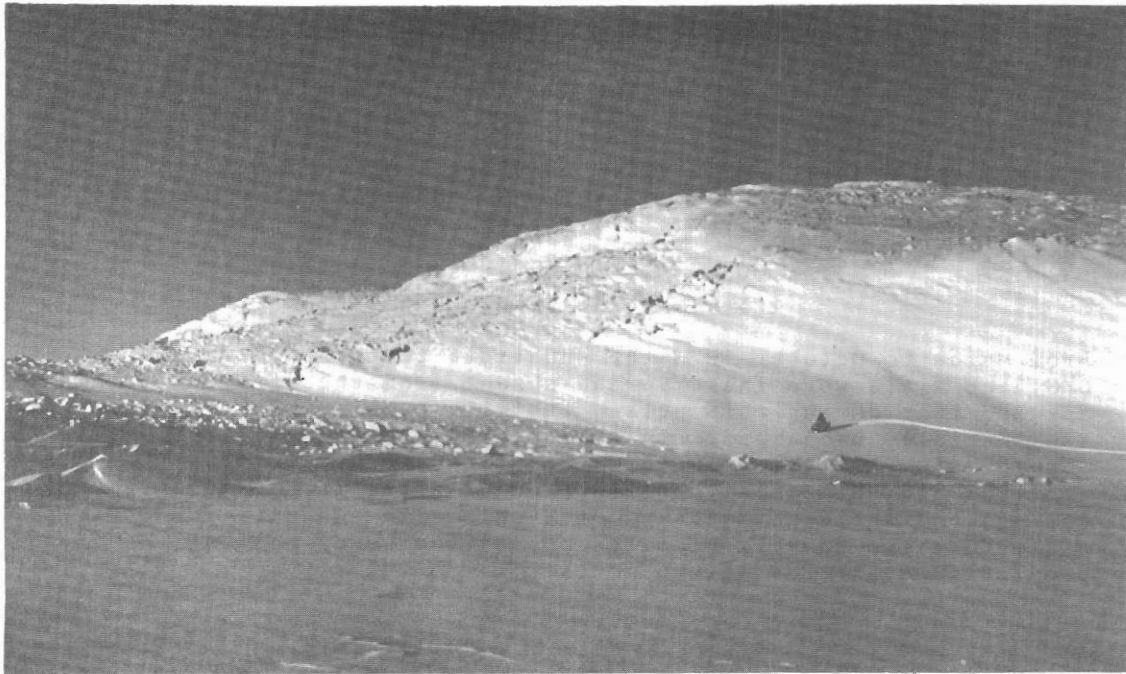


Plate 6. Site B (left) in September 1973. The snowdrift on the right melted during the thaw and water seeped over Site B.



Plate 7. Surface rocks and boulders embedded in the substrate at Site B in April 1973.

Single samples of substrate were collected from sites numbered 1 to 42 (34 and 36 not included) on only one occasion. These sites were sampled in an attempt to include all the terrestrial species which are present. All sites other than Sites A and B were investigated regardless of whether *N. antarcticus* was present or not. *N. antarcticus* occurred at twenty-three of the forty-six sites examined during this study.

4.3 SAMPLING TECHNIQUES

From March to October 1973 the substrate temperature was below 0°C, and mites were inactive and absent from the surface. It was assumed that during this period the mite populations would remain substantially unchanged. In this period, sampling of the mite populations at Sites A and B was confined to determining the vertical and horizontal distribution of mites in the substrate by coring, and the determination of a core size adequate for estimating the numbers of mites per unit area of habitat, or the population densities of the mites.



Plate 8. Pegs (arrowed) marking the 26 m long traverse at Site B in September 1973.

4.3.1 Preliminary Sampling

Population densities at both sites were initially estimated by coring the substrate with cylinders of polythene tubing (internal diameter 8.15 cm, length 10 cm, cross-sectional area 52.2 cm²) sharpened at one end. The cylinders were driven vertically into the substrate as far as the underlying gravel or permafrost would allow, but always to a depth between three centimetres and eight centimetres below the surface. The thickness of the surface layer of fine substrate suitable for coring varied from place to place at Sites A and B. This meant that cores of different lengths were used for quantitative analysis. At Site A, where the fine layer was shallow, cores between three centimetres and five centimetres long were collected. At Site B cores of between five centimetres to eight centimetres long were normally collected because the layer of fine substrate was thicker.

In summer the majority of mites were found in the upper three centimetres of substrate and all cores over three centimetres long were considered suitable for estimating mite density. In winter the mites were inactive and located between one centimetre and five centimetres deep in the substrate. Longer cores were required for estimating mite densities in winter than in summer.

The cylinders were withdrawn with their cores intact, or, if the substrate were very dry and friable, then the contents of the cylinders were spooned and aspirated into glass jars. The aspirated cores, and the cylinders containing intact cores, were sealed in separate glass jars and transported to the laboratory for analysis. Care was taken (as with all cores for quantitative analysis) to transport them in rigid containers and to protect them from unnecessary mechanical disturbance and possible damage.

Four cores, each of area 52.2 cm², were obtained from Sites A and B on 4 and 9 April, respectively, and four cores were collected from Site A on 18 July. The mites were extracted by flotation (Section 4.4), and the physical, chemical and microbiological nature of the substrate in each core was determined (Sections 4.6 and 4.7).

A core surface area of 52.2 cm² was initially chosen to provide enough substrate for physical, chemical and microbiological analysis. These cores also yielded sufficient numbers of mites to estimate the efficiency of the method of extraction of mites by flotation, and the amount of damage done to the mites due to coring.

Nevertheless, apart from providing preliminary estimates of the densities of mites at Sites A and B, the cores yielded unnecessarily large numbers of mites for the estimation of mite density. Greater numbers of cores with a smaller surface area were needed for more precise estimation of mite densities, to avoid oversampling the mite populations, and to limit the very large numbers of mites that would be collected during the main sampling program.

4.3.2 Estimating Horizontal Aggregation

During the analysis of the 52.2 cm² cores it was found that the mites appeared to be aggregated horizontally in the substrate. The degree of horizontal aggregation of inactive mites was

estimated using cylindrical polythene vials (internal diameter 2.11 cm, length 8 cm, cross-sectional area 3.5 cm²) to collect thirty-five cores at Site A on 5 August, and twenty cores at Site B on 16 August. A twenty-five square centimetre quadrat partitioned into 100 subquadrats, each 2.5 cm square, was placed on the substrate. Subquadrats along each of two adjacent axes of the quadrat were numbered consecutively from 0 - 9, and pairs of previously allotted random numbers were used, like the coordinates of a point, to allocate the subquadrats from which the cores were taken. Allocated subquadrats containing rocks that prevented coring had to be omitted. Few subquadrats were omitted for this reason because the quadrat was placed on an area of mite habitat that contained only gravel-sized rocks.

The 3.5 cm² vials were used to collect and transport cores in the same manner as described for the 52.2 cm² cylinders, except that the cores were sealed into the vials with the caps provided. This obviated the need to transport cores in the vials inside glass jars. In August the substrate at Sites A and B was dry and friable. Each core collected was defined by coring the substrate with a tube made from a coring vial and then removed by aspiration into an intact vial for transportation (Plate 9).

Later during summer, the degree of horizontal aggregation of active mites was estimated when diurnal temperatures in the substrate exceeded 0°C. Slightly larger cylindrical polythene vials (internal diameter 2.49 cm, length 8 cm, cross-sectional area 4.9 cm²) were used to collect twenty cores at Site A on 18 December, and sixteen cores at Site B on 22 December. All these cores were withdrawn from the substrate intact, without the need for aspiration, because the substrate was moist at this time of the year; otherwise the same procedures as above were adopted.

4.3.3 Estimating Population Density

In August 1973 a traverse of twenty-six metres in length was permanently established at Site B. Cores of substrate were collected in the larger type of cylindrical polythene vials (internal diameter 2.49 cm, length 8 cm, cross-sectional area 4.9 cm²) at two metre intervals along the traverse. Series of these cores were obtained on eight occasions (2 October, 21 November, 4 December, 1973; 2 January, 16 January, 29 January, 13 February, 27 February, 1974).

Each series of cores was collected at Site B between 12.00 hr and 15.00 hr local geographical time, when maximum temperatures occur at the surface of the substrate on days during summer in Antarctica (Pryor, 1962; Janetschek, 1967). When the cores were collected, measurements of substrate temperature, relative humidity and moisture content were made along the traverse using the methods given in Section 4.7. Cloud cover and wind speed were estimated at Site B on each occasion.

Duplicate cores were taken at the driest and dampest sampling points along the traverse. The duplicate cores were cut into horizontal sections one centimetre thick immediately after collection, and the sections were placed in separate vials for transportation and analysis. These cores were used to record the vertical distribution of mites in the substrate from 21 November 1973, until 27 February 1974.



Plate 9. Aspirating cores in dry substrate at Site B in September 1973.

Cores of 4.9 cm^2 surface area were empirically chosen to estimate mite densities at Site B during the period of mite activity. It was known that at Site B single cores of this size had always contained some mites (frequently more than 100), and that over 100 cores would eventually be collected for analysis. On this basis it was estimated that 4.9 cm^2 cores were about the largest cores that could be used to estimate the density of the mite population without oversampling or obtaining

an unnecessarily large number of mites for analysis.

4.3.4 Recording Vertical Distribution

Seventeen cores of substrate were collected and analysed to record the vertical distribution of mites in the substrate during the period of the study. At Site A single cores were collected on 6 and 27 July, and two cores on 18 November. At Site B three cores were collected on 21 November, and two cores on each occasion thereafter on 19 December, 1973; 16 and 29 January, and 13 and 27 February 1974. All these cores were 4.9 cm² in area, except for the core taken at Site A on 27 July which was 52.2 cm² in area.

The cores from Site B were collected along the traverse as described earlier. In July the substrate at Site A was dry. Intact cores could not be lifted from the substrate with the coring device after it had been driven into the substrate. Neither could the cores be aspirated, as was done in similar circumstances at other times when friable substrate was encountered. The problem was overcome by adding water to the core without disturbing its contents and allowing the core to freeze before removing it for transportation. The frozen core was cut into horizontal sections one centimetre thick, and in the laboratory each section was analysed in the same way as described for the whole cores.

4.3.5 Sampling Under Rocks

On 2 January 1974, when 4.9 cm² cores were collected along the traverse at Site B (as described earlier), seven flat rocks were removed from the surface of the substrate. Mites on the under surfaces of three of the rocks were washed directly into a container with an aqueous solution containing five per cent formalin (by volume), and saturated with magnesium carbonate. Mites from the other four rocks were washed directly into another container with an aqueous solution containing seventy per cent ethyl alcohol (by volume). The horizontal area of habitat occupied by these rocks was estimated by tracing the outline of each rock on to graph paper and summing the number of squares of graph paper enclosed by the pencilled shapes.

This collection of mites was made when population densities were anticipated to be highest during the year, and when the density of mites under rocks could best be compared with the density of mites found in the substrate. The composition of the collection, with respect to the proportions of different stages of mites present, could also be compared with the composition of the collection of mites from cores taken at the same time.

4.3.6 Sampling The Substrate

Samples of substrate for microbiological analysis were collected from all the sites described in Section 4.2. At all Sites except A and B, 200 to 300 gm of the material were scooped into clean new plastic bags. The bags were sealed and transported in cardboard boxes. The samples were stored, frozen and unopened at the laboratory for periods of up to two months until they were analysed.

Eight samples were collected from Site A - four on 4 April and four on 18 July. Four samples were collected from Site B on 19 April, three from Site E, and one from Site F on 20 April, and two from each of Sites C and D on 16 April, 1973. Four samples were actually collected from each of Sites C to F but some replicate samples were not analysed. Samples of substrate from Sites 1 to 42 were collected during field trips in the period from 20 August to 15 December 1973.

4.4 EXTRACTION

All cores of substrate collected in the field were analysed upon arrival at the laboratory, or frozen and stored at a temperature of -15°C . Stored cores were kept for up to several days, until the mites were extracted from them. Frozen cores were individually thawed at a temperature of 3°C , overnight, before analysis in the laboratory at temperatures around 12°C .

An apparatus (Figure 8) was constructed to separate mites from the mineral portion of the cores by flotation in glass-distilled water. The simple apparatus was constructed from a 250 ml Erlenmeyer flask, a rubber stopper and a stirring rod, equipped with a short length of plastic tubing. Initially a saturated solution of sodium chloride was used for flotation, but it offered no apparent advantage over glass-distilled water and subsequently was not used.

The thawed core containing mites was introduced into the empty apparatus and gently dispersed with water. The apparatus then was filled with water and left to stand for several minutes in the open position shown in Figure 8. This period was required to allow the finer mineral particles time to settle out, and for small bubbles of air to rise to the surface of the water. Mites floated to the surface (some were trapped in air bubbles) and were suspended by the meniscus. Dead mites, shrunken carcasses of mites, moulted exoskeletons of mites, mite eggs, some organic detritus and other live organisms, including nematodes and algae, also floated to the surface of the water.

The apparatus was then closed by pulling the rubber stopper up into the neck of the flask as shown in Figure 8. The mites and the other floating material could then be decanted into a Buchner funnel for immediate observation, or into vials for storage. The upper part of the flask was rinsed twice with water after decanting the contents to dislodge any remaining mites.

The technique of extracting mites from mineral substrates by flotation is convenient and rapid, particularly in Antarctica, where the substrate contains only very small amounts of organic material. This technique was first applied to *N. antarcticus* by Gressitt et al., (1964), but these authors did not indicate how efficient the process was. During the present work a 500 gm sample of substrate was extracted as described above (but with an apparatus made from a 1500 ml flask), and the mites obtained were decanted. The apparatus was then opened, the sample was stirred gently, and the apparatus was refilled with water and allowed to stand. After several minutes the apparatus was closed and decantation was repeated as before. This process was repeated

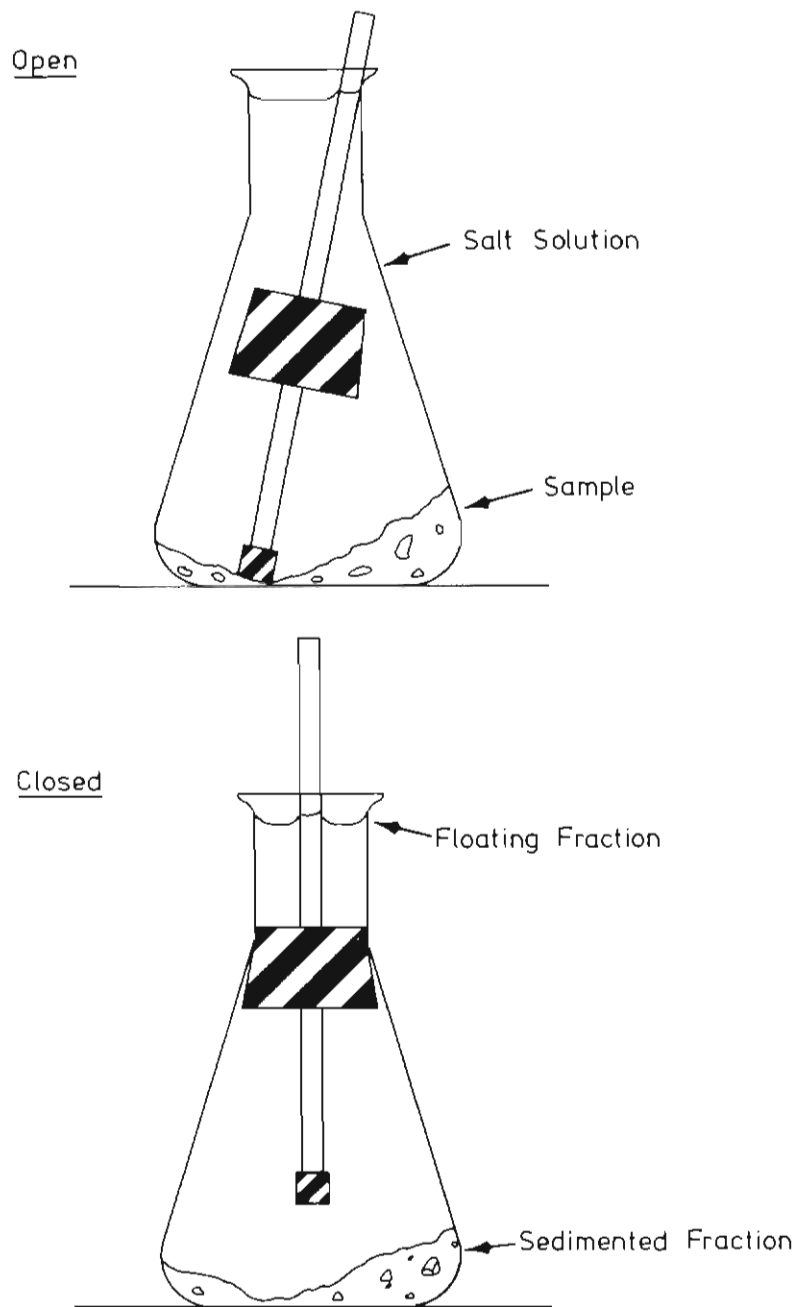


Figure 8. Flotation apparatus.

three times so that decantation was carried out four times using the same sample of substrate. The first time 198, then one, and thereafter no more mites, were obtained in successive decantations. Thus the process was estimated to be 99.5 per cent efficient at extracting all buoyant mites in one decantation.

Janetschek (1967) warned that if the flotation technique is to be applied quantitatively then the samples of substrate should be extracted at the site of collection, or transported carefully to avoid damage to the mites before extraction. The former method was rejected because it was impractical under the conditions experienced during this study.

4.5 COUNTING AND IDENTIFICATION

Phase-contrast microscopy was not available at Davis for the detailed examination and identification of mites. For this reason mites were extracted from the 4.9 cm² cores taken along the traverse at Site B, and preserved for later analysis in Australia. Nevertheless, cores for determining the horizontal and vertical distributions of mites were analysed at Davis for information required to conduct the field work.

Extracted mites were decanted into a nine centimetre diameter Buchner funnel and collected on a Whatman No. 1 filter paper (nine centimetre). If the sample of mites was for analysis in Australia, then the damp filter paper was removed from the funnel with the adhering mites and placed directly into a vial of preservative containing seventy per cent absolute ethyl alcohol and thirty per cent distilled water (by volume). If the sample were to be analysed immediately, then the filter paper was ruled into sixteen equal sectors before the mites were decanted into the funnel. When the mites were decanted the damp filter paper was removed with the mites adhering to it, and placed on the stage of a stereomicroscope. The mites were examined and counted at a magnification of twenty-five times by systematically scanning each of the ruled sectors. This magnification was necessary because unhatched eggs and larvae are approximately 100 microns and lack any dark colouration to contrast them against the white filter paper.

Under the stereomicroscope the material was separated into a number of categories: eggs; fed larvae; unfed larvae; nymphs and adults; black, dehydrated carcasses of mites (dead before collection); moulted cuticles; and mites that had recently died. The legs of live mites contained a bright red pigment that became dull when the mites were dead. This colour change was used to detect mites that were killed by the sampling procedures. The stadia of nymphs, the sex of adults, and the numbers of eggs contained in females, could not be determined by this method, which was primarily used to count mites and detect the timing of events in the mite populations.

Preserved mites were counted and placed into a five per cent aqueous solution of potassium hydroxide to dissolve all soft tissues from the chitinous structures (eggshells and cuticles) which remained. Immature eggs inside females were completely dissolved; but mature eggs remained as pre-larval cuticles within an egg-shell.

After clearing for twenty-four hours, the mites were permanently mounted on glass microscope slides under 51 mm x 22 mm cover slips. Many mites, all originally obtained from the same core of substrate, were mounted on each slide. All the mites from the same core were thus accommodated on one, two or three slides. The mountant used was Hoyer's medium (Baker and Wharton, 1952): 1 part (by volume) glycerol, 1.5 parts gum acacia, 2.5 parts distilled water and 10 parts chloral hydrate. The prepared slides were oven-dried at 50°C for twenty-four hours.

Individual mites were relocated by systematically scanning the slides at a magnification of 100 times with a phase-contrast microscope. As each mite was found it was examined at a magnification of 1000 under an oil immersion objective. Large numbers of mites were mounted on each slide to reduce the amount of manipulation and time required to examine each mite in this way. Each slide was only scanned once. All free-living stages of the mite: larvae, protonymph, deutonymph, tritonymph, male and female, were identified using morphological criteria provided by Lindsay (1972).

Amongst the 10,318 mites that were counted from cores obtained at Site B, 6,789 (65.8 per cent) were identified as one of the six free-living stages, 931 (nine per cent) were unidentifiable, and 2,592 (25.1 per cent) were not relocated on the slides. Some mites were unidentifiable because either they retained opaque deposits of uric acid crystals inside the hysterosome, were poorly oriented, or were obscured by other mites. Some mites that were not relocated could have been overlooked during scanning of the slides. A few slides were prepared with too much mountant and a number of mites were lost from these slides in the excess mountant. Approximately five per cent of the mites from two cores was lost by spillage from three open storage vials before they could be mounted on slides.

Information about the life-stages of mites that were unidentifiable, or not relocated was unavailable. The life-stages of these individuals were assumed to be represented in cores in the same proportions as for mites for which life-stages were known. In Appendix A, tables giving the results of core analyses show the total numbers of life-stages recorded for the identified mites and the corrected totals (based on the above assumption) which represent the numbers of life-stages for all the mites in the cores.

4.6 PHYSICAL AND CHEMICAL MEASUREMENTS

The temperature and relative humidity of air, and the temperature, relative humidity and moisture content of substrate, were measured along the traverse at Site B when cores were collected. These measurements were also made at Site A when cores were collected during 1973, and occasionally at Sites C to F.

Air temperatures were measured with a mercury-in-glass air thermometer to an accuracy of $\pm 0.2^{\circ}\text{C}$, and temperatures in the substrate were measured with a thermistor thermometer (Plate 10). The thermistor thermometer was a portable Wheatstone's bridge equipped with a 100 mV f.s.d. meter with a linear scale and powered by nine volt dry batteries. The temperature sensors were

"F22" S.T.C. thermistors (Radio Parts Pty Ltd., Melbourne) mounted inside glass needles. The thermistors provided a linear response to temperature changes from -30°C to $+20^{\circ}\text{C}$. Temperature was measured to an accuracy of $\pm 0.07^{\circ}\text{C}$ with this thermometer.

The thermistor thermometer was suitable for operation over long periods of time at sub-zero temperatures in the field without battery failure because it consumed only a small amount of power. Temperature measurements were made by driving the sensor into the substrate, or underneath rocks, with minimal disturbance to the surrounding substrate.

A portable, battery-powered, electronic hygrometer ("Rotronic, Hygroskop B") was used to measure the relative humidity in the air and the substrate. The meter (Plate 10) was calibrated with standard solutions of lithium chloride supplied by the manufacturer, and was accurate to plus or minus two per cent relative humidity. The sensor was disc-shaped (diameter fifteen millimetre, five millimetre thick) and mounted on a probe. The probe was pushed obliquely into the substrate to the required depth and the measurement was made on the undisturbed substrate immediately beneath the sensor. The hygrometer would not operate after about one hour in the field at temperatures around -10°C because of battery failure, but continuous operation was possible in temperatures above 0°C .



Plate 10. The portable hygrometer (left), thermistor thermometer (centre) and their sensors (foreground) which were used to measure the relative humidity and temperature of substrate.

The amount of water in the substrate (including ice), as a percentage of the dry weight of a substrate sample, was measured with a moisture meter ("Speedy" Model D1, range zero to twenty per cent - Thomas Ashworth and Co. Ltd). This instrument was designed to produce direct readings of percentage moisture and its operation was unaffected by low ambient temperatures.

A mixture of five parts (by weight) of glass-distilled water and one part of substrate was filtered with Whatman No. 1 filter paper to produce extracts of substrate for chemical analyses. The electrical conductivity of extracts was measured with a platinum electrode conductivity meter ("Metrohm", Model 382), and expressed as a total amount of soluble salts. The pH of extracts was measured at 10°C with a temperature compensating pH meter ("Radiometer", Model PHM 26).

The concentration of chloride ions in extracts was measured by titration with a 0.01N silver nitrate (Strickland and Parsons, 1968).

Levels of phosphate in the extracts were estimated by the ammonium molybdate method; nitrite after reaction with sulphanilimide, and nitrate (after being reduced in a cadmium reducing column) as nitrite (Strickland and Parsons, 1968).

Apart from the microclimatic measurements discussed above, routine observations of weather were not considered necessary to provide information about the climate of Sites A and B. Suitable records of weather data were available from routine observations made by Commonwealth Bureau of Meteorology staff at Davis.

4.7 MICROBIOLOGICAL METHODS

Samples of substrate for microbiological analysis were thawed, unopened, in the collecting bags. On opening the bags quantities of substrate, estimated to be 0.5 gm, were immediately sprinkled into petri dishes (nine centimetre diameter) containing Czapek-Dox agar (Parkinson et al., 1971). A proprietary brand of condiment containing yeast extract ("Vegemite", Kraft, Australia) was used instead of prepared yeast extract to make this agar. Nutrient agar (Difco) was initially used for isolating micro-organisms from substrate but Czapek-Dox agar grew a wider range of micro-organisms more vigorously.

The plates of substrate were incubated at 20°C for up to one month to observe the sporulation of fungal colonies. During this period the plates were observed regularly and the numbers and types of bacterial, streptomycete and fungal colonies grown were recorded. Most bacterial colonies were small, but visible after four days, and became senile in a week. Colonies of streptomycetes were also small, but required more than two weeks for sporulation. Some fungal mycellia grew rapidly, and eventually covered a large area of the agar, obscuring many of the bacterial colonies. Provided that the plates were observed regularly, there was no difficulty in counting all the colonies of different kinds of organisms present. A reference collection was made, by subculturing each type of micro-organism until the return to Australia.

The remainder of each of the substrate samples was weighed and then placed in a sterile 1500 ml Erlenmeyer flask and mixed with five times its weight of sterile glass-distilled water. After allowing the mixture to stand for thirty seconds, a one millilitre sample of the supernatant mixture was withdrawn and diluted to one-tenth, one-hundredth and one-thousandth its original volume. One millilitre of sample at each dilution was spread on to Czapek-Dox and nutrient (Difco) agars. Sterile glassware and sterile glass-distilled water was used for this procedure. Each plate was incubated at 20°C and observed as described above.

A 100 ml portion of the original mixture was then filtered through a Whatman No. 1 filter paper to produce an extract for chemical analysis. The remainder of the sample was saturated with rock salt (NaCl) to extract plants and animals by flotation. Mites, nematodes and small clumps of algae were collected in a Buchner funnel and preserved for later examination. A sample of supernatant was allowed to stand for several minutes and the sediment obtained was examined through a microscope for diatoms and microscopic algae.

Moss and macroscopic algae in the original samples of substrate were removed and treated separately. Animals were extracted from the plants with a Baermann funnel (Southwood, 1969), examined alive, and then fixed in hot neutral formalin (five per cent), or Schaudinn solution (Pantin, 1964).

Fungi isolated from the original cultures were subcultured on four media. The media were: Czapek-Dox agar, malt agar (1.5 gm malt extract in one litre distilled water), sea water agar (ten grams glucose, three grams "Vegemite" in one litre of artificial sea water), and an agar containing ten grams glucose, three grams "Vegemite" in one litre of distilled water. Observing the growth of these fungi on different media permitted most of the replicated subcultures of the same species of fungi to be detected. This technique was necessary because the mycelial characteristics of some fungi (e.g. *C. pannorum*) in the original cultures were quite variable.

Subcultures of fungi were also grown on Czapek-Dox agar and malt agar at temperatures of 3°C, 10°C, 20°C and 26°C. After two weeks the diameters of the mycelia were measured, and the rates of growth of fungi at the different temperatures on each medium were then compared. These results provided a check on the validity of the fungal taxa detected by culturing on different media. A subculture of each species of fungus was kept for later identification in Australia.

Samples of substrate, estimated to weigh 0.5 gm, were plated directly on to Czapek-Dox agar from depths between the surface and two centimetres and between four and five centimetres at Site A on 14 May and 21 December 1973. The plates were incubated at 20°C and observed regularly. The number of mycelia of each species of fungi growing on each plate was recorded. The experiment was designed to indicate the relative abundance of fungal propagules at different depths in the substrate at different times of the year.

On 3 September, thirteen inactive *N. antarcticus* were extracted from substrate by flotation. Five were transferred

from the extraction apparatus and plated, four intact and one squashed, on to Czapek-Dox agar with a sterile needle. Eight were briefly dipped in a solution containing seventy per cent absolute ethyl alcohol and thirty per cent distilled water (by volume); four of them plated intact and four squashed. Two of the latter mites were squashed whilst still wet and two after they had dried. The plates were then incubated for fourteen days at 20°C.

This procedure was designed to show whether mites carried live micro-organisms on their cuticles (intact mites) or inside their bodies (squashed mites). Two of the squashed mites were allowed to dry after being dipped in case the adhering alcohol killed any micro-organisms inside the mites as the mites were squashed. On 3 December a similar procedure was followed, but this time with four active mites. All the mites were squashed directly on to the agar without being washed in the alcoholic solution.

In Australia 73 cultures of bacteria were freeze-dried in triplicate. These bacteria have not been identified. At Davis they were classified by their colour, shape and response to Grams' staining. The two yeast cultures failed before the return to Australia. The two streptomycetes were identified only to generic level. One fungus was identified at Davis (*D. salina*), and six others were identified by Dr. H.J. Swartz, Department of Botany, University of Melbourne.

4.8 EXPERIMENTS ON BEHAVIOUR

On 16 August 1973, a sample of substrate containing inactive mites was collected at Site B at a temperature of -10°C. The sample was taken to the laboratory and heated to a temperature of 25°C under a lamp. Five of the mites which became active and left the sample were collected and then placed in a one by two centimetre observation chamber. The chamber was suspended in a bath containing a mixture of glycerol (forty per cent by volume) and water. The bath was then cooled to a temperature of -16°C and kept in a relative humidity of eighty per cent for twenty-four hours.

After twenty-four hours the bath was allowed to warm slowly to a temperature of 12°C on a bench in the laboratory. During this period of warming the mixture was constantly stirred with a magnetic stirrer, and the change in the temperature of the mixture was measured with a mercury-glass thermometer (accuracy $\pm 0.2^\circ\text{C}$). As the temperature of the mixture increased by $0.7^\circ\text{C}/\text{min}$ the behaviour of the mites inside the chamber was observed through a stereomicroscope. After about twenty minutes when the observations were completed, the bath containing the mites in the chamber was again stored at a low temperature. The procedure was repeated after storing the bath for three days at a temperature of -19°C and again after six days at 2°C.

The same method was used to observe the behaviour of summer-collected mites kept at low temperatures. Five active mites were collected at 6°C from under rocks at Site A on 6 January 1974. The mites were placed directly into the chamber when the

bath mixture was at a temperature of -10°C and then kept at -10°C for one-and-a-half hours before being rewarmed as described in the last paragraph. Later rewarming was carried out after the mites were stored at temperatures of -10°C for thirty-six hours, and -15°C for sixty hours.

After these experiments had been carried out, the probe of the thermistor thermometer (Section 4.6) was placed inside the chamber and the warming procedure was repeated. This allowed the change in temperature inside the chamber to be calibrated against the change in the temperature of the bath, so that the temperature of the mites during the experiments could be estimated.

To observe the behaviour of active mites being cooled to low temperatures, a group of five mites was collected from under rocks at 6°C in Site A on 9 January 1974. The mites were placed in the observation chamber when the bath mixture was at a temperature of 6°C . The bath was then cooled to a temperature of -15°C during a period of twenty-four hours. During this period the temperature of the bath was measured hourly, for the first three hours, and the behaviour of each mite was noted.

5. RESULTS

5.1 HABITAT

Nanorchestes antarcticus was found in valleys along meltwater courses, and in similar lowland situations where the drainage of freshwater from snowdrifts moistened substrate during the spring thaw (Plate 11). Suitable areas of habitat were confined by the limits of seepage during the thaw.

Substrate that did not receive meltwater during the thaw usually contained less than 0.5 per cent water by weight throughout the year, and was not inhabited by *N. antarcticus*. On the steep slopes of mainland hills and nearby offshore islands snowdrifts were absent or small, and meltwater from the slopes drained rapidly into valleys or the sea below during the thaw. At these sites the substrate was either permanently dry or moistened only briefly during the thaw, and hence did not support *N. antarcticus*.

The main source of water for the surface of the land at the Vestfold Hills is from the snowdrifts that form in winter. They are formed by the prevailing north-easterly winds on the lee

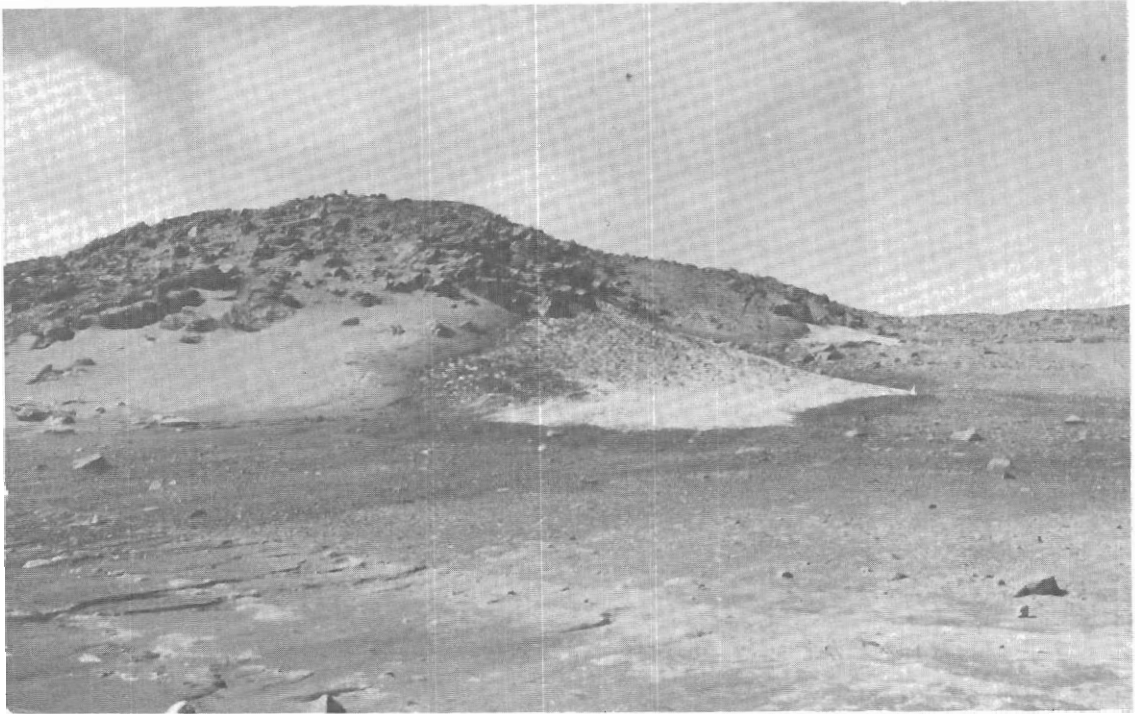


Plate 11. The remains of a snowdrift in December 1973. The habitat of *N. antarcticus* is confined to the damp substrate in the foreground.

sides of rocks and hills, and on melting yield much of their water to the surrounding substrate. The larger snowdrifts take the longest time to melt completely and supply the surrounding substrate with water from October to December or January.

In the summers of 1972-73 and 1974-75 some large snowdrifts did not melt completely until about the end of January. Persistent snowdrifts were most noticeable at Davis where they had been formed in the lee of buildings, but large snowdrifts also persisted at other sites in the Vestfold Hills. During the summer of 1973-74 (in the period of this study), snowdrifts around Davis, and elsewhere in the Vestfold Hills, had melted completely by the beginning of January. This meant that the substrate at Sites A and B, and elsewhere in the habitat of *N. antarcticus*, began to dry out earlier in the summer of 1973-74 than in the summers immediately before or after it.

A large snowdrift near Site B began to thaw at the end of October 1973, and water from the snowdrift drained over the site and across the sampling traverse. In November, when this flow of water was greatest, the central portion of the traverse was often awash during the warmest time of the day. At this time the mites were submerged in water-saturated substrate or trapped in pockets of air beneath rocks at the surface of the substrate. During the coldest time of the day a thin layer of ice formed at the surface of the water flowing over the substrate and the flow of meltwater abated, but water continued to seep through the substrate beneath the ice.

Table 2 shows the amounts of water contained in the substrate when cores were collected along the traverse at Site B. On 21 November water intermittently flowed across the traverse at the surface of the substrate over the positions indicated in Table 2, but seeped into the lower layers of substrate all along the traverse. The results in Table 2 were obtained from samples from the top three centimetres of substrate, but the amount of moisture in the substrate varied widely with the depth at some points on the traverse. For example, at twenty-two metres on 21 November, the surface substrate contained 0.2 per cent water; at a depth of two centimetres the substrate contained 2.4 per cent water, and at a depth of six centimetres it contained seven per cent water. Thus the results shown in Table 2 serve only as a guide to the amount of water in the substrate at that time.

Table 3 gives the temperatures of air, rocks and substrate along the traverse around noon on days when cores of substrate were collected at Site B. Measurements were made at two metre intervals along the traverse, but only a representative temperature or range of temperatures is given for each vertical position on the profile of the traverse in Table 3.

Steep, but stable, thermal gradients existed between the air, the surface of the substrate, and deep substrate over the period of measurement, except when the rapid flow of air or water across the traverse caused local differences in the distribution of heat.

The highest temperatures were consistently found in the top one centimetre of the substrate, and beneath rocks at the surface - where most mites occurred in summer. On 2 January 1974, a cloudless day with almost no breeze, a thermal gradient of 16.0°C

Date	Distance along traverse (m)												Mean				
	24	22	20	18	16	14	12	10	8	6	4	2		0	-2		
15 Sept. 1973																	
	(between 0.0 and 0.5)																
2 Oct. 1973																	
	(between 0.0 and 0.5)																
21 Nov. 1973	-	2.4	4.3	13.1	*	*	10.0	10.9	*	*	*	*	*	*	*	*	-
4 Dec. 1973	-	-	13.7	-	13.7	-	13.7	-	13.7	-	-	-	8.6	-	-	-	-
18 Dec. 1973	10.3	12.9	13.0	-	13.1	-	13.0	7.8	5.9	4.9	4.8	6.7	3.4	6.9	7.7		
2 Jan. 1974	6.0	-	8.2	-	8.2	-	3.6	-	6.3	-	9.4	-	5.7	-	6.8		
16 Jan. 1974	6.7	-	4.7	-	5.3	-	1.2	-	1.2	-	2.2	-	1.1	0.9	2.9		
29 Jan. 1974	5.5	-	6.4	-	5.3	-	2.4	-	1.9	-	2.8	-	3.8	2.8	5.9		
13 Feb. 1974	6.4	-	4.3	-	4.5	-	3.2	-	2.1	-	2.2	-	2.7	0.3	3.2		
27 Feb. 1974	3.8	-	2.9	-	3.7	-	1.0	-	1.0	-	2.3	-	1.4	0.9	2.1		

(* = water flowing over substrate)

Table 2. The percentage weight of water in substrate along the traverse at Site B on days when cores were collected.

Date	Air Temperature			Surface Temperature			Temperature in Substrate				
	Davis (1m)	Site B (1m)	Under Rocks	On Substrate	1cm	2cm	3cm	4cm	5cm		
15 Sept. 1973	-12.8	-12.8	-10.0	-3.9	-10.0	-	-	-	-		
2 Oct. 1973	-9.5	-6.7	-7.0	-1.0/0.5	-1.7/0.0	-3.5/-4.1	-	-	-		
21 Nov. 1973*	-0.2	0.5	2.3	4.2	4.0/5.8	1.8/4.0	0.7/2.6	0.4/1.3	-		
21 Nov. 1973+	"	"	"	13.0	14.7	8.5/9.9	6.4/6.9	5.8/6.5	6.5	5.9	
4 Dec. 1973	-3.7	-2.0	0.9	6.5	4.7	2.5/4.3	1.6/3.4	0.5/2.5	0.2/1.3	0.0	
18 Dec. 1973	0.4	1.0	5.0	-	10.3	11.4	11.0	10.7	10.2	9.7	
2 Jan. 1974	0.5	2.0	5.0	18.0	18.0	17.2	16.9	16.1	15.4	-	
16 Jan. 1974	4.0	6.9	9.8	-	14.5	10.9	10.2	10.0	9.5	8.8	
29 Jan. 1974	1.0	-0.3	4.7	-	10.8	8.5	6.2	6.8	6.2	5.3	
13 Feb. 1974	-3.0	-3.0	1.5	3.0	3.2	3.5	2.6	0.8	0.0	-0.2	
27 Feb. 1974	0.0	0.0	2.0	-	2.5/6.2	0.4/1.8	-0.2/1.9	0.2/0.5	-0.2/0.0	-0.3	

(Temperatures at flooded *(0m) and unflooded +(22m) parts of the traverse.
Range of temperatures is indicated by /).

Table 3. Air and substrate temperatures (^oC) at Davis, and along the traverse at Site B on days when cores were collected.

existed between the surface of the substrate (18.0°C) and the air (2.0°C) one metre above. A similarly steep gradient of 14.8°C occurred at Site A on 7 January 1974, when a record maximum air temperature (1.5 m) of 12.7°C occurred at Davis station in the early afternoon. The temperature recorded at the surface of the substrate at this time was 27.5°C. Over the summer the temperature recorded at the surface of the substrate at about noon was between 5°C and 15°C higher than the air temperature one metre above the substrate. The high temperature at the surface of the substrate was caused by direct isolation and was attenuated by cloud, wind, and water flowing across the traverse.

In the laboratory, ten of the sixty-two mites extracted on 3 October 1973 from two cores taken on 2 October 1973 were active. Temperatures in the top one centimetre of substrate at Site B were close to 0°C at this time. Mites that had been inactive in the substrate during winter apparently were being reactivated by temperatures above 0°C as the deeper part of the substrate was warmed. Correspondingly, temperatures in the substrate on 27 February 1974 were also near 0°C, and were soon to remain below 0°C from early March until the following October. By inference from experiments discussed later, the mites retired to the lower layers of substrate at about this time and remained inactive during winter.

Table 4 shows that the relative humidity of the air one metre above the substrate at Site B was less than the corresponding relative humidity of air measured at Davis. Site B was slightly warmer than Davis (Table 3), and this fact may partly account for the lower relative humidity. One centimetre above the substrate at Site B, where the highest air temperatures were detected, the relative humidity of the air was also consistently low. Nevertheless, just below the surface of the substrate the air was saturated or nearly saturated even in February, the driest month when mites were active.

Snow fell on thirteen days during February 1973, and on fifteen days during February 1974, but during this month heavy snowfalls of over two centimetres occurred only in the week prior to the last sampling date.

As in other lowland areas of the Vestfold Hills, most of the substrate at Site B is composed of glacial till, ranging in size from glacial flour to erratics. Other particles originated from ice-shattered rocks or wind-blown material, but all appeared to have been formed from the country rock types. A thin layer of sand-sized particles covered Site B. The particles were pieces of biotite, garnet, silica and other minerals that are common in the bedrock. This sandy material appeared to have been deposited with snow as a wind-borne sediment in the large snowdrift above Site B, and then spread over the site by the joint action of wind and meltwater. Because the site was sloped, and well drained, ice polygons caused by the freeze-thaw cycle were absent.

At other sites where *N. antarcticus* occurred, the substrate below large snowdrifts also appeared to have been supplemented with wind-borne sediment. For this reason the occurrence of *N. antarcticus* may be positively correlated with the occurrence of a sandy substrate; but sand is not considered as a necessary

Date	R.H. (%) in Air			R.H. (%) in Substrate		Cloud (tenths)	Wind (m/sec.)
	Davis (1m)	(1m)-Site B)-(1cm)	Site B(0-1cm)	Site B(0-1cm)	Site B(0-1cm)		
15 Sept. 1973	72	27	32	89 to 94	0	5.0	
21 Oct. 1973	43	31	38	65 to 100	4	7.5	
4 Dec. 1973	41	27	32	100	1	7.5	
18 Dec. 1973	53	38	32	100	1	4.0	
2 Jan. 1974	77	29	34	94	0	0.5	
16 Jan. 1974	63	-	-	100	4	5.0	
29 Jan. 1974	68	40	30	100	5	2.5	
13 Feb. 1974	-	30	30	100	10	0.5	
27 Feb. 1974	-	30	25	100	10	2.5	

Table 4. Relative humidities (R.H.%), wind speed and cloud cover at Site B on days when cores were collected. Standard R.H. data for Davis are included for comparison.

requisite of the habitat of the mite (Table 1 of Appendix B).

Apart from the sandy layer, the substrate had none of the structure of a soil. Organic material was present only in minute quantities - insufficient to affect the structure of the substrate. For this reason the substrate is not referred to as soil.

Some chemical characteristics of the substrate at Sites A to F are shown in Table 5. *N. antarcticus* occurred at all the sites except Site C - where suitable habitat was not available for this mite. The number of mites found in each sample (from a 52.2 cm² core) are given in Table 5.

A slightly acidic substrate was found at all sites, except Site F, which was clearly alkaline. Site F was located inland at the edge of a poorly-drained tarn, and the substrate contained large amounts of soluble salts.

The total amounts of soluble salts and chloride ions found at Sites A to E show a decrease from the offshore island Site C, to the coastal Sites A and B, and to Sites D and E further inland. The decrease is due to the differential rate of deposition of electrolytes from seawater aerosol transported by winds. Nevertheless, some of the electrolytes are autochthonous.

Table 5 shows that within each site samples which contained the largest numbers of mites yielded the smallest amounts of dissolved salts, and chloride ions, and vice versa.

The mean values for pH, total dissolved salts, and chloride ions from Site A are similar to those from Site B. The amount of phosphate ion at Site A was greater than at Site B probably because the substrate at Site A contained foreign wood debris from Davis station. The percentage of moisture in the substrate at Site B was greater than at the other sites in April 1973 (when the samples were collected), and similar to that found at Site B on 27 February, 1974 (Table 2).

The largest amount of phosphate ion was found at Site C, which was in a petrel nesting colony on Bluff Island. A small amount of nitrate ion was present at all sites, but the largest amount was found at Site E near another petrel nesting colony. Nitrite was not present in measurable amounts in substrate from any of the sites.

5.2 BEHAVIOUR AND THERMAL PHYSIOLOGY

At the Vestfold Hills *N. antarcticus* was first observed on 30 January 1973 walking on the undersides of rocks removed from the surface of the substrate. Thereafter, active mites were found under rocks whenever the maximum diurnal temperature of the substrate exceeded 0°C. By March, when the temperature of the substrate finally failed to exceed 0°C diurnally, no mites were found under rocks. The mites did not reappear under surface rocks until October 1973, when temperatures once again exceeded 0°C (Section 5.1, Table 3).

In November 1973 when the substrate was saturated with water (Section 5.1, Table 2), mites were observed supported on the meniscus of water at the surface of the substrate. The mites could walk and jump on the surface of the water, but most were observed walking inside air bubbles in the water or under rocks

No. mites* (/52.2cm ²)	Total Dissolved salts (ppm)	Cl (ppm)	pH (10°C)	PO ₄ (ppm)	NO ₃ (ppm)	Water (% - April)
<u>SITE A</u>						
198	612	249	6.40	-	-	-
191	729	274	6.10	-	-	-
142	750	274	6.05	77	1.1	-
129	921	328	5.72	-	-	0.34
104	1697	603	6.31	-	-	0.47
70	2056	778	5.90	-	-	0.82
29	1236	443	6.08	-	-	-
0	1163	425	5.94	-	-	0.36
Mean:	1146	422	6.06			
<u>SITE B</u>						
584	237	62	6.32	-	-	2.10
231	248	80	5.55	-	-	-
102	310	106	6.20	-	-	1.85
63	3891	1494	6.28	23	1.0	-
Mean:	1172	435	6.16			
<u>SITE C</u>						
0	3181	1195	6.34	168	1.1	0.45
0	2255	808	5.97	-	-	-
Mean:	2718	1001	6.15			
<u>SITE D</u>						
1	1239	67	6.38	-	-	0.45
0	553	116	6.39	96	0.7	0.87
Mean:	896	92	6.38			
<u>SITE E</u>						
1	327	71	6.34	-	-	0.40
0	220	44	6.12	20	1.6	0.30
0	194	87	6.19	-	-	0.35
Mean:	247	67	6.11			
<u>SITE F</u>						
0	2007	621	8.78	21	0.8	-

* The number of mites found in each sample
Table 5. Chemical characteristics of the substrate at
five sampling sites in the Vestfold Hills.

lying on water-saturated substrate.

From March to September 1973, most mites extracted from substrate by flotation in water at 12°C in the laboratory failed to become active. When mites were being counted during core analysis, only three immature individuals of 3,794 extracted mites were seen moving, one in March, one in July, and the other in August. In contrast, ten of sixty-two mites collected on 2 October 1973 were active after collection and extraction on that day. Thereafter, from November 1973 to February 1974, all live mites were active after extraction.

To find the minimum temperatures at which cold-immobilized winter-collected and summer-collected mites regained their activity, mites were rewarmed as described in Section 4.8. The procedure was repeated using the same mites in successive experiments immobilized for different periods of time at different temperatures (Figures 9, 10). Winter-collected mites (Figure 9) first began to move single legs at 9°C, and did not always begin to walk as soon as they began to move. In the field the substrate more than one centimetre below the surface (where mites were dormant in winter) did not reach 9°C until mid-November 1973 (Section 5.1, Table 3), six weeks after the mites became active.

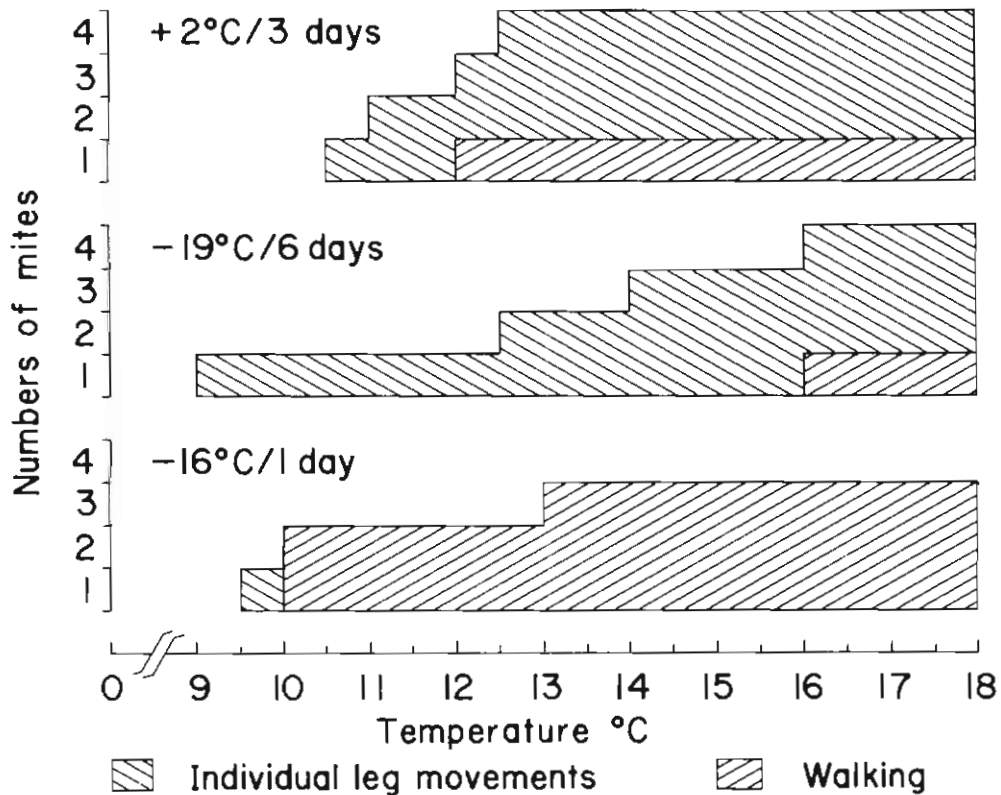


Figure 9. Re-activation of winter-collected mites after the pretreatment indicated.

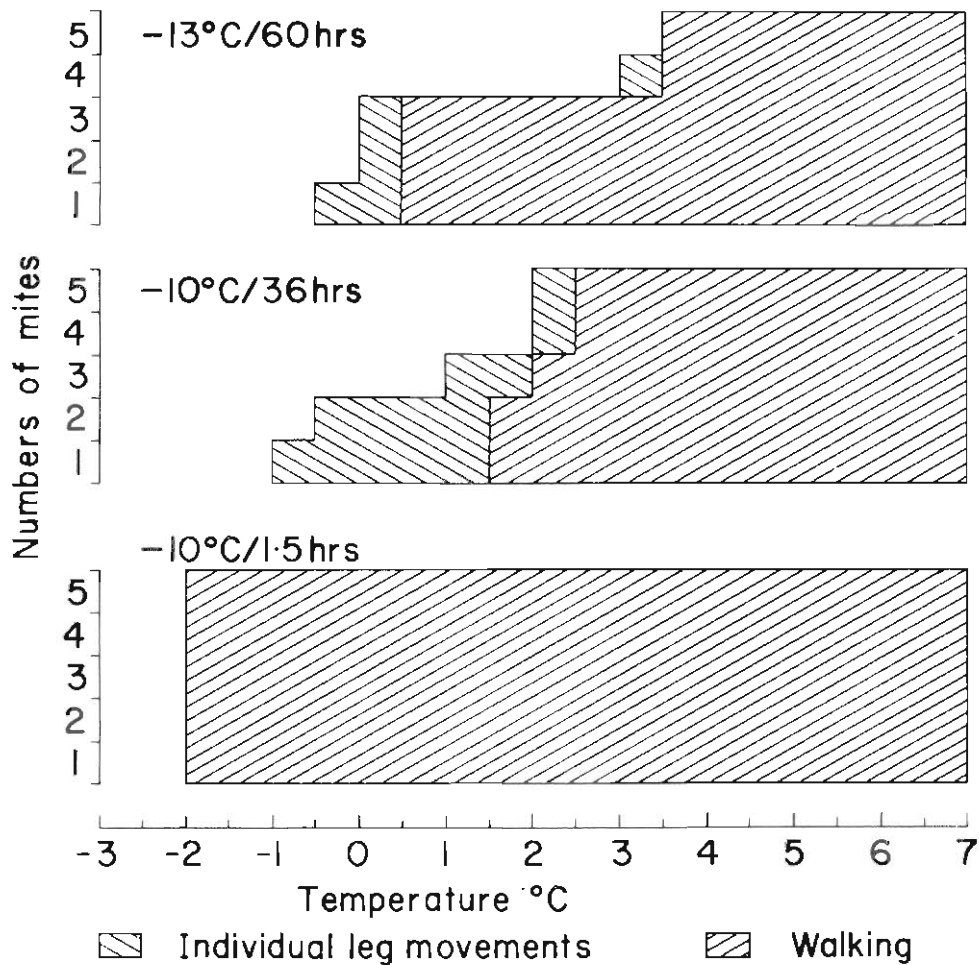


Figure 10. Re-activation of summer-collected mites after the pretreatment indicated.

Summer-collected mites (Figure 10) cold-immobilized for one-and-a-half hours at -10°C , walked, albeit slowly, on being re-warmed to -2°C . As the temperature continued to rise past 0°C the mites quickly regained a normal gait. Summer-collected mites, cold-immobilized for thirty-six hours at -10°C or sixty hours at -13°C (Figure 10), first began to move single legs at -1°C , and began to walk only at temperatures above 0°C .

The rate of cold-immobilization in five active summer-collected mites was observed during a period of twenty-four hours as they cooled from 6°C to -15°C (Table 6).

These observations suggest that active mites only become completely immobile two to four hours after being cooled below 0°C .

<u>Time (hrs)</u>	<u>Temperature (°C)</u>	<u>Behaviour</u>
0	+6	All walking rapidly
1	-5	All walking slowly
2	-9	Two inactive; three stationary but moving legs
3	-11	Four inactive; one moving a leg
24	-15	All inactive

Table 6. Activity of mites during cold-immobilization.

5.3 VERTICAL DISTRIBUTION

All cores analysed for vertical distribution of mites in the substrate were collected in the early afternoon when maximum daily temperatures occurred at the surface of the substrate. The results of these core analyses are shown in Table 7. Analyses of the first two cores from Site A indicate that in winter mites occurred mainly at a depth of one to five centimetres with very few in the upper one centimetre of substrate. In the remaining cores, which were collected in summer, most mites were found in the upper one to two centimetres, and very few occurred below three centimetres.

The vertical distributions of mites and eggs in two cores taken from Site A (one on 27 July and another on 18 November 1973), are compared in Figure 11. Mites in the second core were sorted into two groups according to length: those over 160 microns long (adults and nymphs), and those under 160 microns long (mainly larvae). The two groups, plotted separately as semi-log relationships with depth, produce two straight lines with similar slopes (Figure 11). Mites in these two groups were vertically distributed in the substrate in the same way.

Between 18 November 1973 and 13 February 1974, thirty-eight eggs containing fully-developed larvae were found in the cores, all within four centimetres of the surface of the substrate, and most in the top three centimetres (Table 7).

At Site B on 2 January 1974, 2,292 mites were washed from the undersides of seven flat rocks lying on an area of 144.5 cm² of substrate. This large number suggests that many of the mites found by core analysis in the upper centimetre of substrate may congregate on the undersides of rocks lying on the surface itself. The density of mites under the rocks was 15.8 mites/cm², which is similar to the densities of mites obtained by coring the substrate with tubes 2.49 cm in diameter (Section 5.5).

No experiments were performed to determine whether the mites undertook diurnal vertical migrations in the substrate.

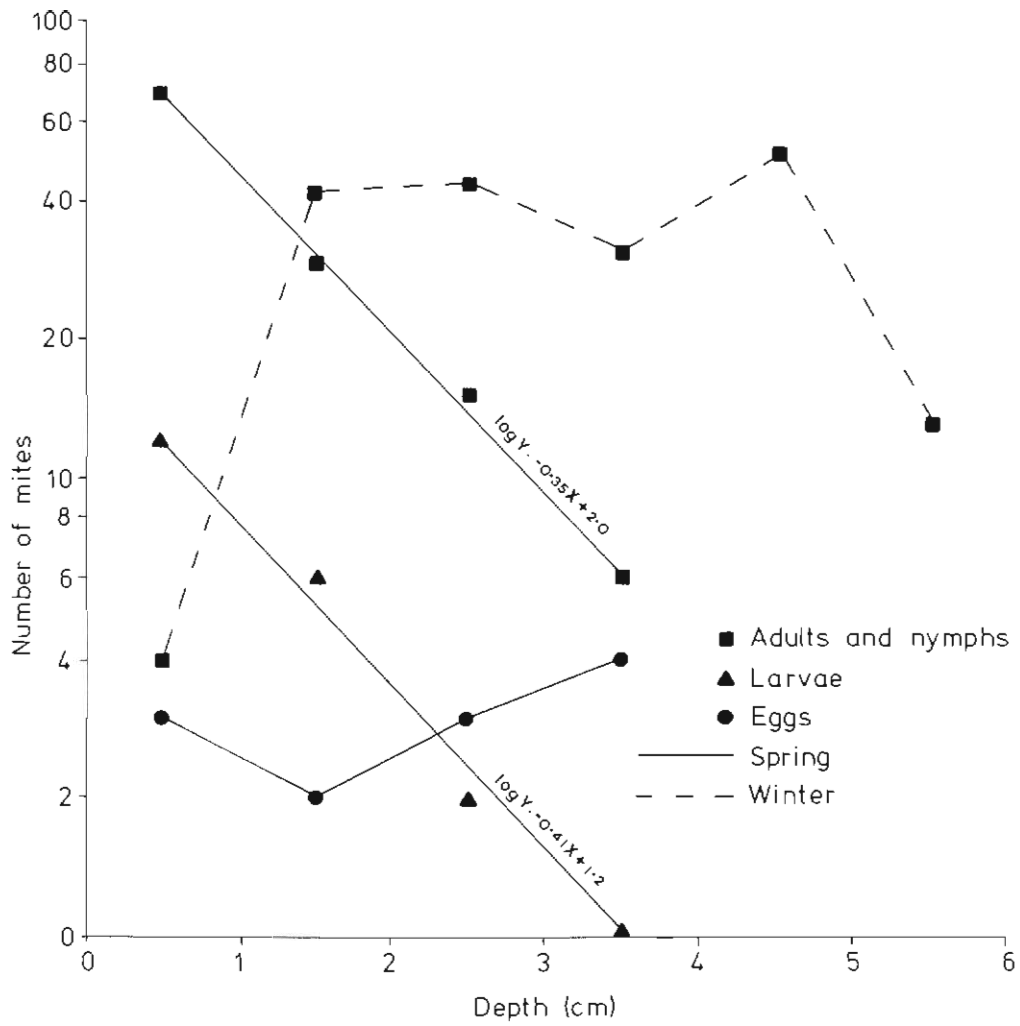


Figure 11. The numbers of mites found at different depths in cores taken from Site A on two occasions during 1973.

DATE	D E P T H (cm)						TOTAL
	0.0 - 1.0	1.1 - 2.0	2.1 - 3.0	3.1 - 4.0	4.1 - 5.0	5.1 - 6.0	
<u>SITE A</u>							
6 July 1973	0.0	31.7	26.3	31.5	10.5	0.0	19
27 July 1973	2.1	22.4	23.5	17.5	27.9	7.1	183
18 Nov. 1973	44.2(5)	32.7(5)	23.1(8)	-	-	-	52(18)
18 Nov. 1973	52.3(3)	23.4(2)	16.2(3)	8.1(4)	-	-	111(12)
<u>SITE B</u>							
21 Nov. 1973	28.2	33.8	38.1	-	-	-	71
21 Nov. 1973	54.5	34.1(1)	6.8	4.5	-	-	43(1)
21 Nov. 1973	87.1(2)	9.6(1)	3.2(1)	-	-	-	63(4)
19 Dec. 1973	89.6	10.3	0.0	0.0	-	-	29
19 Dec. 1973	92.3	2.6	3.8	1.3(1)	-	-	78(1)
16 Jan. 1974	(98.7)	(1.3)	76
16 Jan. 1974	(80.0(1))	(20.0)	20(1)
29 Jan. 1974	(93.0)	6.1	0.9	0.0	230
29 Jan. 1974	(68.2)	(9.1)	44
13 Feb. 1974	(52.0)	40.0	4.0	-	25
13 Feb. 1974	(98.0(1))	1.0	1.0	-	98(1)
27 Feb. 1974	(47.2)	(25.0)	36
27 Feb. 1974	(83.3)	(11.1)	18

Table 7. The vertical distribution of mites in cores of substrate. (Percentages of the total number of mites are shown. Integers in brackets show the numbers of eggs found).

5.4 HORIZONTAL DISTRIBUTION

The cores taken from the twenty-five square centimetre quadrats were analysed, and the numbers of mites determined (Table 8). The frequency distribution of mites in each series of cores was compared with the Poisson distribution by calculating their indices of dispersion (Southwood, 1969). The indices are significantly greater than unity in each case. This finding demonstrates that, at both sites in summer and winter, the mites were horizontally aggregated in the substrate more than would be expected if they were distributed at random. This aggregation is independent of surface rocks because most of the rocks were too large to be taken in the cores (i.e. over 2.5 cm in diameter).

The densities of mites in these series of cores (Table 8) ranged from 1.26 mites per square centimetre (Site A, 5 August) to 16.58 mites per square centimetre (Site B, 22 December). Thus mites were horizontally aggregated in the substrate over a wide range of population densities. According to the indices of dispersion (Table 8) the degree of aggregation of mites is greater at higher population densities.

Mites from cores taken in quadrat at Site B on 16 August were counted and identified according to life stage. Table 9 gives the frequencies of all the free living life stages in eighteen cores. The frequency distributions of the life stages (Table 9) in the cores were compared with the Poisson distribution by calculating their indices of dispersion (Southwood, 1969). For males, females, protonymphs and larvae, indices of dispersion were significantly greater than unity (Table 9), which demonstrates that these life stages were distributed horizontally in a contagious way.

The largest indices of dispersion were for adults (Table 9) which were more clumped than were the immature stages. The distributions of tritonymphs and deutonymphs gave indices of dispersion which were not significantly different from unity. The horizontal distributions of these two life stages were not significantly different from a random distribution, and were therefore more uniformly distributed in the substrate than were the other life stages.

5.5 ABUNDANCE

As some stages of mites are aggregated horizontally in the substrate, cores with larger surface areas may give better estimates of the mean densities of mites than the same area based on a number of smaller cores. Mean densities of mites at Site A (where mites were sparse) were estimated with cores of two different sizes (Table 10). The cores with the smaller area appear to have underestimated the mean density of mites by about fifty per cent, although the difference between the two mean densities in Table 10 is not statistically significantly different from 1:1 ($\chi^2 = 0.9$, $P = 0.4$). The ranges of the numbers of mites found¹ in cores of different sizes at Sites A and B are shown in Table 11.

SITE	WINTER				SUMMER			
	A		B		A		B	
DATE	5 August		16 August		18 December		22 December	
CORE AREA	3.5 cm ²		3.5 cm ²		4.9 cm ²		4.9 cm ²	
FREQUENCY	Cores	Mites	Cores	Mites	Cores	Mites	Cores	Mites
	f	x	f	x	f	x	f	x
	3	0	1	10	3	2	1	35
	5	1	2	20	1	3	1	38
	3	2	1	24	3	4	1	39
	7	3	1	31	1	5	1	44
	3	4	1	33	4	6	1	46
	3	5	1	34	2	7	1	49
	3	6	1	35	1	12	1	51
	4	8	1	38	1	22	1	64
	2	11	1	39	1	24	1	76
	2	12	1	41	1	25	1	78
			1	52	1	27	1	79
			1	55	1	36	1	90
			2	56			1	108
			1	57			1	161
			1	60			1	156
			1	63			1	177
			1	72				
			1	87				
INDEX								
DISPERSION	2.7*		7.7*		9.9*		26.6*	
MITES/cm ²	1.26		12.74		2.14		16.58	

* Significantly different from 1.0 (χ^2_1 P < 0.05)

Table 8. The horizontal distribution of mites in substrate.

Males		Females		Triton.		Deuton.		Proton.		Larvae	
f	x	f	x	f	x	f	x	f	x	f	x
1	1	2	1	2	1	2	0	6	0	6	0
4	2	1	2	3	2	3	1	3	1	4	1
1	4	2	3	2	3	7	2	4	2	4	2
2	5	1	4	2	4	4	4	1	3	3	4
1	6	1	5	1	5	1	5	1	5	1	5
1	8	2	6	3	6			1	6		
1	11	1	7	4	7			1	7		
2	13	3	8	1	8			1	11		
1	14	1	10								
1	15	1	11								
2	16	1	12								
1	19	1	16								
		1	25								

INDEX DISPERSION

4.3*	4.6*	1.2(NS)	1.1(NS)	3.9*	1.7*
MITES/cm ²					
2.44	2.15	1.28	0.60	0.68	0.46

* Significantly different from 1.0 (χ^2_1 , P < 0.05)

NS Not significantly different from 1.0 (χ^2_1 , P > 0.05)

Table 9. The horizontal distribution of free living stages of mites (18 x 3.5 cm² cores, Site B, 16 August 1973).

Date	Core Area (cm ²)	No. of Cores	Total Area (cm ²)	Mean Density (mites/cm ²)
27 July	52.2	5	261	2.93
5 August	3.5	35	122.5	1.28

Table 10. A comparison of the mean densities of mites obtained with cores of different areas.

Site	3.5cm ² or 4.9cm ² cores	52.2cm ² cores
A		
Winter	0 - 12	29 - 223
Summer	2 - 36	Not used
B		
Winter	10 - 87	63 - 584
Summer	2 - 321	Not used

Table 11. The numbers of mites obtained from cores at Sites A and B.

Changes in the abundance of mites at Site B were measured during summer with 4.9 cm² cores. The numbers of mites found in each of these cores ranged from 2 to 321 (Table 11). The results of analyses of these cores are given in Appendix A. The mean densities of mites obtained in all series of cores are summarized in Figure 12.

During preliminary sampling at Site B on 9 April 1973, four 52.2 cm² cores produced a mean density of 4.69 ± 2.15 mites per square centimetre (Figure 12). On 16 August 1973, eighteen smaller cores (surface area 4.9 cm² from a quadrat at Site B contained a mean density of 9.11 ± 1.24 mites per square centimetre (Figure 12).

Series of cores (surface area 4.9 cm²) were collected along the traverse at Site B on eight occasions from 2 October 1973 to 27 February 1974. Mean densities of all mites from these cores showed that two marked changes occurred in the abundance of mites during that period (Figure 12). The mean density of mites at Site B increased from 9.73 ± 1.87 mites per square centimetre (2 October) to 20.35 ± 3.93 mites per square centimetre (21 November) during a period of fifty days, and decreased from 19.90 ± 4.43 mites per square centimetre (16 January) to 6.06 ± 0.80 mites per square centimetre (27 February) in forty-two days. In the fifty-six days between these two changes in mite abundance, maximum mean density of 20.96 ± 4.80 mites per square centimetre (4 December), and minimum mean density of 16.49 ± 2.68 mites per square centimetre (2 January) was measured (Figure 12).

On 22 December 1973 a series of sixteen cores (surface area 4.9 cm²) taken from a twenty-five centimetre square quadrat at Site B near the traverse, produced a mean density of 16.53 ± 2.43 mites per square centimetre.

This mean density is not significantly different ($t_{28} = 0.02$, $P > 0.9$) from the mean density of mites obtained from cores collected along the traverse on 2 January (16.49 ± 2.68 mites per square centimetre).

On 2 January, 2,292 mites were collected from the undersides of rocks lying on a total area of 144.5 cm² of mite habitat near the traverse at Site B. This collection provided a mean density

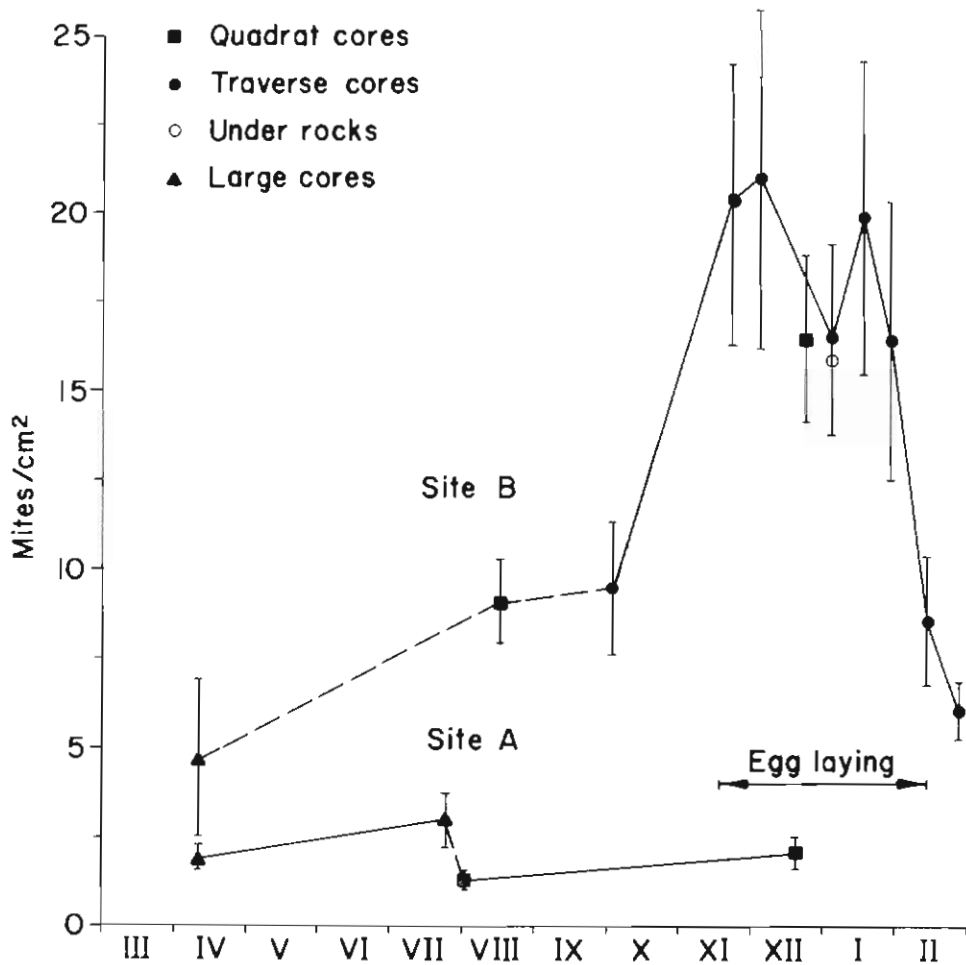


Figure 12. Mean densities of mites in cores from Sites A and B. (Vertical bars represent standard errors of means). Roman numerals refer to months.

of 15.86 mites per square centimetre from under rocks - which is not significantly different ($\chi^2 = 0.03$, $P > 0.7$) from the mean density (16.49 ± 2.68 mites per square centimetre) from cores taken along the traverse on the same occasion.

High mean densities of mites were obtained from cores at Site B from 21 November 1973 to 29 January 1974; a period of seventy days was examined by using an approximate test of equality of means when variances are heterogeneous (Sokal and Rohlf, 1969, p.372). The test demonstrated that samples on which the mean densities are based were drawn from sampling populations whose means were not significantly different ($F_{30}^4 = 0.33$). Thus the mean densities obtained during the

seventy day period were represented by an average summer mean density of 18.81 ± 3.95 mites per square centimetre.

The maximum and minimum mean densities of mites recorded during the seventy day period were 20.96 ± 4.80 mites per square centimetre (4 December) and 16.38 ± 3.93 mites per square centimetre (29 January) (Figure 12). The mean densities of mites at the end of winter dormancy in 1973 and at the beginning of winter dormancy in 1974 were 9.41 ± 1.87 mites per square centimetre (2 October) and 6.06 ± 0.80 mites per square centimetre (27 February) (Figure 12). These mean densities, including the average summer mean density, subsequently were used in the calculation of population biomass and respiration in Section 6.3.

5.6 POPULATION COMPOSITION

Over 10,318 mites were obtained from traverse cores at Site B. Amongst the 7,726 mites that were individually examined, 6,789 were each identified as one of the six free-living stages. Adult mites numbered 2,645, and the proportion of males to females (1,332 males and 1,313 females) was not significantly different from 1:1 ($\chi^2_1 = 0.14$).

The mean densities of all life-stages of mites from cores taken at Site B between 2 October 1973 and 27 February 1974 are given in Appendix A. The mean densities are plotted against date of collection in Figure 13, and by life-stage in Figure 14. The period of time spanned approximately corresponds to the active period of the mites. At the beginning and the end of this period the mature stages of mites were more abundant than the immature stages (Figures 13 and 14).

The maximum mean densities of larvae (3.92 mites per square centimetre) and protonymphs (3.69 mites per square centimetre) occurred on 4 December (Figure 13). A secondary maximum mean density of larvae (2.92 mites per square centimetre) occurred later on 16 January, but the mean densities of protonymphs from 4 December until 16 January are not significantly different ($t_{26} = 0.05$, $P > 0.9$).

After 4 December, the maximum mean density of deutonymphs (3.98 mites per square centimetre) and tritonymphs (3.08 mites per square centimetre) occurred on 16 January (Figure 13). Prior to 4 December a greater maximum mean density of tritonymphs (3.49 mites per square centimetre) occurred on 21 November, but the mean density of deutonymphs increased steadily from 2 October to 16 January.

The mean density of males remained almost constant until 16 January, but then decreased steadily until 27 February (Figure 13). At the beginning and the end of the active period the mean densities of adults of both sexes were similar. Nevertheless, the mean density of females in the cores fluctuated widely during the intervening summer period, between a maximum of 5.85 mites per square centimetre on 21 November and a minimum of 2.34 mites per square centimetre on 2 January (Figure 13).

The mean densities of adults collected from under rocks on 2 January were greater than the mean densities of adults from cores taken on the same occasion (Figure 13). Females were

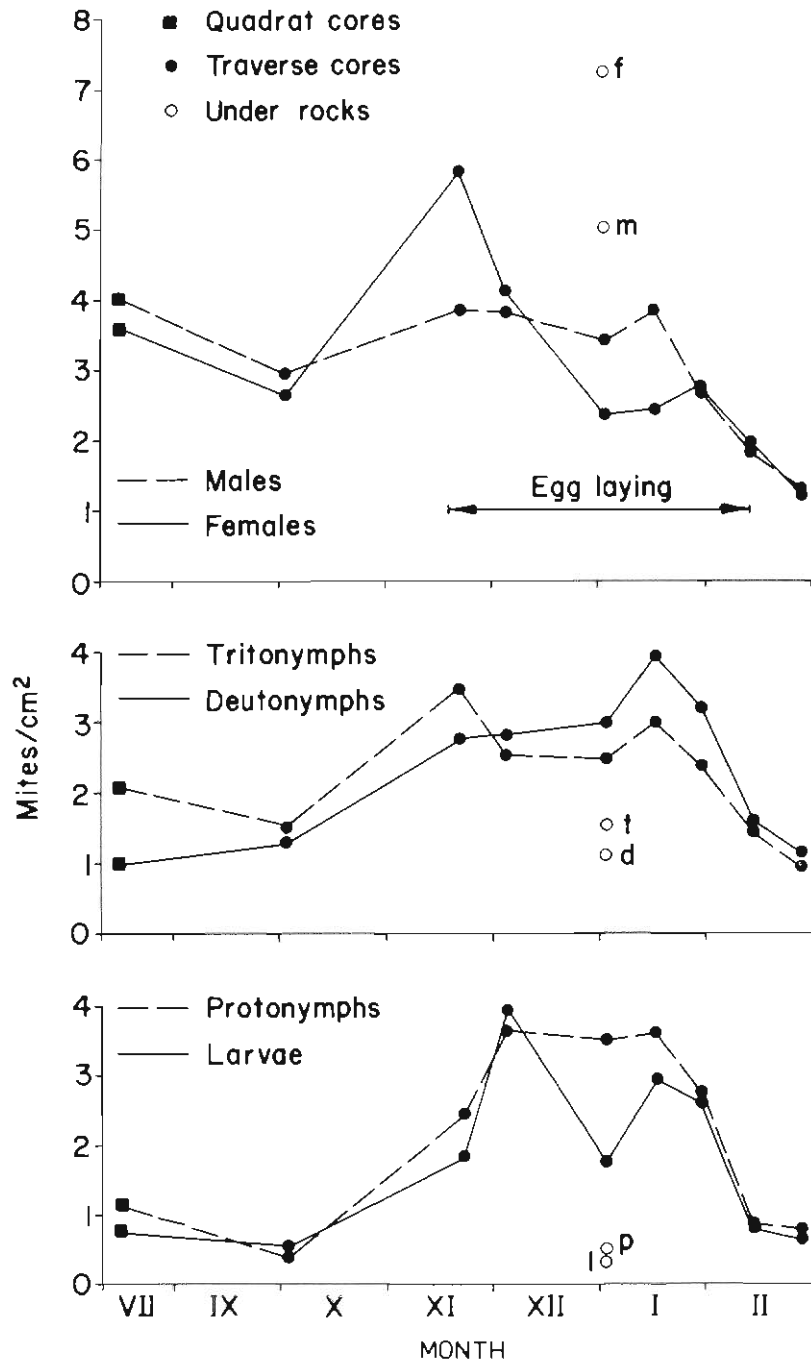


Figure 13. Abundance of freeliving stages of mites at Site B. Roman numerals refer to months.

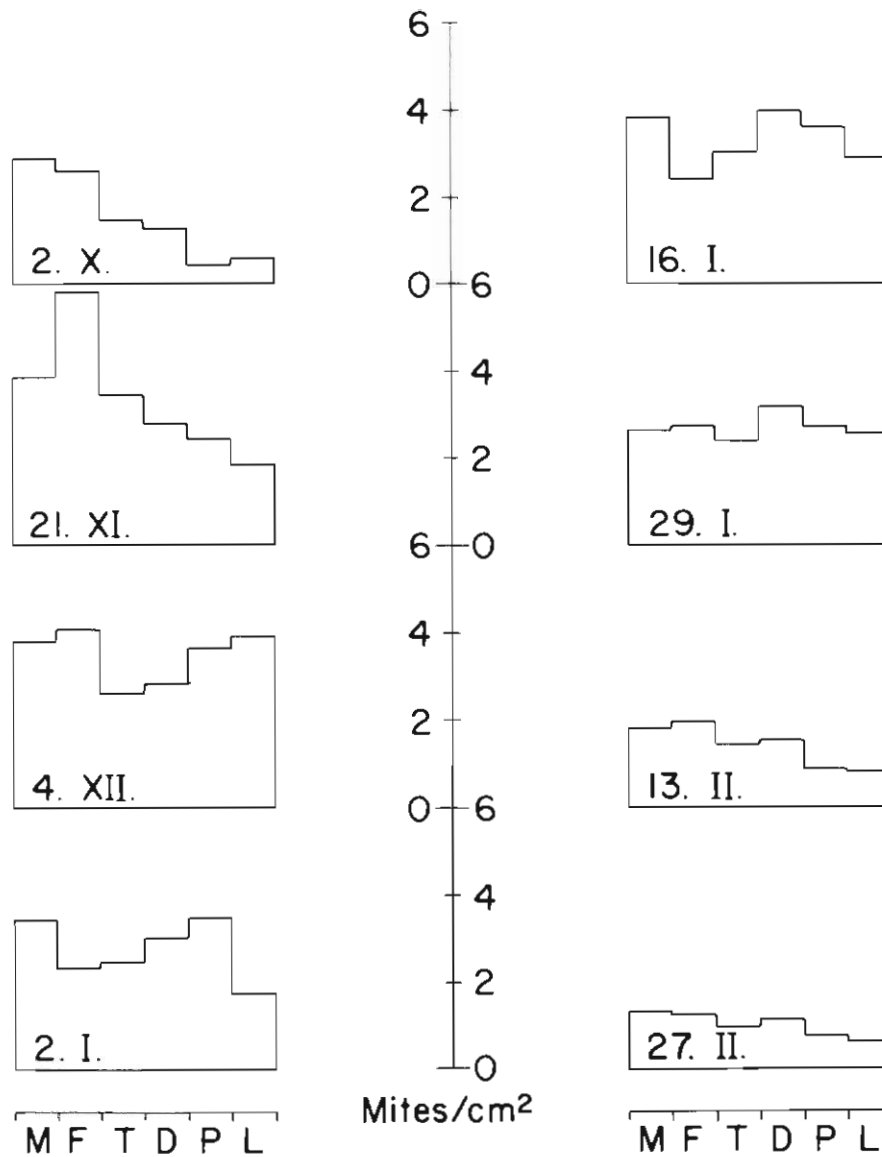


Figure 14. Abundance of free living stages of mites at Site B. (M = males, F = females, T = tritonymphs, D = deutonymphs, P = protonymphs, L = larvae). Roman numerals refer to months.

abundant under rocks on this occasion, and gave the highest mean density (7.24 mites per square centimetre) recorded for any life-stage of the mite. All immature stages of the mite were less abundant under rocks than in cores on this occasion, but the adults were more abundant (Figure 13).

The mean densities of all stages in cores decreased steadily from 16 January to 27 February 1974 until they were below the mean densities recorded on 2 October 1973, i.e. at the end of the previous winter (Figures 13 and 14).

All free-living stages of the mite were found in the substrate during the winter (e.g. Section 5.4, Table 8). Eggs were found in the substrate only from 18 November, 1973 until 13 February, 1974 (Section 5.5, Figure 12; Section 5.7).

Black dehydrated carcasses of mites were commonly extracted from cores containing live mites. The carcasses were the remains of mites that had died in the substrate prior to sampling and were found in cores from both Sites A and B. The numbers of carcasses in cores were not counted.

5.7 REPRODUCTION

Over 4,562 mites were extracted from cores taken at Sites A and B from March 1973 to 2 November 1973. All active life-stages of mites were found in these cores (e.g. Core analysis summary, 16 August, 19 September, 2 October, 2 November in Appendix A). No laid eggs were found in any of the cores during this period, which suggests that eggs were not laid in the substrate during this period and that no larvae in eggshells over-wintered in the substrate.

The maximum diameters of eighteen developing embryos from six females collected in the field on 29 August and 3 September are given in Table 12. Two of these embryos are shown in Plate 12.

The embryos have large cream-coloured yolks with a hyaline blastodisc attached to one side of the yolk (Plate 12). The largest blastodisc was 50 microns long (Table 12). Only one egg (containing a larva enclosed in an eggshell) was found in a female (Table 12); the first egg observed in a female during

FEMALE		EMBRYOS			
No.	Length	First	Second	Third	Fourth
1	290	95e	32y + b	40y + b	-
2	290	69y + b	60y + b	65y + b	-
3	300	80y + b	60y + b	40b, 40y	-
4	300	30b, 50y	33b, 58y	28b, 55y*	-
5	350	10b, 70y	20b, 60y	-	-
6	260	25b, 68y	25b, 77y	50b, 45y	50b, 45y

* (See Plate 12).

Table 12. Maximum diameters of embryos and eggs in six females (All measurements in microns)
e = diam. of egg, *b* = diam. of blastodisc,
y = diam. of yolk.

winter. The data in Table 12 suggest that over-wintering females carry three to four immature embryos (and occasionally an egg), at different stages of development, a month before their activity is regained in October (Section 5.2).

Eggs were found in two of sixty-nine females collected on 16 August, but none was found in sixty-six females collected on 2 October, or in seventy-two females collected on 2 November (Table 13). These data suggest that most eggs are formed in females after 2 November, at least one month after the females first become active after over-wintering. Eggs were first found in the substrate at Site A on 18 November, and at Site B on 21 November.

The percentages of egg-bearing females in cores at Site B during summer are given in Table 13. The numbers of eggs found in females ranged from one to five (Table 13). On 21 November 13.8 per cent of females contained eggs, and by 2 January a maximum of 38.8 per cent of females contained eggs (Table 13). The percentage of egg-bearing females decreased from 2 January to 29 January until none occurred in February (Table 13). Laid eggs were found in the substrate at Site B until 13 February (Section 5.3, Table 7).

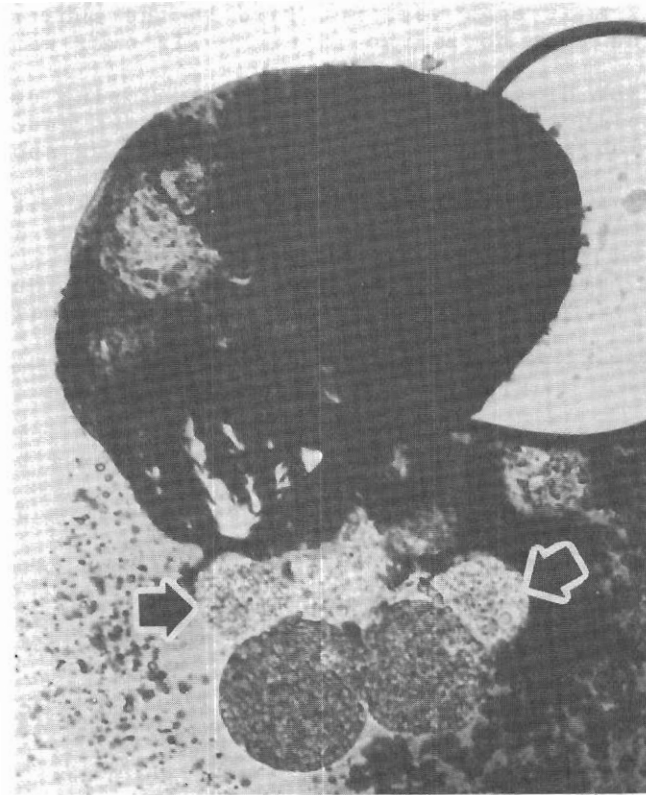


Plate 12. Two embryos (arrowed) attached to large yolk-sacs (x 100).

Date	Females			Eggs					
	Total	Non-Gravid (%)	Gravid (%)	Total	1	2	3	4	5
16 Aug.	71	97.1	2.8	3	1.4	1.4			
2 Oct.	66	100	0	0					
2 Nov.	72	100	0	0					
21 Nov.	160	86.2	13.8	37	7.6	3.1	3.1		
4 Dec.	161	60.2	34.7	109	14.3	9.3	9.9	1.2	
2 Jan.	116	61.2	38.8	106	4.3	20.7	9.5	4.3	
2 Jan. *	340	37.9	62.1	571	8.8	18.2	18.5	15.3	1.2
16 Jan	109	86.2	13.8	33	2.8	5.5	5.5		
29 Jan.	85	87.1	12.9	21	7.1	1.2	3.5	1.2	
13 Feb.	67	100	0	0					
27 Feb.	65	100	0	0					

Table 13. Distribution of eggs in females obtained from cores and from under rocks* at Site B.

On 2 January 61.2 per cent of females collected from beneath rocks contained eggs and the mean number of eggs per gravid female was 2.64 (Table 13). The rocks were too large to be included in core samples and carried approximately three times the mean density of females found in cores on that day (Section 5.6, Figure 13).

Eggs are laid up to four centimetres deep in the substrate (Section 5.3; Table 7). Three laid eggs were ovoid and their maximum and minimum axes measured in microns were 106 x 73, 103 x 60, and 103 x 68 respectively. Laid eggs contain larvae enclosed in hyaline egg shell, and hatch in the substrate. Newly-hatched unfed larvae are colourless, except for the hysterosoma which is coloured pale orange.

5.8 OTHER ORGANISMS

Eight species of vertebrates (seals and birds) breed at the Vestfold Hills (Johnstone et al., 1973). *N. antarcticus* rarely occurs at the breeding sites of these vertebrates, probably because they are located on steep rocky slopes, on islands or mainland hills, where the habitat is unsuitable (Section 5.1).

The soil mite *Tydeus erebus*, which is locally abundant only under rocks around the breeding colonies of birds, or at sites rich in moss and lichen (Rounsevell, 1977), also is absent from the habitat of *N. antarcticus*. *N. antarcticus* was found near

sites supporting *T. erebus* only where suitable habitat adjoined the sites.

Organisms found in the habitat of *N. antarcticus* belong to groups that are primarily edaphic or aquatic (Appendix B, Tables 1 and 2). Fungi, actinomycetes, bacteria and yeasts found at each site are listed in Appendix B, Table 2. Bacteria were the most common group; gram-negative achromatic bacilli being found at forty-one of forty-six sites. Four forms of sessile, gram-negative, chromogenic bacilli or cocci were less common. All forms of bacteria isolated occurred at Sites A and B, and were often found at other sites which support *N. antarcticus* (Appendix B, Table 2). All these forms of bacteria grew at temperatures between 0°C and 25°C on Czapek - Dox agar.

Actinomycetes were represented by two unidentified species of *Streptomyces*, one forming a grey-green mycelium (species 1) and the other a pink mycelium (species 2). Both species were common at sites A and B, but species 1 was more common and was found at a greater number of sites containing *N. antarcticus* than species 2 (Appendix B, Table 2).

Eight species of fungi were isolated from the study sites (Table 2 of Appendix B), but only six species were obtained from localities shared with *N. antarcticus*. The most common species, *Chrysosporium pannorum*, occurred at twenty-three of forty-six sites (Table 2 of Appendix B), including Sites A and B (along with an unidentified species denoted "F8"). *C. pannorum* is common in substrate elsewhere in Antarctica (Tubacki, 1961; Corte and Daglio, 1963; Tubacki and Asano, 1965). *Thelebolus microsporus* was also found at Site A and at nine other sites near the nesting colonies or moulting sites of birds and seals. *T. microsporus* has previously been recorded from cold climates, and occurs in the intestinal tracts of vertebrates (von Arx, pers. comm.). *T. microsporus* was observed sporulating amongst feathers and detritus on rocks around the entrance to a petrel nest at Site E. *Dendrophyellia salina* was found only at Site B. *D. salina* occurs amongst soil algae and moss elsewhere in Antarctica (Tubacki and Asano, 1965) and is common in the intertidal zone (Pugh, 1962). *Phialophora melinii* occurred only at Site A, where it was abundant in a substrate containing chips of wood and sawdust. *P. melinii* may have been introduced to Davis station on wooden crates made of a species of *Pinus*. Species of *Phialophora* commonly inhabit softwoods (Davidson, 1935; Schol-Schwarz, 1970). *Acremonium strictum* (in lit. *Cephalosporium acremonium*) and *Cladosporium cladosporioides* were rare, being found at one or two sites at which *N. antarcticus* did not occur (Table 2 of Appendix 2). "PP", an unidentified fungus which did not sporulate, was found only at Site E (Table 2 of Appendix 2).

The only fungus that was visible in the field was *Acremonium strictum*. This fungus was found growing as a white mass of hyphae on the hide of a dehydrated carcass of a Southern Elephant Seal *Mirounga leonina*.

The relative abundance of fungal propagules in substrate at Site A varied with depth and season (Table 14). Fungal propagules were less common at the surface of the substrate in winter than in summer; *C. pannorum* was most abundant on the surface in summer, and *P. melinii* occurred on the surface only in summer (Table 14).

Depth (cm)	Date			
	May 1973		December 1973	
0 - 2	<i>C. pannorum</i>	3	<i>C. pannorum</i>	14
	<i>T. microsporus</i>	3	<i>T. microsporus</i>	3
	<i>P. melinii</i>	0	<i>P. melinii</i>	14
4 - 5	<i>C. pannorum</i>	3	<i>C. pannorum</i>	4
	<i>T. microsporus</i>	2	<i>T. microsporus</i>	0
	<i>P. melinii</i>	27	<i>P. melinii</i>	

Table 14. The numbers of fungal mycellia grown from 0.5 gm of substrate on Czapek-Dox agar at 20°C.

Cultures of *T. microsporus* and *C. pannorum* grew best at between 10°C and 20°C, and *P. melinii* at above 20°C. No fungi grew at -5°C, but after thawing, cultures of *T. microsporus* and *P. melinii* had grown visibly after twenty-four hours at 20°C, and *C. pannorum*, after forty-eight hours at 20°C.

C. pannorum is the only soil fungus at the Vestfold Hills which is widespread and common (Table 2 of Appendix B), and it grows well in the temperatures found at the surface of the substrate in summer (Table 3).

One species of yeast (an orange-coloured form) was obtained from Site 2 (Table 2 of Appendix B). The solid media used to isolate other soil micro-organisms (Section 4.7) probably were unsuitable for yeasts.

Protozoans, rotifers and nematodes have been reported from the Vestfold Hills (Johnstone et al., 1973; Korotkevich, 1964). A variety of species in each of these groups, including tardigrades, was found in freshwater habitats during this study. Species in these groups were found at seven of the forty-six terrestrial sites (Table 1 of Appendix B), and were represented by fewer species than in freshwater habitats. Because of their small size or comparative rarity in the substrate, members of these groups were not systematically sought. Only one relatively large species of nematode (1.3 mm long) was readily detected by flotation during the extraction of mites from cores.

At least three species of ciliates and one species of rhizopod occurred in freshwater tarns, but only the latter was observed at a terrestrial site (Site B). One species of sessile rotifer, one species of loricate rotifer, and two species of bdelloid rotifers, were found in freshwater habitats, but only one bdelloid form occurred in moss and moist substrate in the habitat of *N. antarcticus* (Table 1 of Appendix B). This species was very abundant in a substrate containing an abundant green algae *Prasiola* on Gardener Island (Site 23), where *N. antarcticus* did not occur. At Site 23, an estimated number of 500 rotifers/gm of air-dried substrate occurred; but the rotifer was found only occasionally at Site B.

Two unidentified species of nematodes were found in freshwater and moss habitats at the Vestfold Hills, but only one species occurred in substrate at Sites A, B, 33 and 35 (Table 1 of Appendix B). This species was commonly extracted along with

N. antarcticus from cores taken at Site B, and was the only potential predator of mites found at Sites A and B. No evidence of mite predation was found, and nematodes generally occurred only in the wettest parts of the mite habitat.

Tardigrades were found singly in samples of moss or clumps of freshwater algae and were not present in substrate in the habitat of *N. antarcticus* (Table 1 of Appendix B).

Specimens of the above microfauna were collected and preserved, but were not identified for the purpose of this study.

Most of the lichens known from the Vestfold Hills (Johnstone et al., 1973) grow on rocks, and none is well represented in the habitat of *N. antarcticus*. Patches of moss often occurred with the habitat of *N. antarcticus* but most were restricted to small areas. Mites were not found amongst the moss, and very few were found living in substrate beneath the moss. The presence of moss and some species of lichens at the sites studied is indicated in Table 1 of Appendix B.

A wide range of soil-dwelling algae was encountered within (and outside) the habitat of *N. antarcticus* (Table 1 of Appendix B). Difficulties were encountered in describing and recognising different species of algae, particularly the coccoid forms of green and blue-green algae, because they are unicellular and microscopic. Soil algae are the main source of food for some antarctic mites, including *N. antarcticus* (Fitzsimons, 1971a).

The largest alga found (two to three centimetres in diameter) was a species of *Nostoc* which grows on the surface of the substrate at Site B in areas saturated by meltwater in summer; but is represented as hormogonia (0.2 - 0.3 mm in diameter) in winter. This species also grew in the substrate at nine other sites (Table 1 of Appendix B). Filamentous blue-green algae (mainly Oscillatoriales) were abundant; but only one species was identified (*Microcoleus vaginatus*). Filamentous and coccoid blue-green algae grew under the edges of rocks which were lying on the substrate in mite habitat. Only one species of soil diatom was common in the substrate, and it was found at a number of sites including Sites A and B (Table 1 of Appendix B). Near the breeding and moulting sites of birds, a nitrophilic species of green algae (*Prasiola*) occurred, sometimes in association with *N. antarcticus*; but it was uncommon in areas of mite habitat distant from the sites of vertebrate activities (Table 2 of Appendix B). *Nostoc*, forms of Oscillatoriales, coccoid blue-green algae, diatoms and *Prasiola* occurred in order of decreasing frequency at sites where *N. antarcticus* was found.

Nanorchestes antarcticus was found at twenty-three of forty-five sites which were examined for the presence of organisms and scored according to type of substrate (e.g. silt, sand or grit). The frequencies of occurrence of organisms and substrates at all the sites and those sites where *N. antarcticus* was found are given in Table 15. The most common organisms and substrates at all sites were white bacilli, sand, algae, *C. pannorum*, *N. antarcticus*, yellow bacilli and *Streptomyces* (sp.1) in order of decreasing frequency (Table 15). The frequencies of occurrence of these organisms and substrates are not significantly different from the frequency of occurrence of *N. antarcticus* at sites where *N. antarcticus* was found. The remaining organisms and substrates shown in Table 15 were least common and their

	Frequency (%) at sites with <i>N. antarcticus</i>	χ^2_1 *	Frequency (%) at all sites
<i>N. antarcticus</i>	100	-	51
White bacilli	91	NS	91
Sand (>0.1 mm, <1 mm)	78	"	64
Algae	78	"	60
Streptomyces (sp.1)	70	"	49
<i>C. pannorum</i>	61	"	53
Yellow bacilli	61	"	51
Pink coccoid bacteria	43	S	44
Streptomyces (sp.2)	39	"	24
Microfauna	30	"	29
<i>T. microsporus</i>	22	"	22
Moss	26	"	20
Lichens	26	"	20
Orange bacilli	26	"	27
Lemon bacilli	17	"	27
Grit (>1 mm)	17	"	38
F8 (fungus)	9	"	4
Silt (<0.1 mm)	9	"	7
Vertebrates	4	"	15
PP (fungus)	4	"	2
<i>D. salina</i>	4	"	2
<i>P. melinii</i>	4	"	2
<i>A strictum</i>	4	"	2
<i>C. cladosporoides</i>	0	"	4

* Null Hypothesis - Expected frequency of occurrence at twenty-three sites where *N. antarcticus* occurs is twenty-three (100%)
NS, P > 0.05; S, P < 0.05.

Table 15. The frequencies of occurrence of organisms and substrate types at twenty-three sites where *N. antarcticus* was found, and all forty-five sites examined.

frequencies of occurrence at sites where *N. antarcticus* was found are significantly less than the frequency of occurrence of *N. antarcticus*. The organisms which are most common in the habitat of *N. antarcticus* are also the most common organisms found at all the sites examined in the Chalikosystem of the Vestfold Hills.

5.9 FOOD

During the winter of 1973, mites were inactive in the substrate until the end of September (Section 5.2). In fed mites the contents of the gut are visible through the cuticle as a dark mass (Gressitt and Shoup, 1967). Dark masses were not apparent in any of the 3,794 mites extracted during winter.

On 29 August nine inactive individuals were collected from Site A, squashed in water under a coverslip and examined through a microscope. Globules of a yellow water immiscible liquid, and small (one to two micron) pieces of crystalline material and dark amorphous solids were obtained from the bodies of all the mites. The crystalline material is considered to be uric acid because it dissolved in potassium hydroxide. Uric acid, a waste product of metabolism, is found in *N. antarcticus* (Womersley and Strandtmann, 1963). The dark amorphous solids appeared to be the remains of long-undigested food.

Active individuals of *N. antarcticus* eat algae in summer (Fitzsimons, 1971a). No algae or other food was found in *N. antarcticus* during winter - which suggests that the inactive mites did not eat.

Dark masses of food, visible through the cuticles of mites collected in the field, were first noted on 21 November. From this time until 8 January, and as soon as possible after collection in the field, a total of twenty-four mites were squashed in water under coverslips, and their gut contents examined through a microscope. Five adult mites examined on 3 December contained green amorphous algal material which was unidentifiable; and another mite contained entire spherical cells (mean diameter, six microns) of *Nostoc*. The gut contents of the remaining eighteen mites examined also contained green or brown amorphous algal material. Entire green or brown algal cells four to fifteen microns in diameter were observed in some of the mites but the algae were unidentifiable. Portions of diatoms and of representatives of Oscillatoriales, which are readily identifiable, were not observed in these mites. Thus the majority of the amorphous algal material appeared to have been forms of coccoid green algae or blue-green algae like *Nostoc*.

The natural diet of *N. antarcticus* may include soil fungi (Janetschek, 1967), although fungal hyphae were not found amongst the gut contents of mites examined by Fitzsimons (1971a).

Agar plates on which thirteen winter-collected and four summer-collected mites were placed (Section 4.7) did not grow colonies of fungi or bacteria. Substrate samples from Sites A and B, at which active mites collected, produced a range of fungal and bacterial colonies (Table 2 of Appendix B) on the same agar medium.

6. DISCUSSION

6.1 HABITAT

The habitat of *N. antarcticus* at the Vestfold Hills is mainly confined to substrate receiving meltwater from snowdrifts that thaw during spring. The amount of habitat available depends on the area of land moistened by seepage during the thaw. The greatest accumulation of snow at the Vestfold Hills occurs in winter, but the prevailing winds sweep the land bare before the thaw, leaving compacted snow on the leesides of hills and other obstructions. Topographic features determine the locations of annual snowdrifts which support populations of *N. antarcticus*. Annual variations in the size, and the duration of thawing of snowdrifts, will affect the supply of water available in the habitat of the mite during summer.

Antarctica is a dry continent receiving an average annual accumulation of snow equivalent to 14.5 cm of water. Accumulation is generally greater at the coast than inland (Rubin and Weyant, 1965). Davis station annually receives 6.5 cm of water as accumulated snow (Mellor, 1967), which is a similar amount to that received at the South Pole (Siple, 1958); but the nett accumulation of snow does not determine the number and size of local snowdrifts. Regardless of latitude, local topography and prevailing winds form snowdrifts in the Chalikosystem, including areas where there is no nett accumulation of snow, such as the coast of Mac.Robertson Land (Mellor, 1967). Thus moist substrate suitable for *N. antarcticus* should be available throughout the Chalikosystem at localities where snowdrifts thaw annually.

N. antarcticus is usually reported from substrate which has been moistened by meltwater or patches of melting snow (Tyndale-Biscoe, 1960; Gressitt et al, 1963; Wise et al., 1964; Strandtmann et al., 1967; Strong, 1967; Strandtmann and Pittard, 1968; Rounsevell, 1974) and has not been found in substrate that is permanently dry. *N. antarcticus* occurs at 85°32'S, and is the southernmost known terrestrial arthropod; but even at this latitude it is found only where there is local melting of snow or ice (Wise and Gressitt, 1965). Janetschek (1967, 1970) concludes that the single, most important, requirement for life in the Chalikosystem is the availability of water as a liquid or moisture, which requires the local temperature to rise above 0°C at times. The distribution of the habitat of *N. antarcticus* supports this conclusion.

Antarctic substrates are usually alkaline (Tedrow and Ugolini, 1966). With the exception of one site, all those sites where *N. antarcticus* was found during the present study contained substrates that were mildly acidic. In South Victoria Land *N. antarcticus* is found in mildly alkaline substrates (Spain, 1971; Wise and Spain, 1967). This difference in pH probably reflects the difference between the mineralogy of the bedrock in the two parts of the Chalikosystem. In the range encountered pH probably has little effect on determining the habitat of *N. antarcticus*. Large amounts of soluble salts are

usually found in Chalikosystem substrates (Tedrow and Ugolini, 1966), and this is probably associated with the dryness of the environment (Spain, 1971). In the present study the greatest numbers of *N. antarcticus* were found in substrate containing the least amount of soluble salts. If the mites are more numerous in substrate where the available water levels are highest, then low concentrations of soluble salts could be expected. Spain (1971), and Wise and Spain (1967) observed the alternative situation - that soils which do not support arthropods have a considerably higher salt content than those that do.

During this study part of the substrate in the habitat of *N. antarcticus* was saturated with water at the height of the thaw in November. The substrate steadily desiccated until the end of February when maximum diurnal temperatures in the substrate just exceeded 0°C. On this occasion the substrate contained 2.1 per cent moisture and the mites had not begun to leave the surface. Wise et al. (1964) and Janetschek (1967) found that *N. antarcticus* (and other arthropods) did not occur in substrate which contained less than two per cent moisture. Janetschek (1970) suggests that sites must contain a moisture content of at least two per cent to support arthropods; but failed to emphasize that this applies only after the thaw and during the Antarctic summer when maximum diurnal temperatures exceed 0°C.

During winter the amount of moisture in the substrate continued to decrease, and the inactive mites overwintered at least one centimetre below the surface. Just before the thaw began in October, the substrate contained between zero and 0.5 per cent moisture - a level which continuously prevailed in areas free of meltwater outside the habitat of *N. antarcticus*. The relative humidity of the air in the upper one centimetre of substrate at this time was between 89 and 94 per cent. Because temperatures remained below 0°C, overwintering mites which were at least one centimetre below the surface probably survived the winter in relative humidities of about ninety per cent, despite the small amount of moisture in the substrate. At sub-zero temperatures only a small amount of moisture is required to saturate air. Moisture lost to the atmosphere from the top one centimetre of substrate may be replenished by sublimation from ice in the permafrost deeper in the substrate. If the permafrost is a source of sufficient moisture to maintain high humidities deep in the substrate this feature may explain why the mites overwinter between one and five centimetres below the surface.

Wise et al. (1964) and Janetschek (1967) found that in summer the diurnal range of relative humidity measured in the top centimetre of substrate was almost as wide as that obtained from measurements throughout the summer. This measurement did not reveal any correlation between the occurrence or non-occurrence of arthropods at a site (Wise et al., 1964; Janetschek, 1967). During the present study air in the top centimetre of substrate was usually saturated with moisture after noon in the period of summer following the thaw.

Laboratory experiments demonstrated that summer-collected *N. antarcticus* were active at temperatures above 0°C, but become inactive after two to four hours at temperatures below 0°C. In the field, mites were probably active only on days when the

temperature of the substrate exceeded 0°C, and then only for the period of the day when temperatures at the surface of the substrate were above 0°C. Fitzsimons (1971b) observed normal motor activity in *N. antarcticus* at temperatures from -23°C to +31°C, although the duration of activity at sub-zero temperatures is not stated. The maximum temperature measured in the substrate at the Vestfold Hills during summer 1973-1974 was 27.5°C, i.e. below the upper lethal temperature of 37.2°C for *N. antarcticus* (Fitzsimons, 1971b). The lower lethal temperature of *N. antarcticus* has not been determined. Fitzsimons (1971b) found that eight of twenty individuals of *N. antarcticus* remained alive after storage at -41°C for nine days. The cause of death in the twelve mites which did not survive is uncertain.

During the present study inactive winter-collected mites became active in the laboratory at temperatures above 9°C during heating at a rate of 0.7°C/min. This behaviour contrasts with that of summer-collected, cold-immobilized mites which became active at 0°C under the same conditions. It is probable that the inactive winter-collected mites required a slower rate of heating to become physiologically prepared for motor activity. This finding suggests that winter dormancy in *N. antarcticus* is a special physiological state as well as a state of inactivity. Only 0.001 per cent of winter-collected mites were active after extraction at 12°C in the laboratory. The process of extraction (immersion in water) probably killed most of these mites.

The annual period of activity of *N. antarcticus* is determined by the length of time during which substrate temperatures exceed 0°C. At the Vestfold Hills the first and last days of the 1973-1974 summer, when maximum diurnal temperatures measured in the substrate exceeded 0°C and mites were active, were 149 days apart. These dates were 2 October 1973 and 27 February 1974. The actual period of summer activity in mites was probably slightly longer, but at most in the order of five months. The length of this period of activity varies with latitude. At Palmer Station (64°46'S, 64°04'W), individuals of *N. antarcticus* are active on most days throughout the year (D. Berry, pers. comm.). At McMurdo Station (77°53'S, 166°44'E), the annual period of activity for soil microarthropods during summer is 96 days (Wise and Spain, 1967). The length of the active period for *N. antarcticus* at its southernmost recorded locality (85°32'S, 153°W) is probably in the order of two months.

6.2 OTHER ORGANISMS

Species of soil algae are the main food of *N. antarcticus* and are the only organisms so far identified from the gut contents of individual mites. Species of *Prasiola*, non-filamentous cyanophytes, *Protococcus*, diatoms and *Oscillatoria* have been identified from *N. antarcticus* (Fitzsimons, 1971a). At the Vestfold Hills, a species of *Nostoc* is also eaten by the mite (Rounsevell, 1974). Fitzsimons (1971a) suggests that the type of algae taken by *N. antarcticus* is largely determined by its abundance and availability, rather than by any preferential selection by the mites.

In the present study species of soil algae were found at seventy-eight per cent of the sites where *N. antarcticus* occurred. Apart from *N. antarcticus* and species of achromatic gram-negative bacteria, soil algae were the most common organisms found in the habitat of the mite. Soil algae are characteristic of the Chalikosystem wherever arthropods occur (Janetschek, 1963), and have been found further south than the southernmost part of the known range of *N. antarcticus* (Cameron, 1972).

Janetschek (1967), Strong (1967) and Gressitt and Shoup (1967) suggest that *N. antarcticus* eats soil fungi, probably because Wise et al., (1964) grew a species of *Penicillium* from the bodies of mites (*Stereotydeus mollis*) squashed on agar media. No fungi grew from individuals of *N. antarcticus* similarly prepared by Fitzsimons (1971a), and during the present study.

The most common and widespread species of fungus at the Vestfold Hills is *Chrysosporium pannorum*, which occurred at sixty-one per cent of the sites containing *N. antarcticus*. In summer this fungus is most abundant in the upper two centimetres of substrate, where *N. antarcticus* occurs; and the fungus grows most prolifically at temperatures between 10°C and 20°C - which are in the range of maximum diurnal temperatures at the surface of the substrate. If *N. antarcticus* eats fungi, then this species would be the most readily available taxon at the Vestfold Hills.

Coccoid bacteria have been observed growing on agar media on which individuals of *N. antarcticus* were squashed (Fitzsimons, 1971a). No bacteria grew from individuals of *N. antarcticus* similarly prepared during the present study. At the Vestfold Hills a species of pink coccoid bacterium was found at only forty-three per cent of the sites where *N. antarcticus* occurred. Species of achromatic gram-negative bacilli were found at ninety-one per cent of the sites containing *N. antarcticus*, and these were the organisms most commonly associated with the habitat of the mite. It has not been demonstrated that bacteria are eaten by *N. antarcticus* or are symbiotic or commensal on the mite. Nevertheless, bacteria may be concomitantly ingested with algae because they live on the surfaces of these plants (Cameron and Devaney, 1970).

Other common microorganisms in the habitat of *N. antarcticus* at the Vestfold Hills are a species of *Streptomyces* and a yellow gram-negative bacillus. These species were found at seventy and sixty-one per cent of the sites containing *N. antarcticus*, respectively.

No other soil microarthropods occur in the habitat of *N. antarcticus* at the Vestfold Hills. The prostigmatic mite *Tydeus erebus* is the only other soil microarthropod known from the Vestfold Hills, and populations of this species are principally confined to rocky slopes adjoining bird nesting colonies, and to areas supporting mosses and lichens (i.e. the Bryosystem) (Rounsevell, 1977).

The most abundant form of microfauna found in the habitat of *N. antarcticus* at the Vestfold Hills was a species of nematode. This species was found at seventeen per cent of the sites containing populations of *N. antarcticus*, but was confined to

that part of the habitat of the mite which was flooded during the thaw. The diet of this species of nematode is not known.

There are no obvious predators of *N. antarcticus* at the Vestfold Hills. Neither are there any other organisms which are effective competitors for the food of *N. antarcticus*. The population ecology of *N. antarcticus* at the Vestfold Hills is apparently unaffected by other species of consumers. The only other common organisms in the habitat of *N. antarcticus*, apart from algae, are species of fungi, actinomycetes and bacteria, and these organisms are probably most important as decomposers.

Most species of soil microarthropods in Antarctica live in association with bird nesting colonies, or in areas of Bryosystem, and their habitats are similar to that of *T. erebus* at the Vestfold Hills. *N. antarcticus* may compete for food with these species only where it also occurs in the Bryosystem or near bird nesting colonies.

N. antarcticus is characteristic of the Chalikosystem and is often the only arthropod present (Janetschek, 1967). In Victoria Land *Stereotydeus mollis* is a common and widespread species of mite which is often found in the habitat of *N. antarcticus* (Gressitt et al., 1964; Gressitt and Shoup, 1967). *S. mollis* is phytophagous and eats the same kinds of algae as does *N. antarcticus* (Fitzsimons, 1971a). Nevertheless, in many places in the Chalikosystem, the habitat of *N. antarcticus* does not support populations of *S. mollis* (Gressitt and Shoup, 1967).

The collembolan *Gomphiocephalus hodgsoni* occasionally is found in the habitat of *N. antarcticus* in Victoria Land (Gressitt et al., 1964). This species eats soil algae and soil fungi (Fitzsimons, 1971a).

Most species of predatory mite in Antarctica occur in the Bryosystem, where species of Collembola are their main prey (Strong, 1967). In the Chalikosystem species of predatory mites generally do not occur in the habitat of *N. antarcticus*; and none is known to eat *N. antarcticus*. Thus in the Chalikosystem generally, as at the Vestfold Hills, populations of *N. antarcticus* are unaffected by other species of soil microarthropods.

6.3 POPULATION ECOLOGY

In this study cylindrical cores from three to eight centimetres long and with an area of cross-section of 4.9 centimetres square were used to estimate the population densities of *N. antarcticus*. Shallow substrate and rocks embedded in the substrate prevented eight centimetre-long cores from being consistently obtained. During summer, when most cores were taken, the results from all cores were comparable, regardless of core length, because most mites occurred in the top two centimetres of substrate. During the winter mites were dormant at depths between one and five centimetres in the substrate. Thus only the results from cores that were five centimetres or longer, were comparable in winter, and cores of this length were not always obtained. Nevertheless, only preliminary estimates of population densities were made during winter. Because the mites were dormant in winter, their population densities were assumed to be constant. As discussed

above, the location of dormant mites, and the conditions they experienced in the substrate, suggested that the amount of winter mortality in the population was negligible.

Individuals of *N. antarcticus* are horizontally aggregated in the substrate, with the degree of aggregation increasing with increasing population densities. The cause of aggregation is not known, but may be due to the irregular distributions of moisture, heat or food in the substrate. These aggregations partly influenced the choice of a cross-sectional area for cores to estimate population densities. At a population density of two to three mites per square centimetre, cores of 3.5 cm² area underestimated the population density by about fifty per cent. This underestimation was probably caused by the contagious horizontal distribution of the mites. To avoid further serious underestimation, cores 4.9 cm² in cross-section were chosen to estimate the density of a population containing in the order of ten to twenty mites per square centimetre. It is not known how well the 4.9 cm² cores estimated the higher population densities, but each always contained some mites, and often more than 100 mites.

All mobile lifestages of *N. antarcticus* overwinter, but larvae and protonymphs are less abundant than the older lifestages in winter, and at the beginning and the end of summer. Eggs develop in the female until they contain larvae. Larvae encapsulated in eggshells are laid, and hatch, in the substrate. After laying commences in summer the abundances of immature stages reach successive maxima in the order of their age. Eggshells containing larvae are laid only during summer, but embryos are present in females during winter. Fertilization of eggs probably occurs in the summer preceding that in which the larvae are laid. At the end of summer, late-hatched larvae and other immature stages, develop only into more mature stages during the following summer.

Most female mites began laying larvae about one month after becoming active, and ceased laying about one month before they resumed dormancy. During the laying period each gravid female progressively laid a total of three or four larvae. At the peak of laying, thirty-eight per cent of females in the substrate, and sixty-two per cent of females under rocks, were gravid. At this time the population densities of mites under rocks, and in substrate, were similar. Thus, approximately fifty per cent of all females in the population bred during this study.

At the latitude 77° 53'S, where the length of the active season is three months, Lindsay (1972) found that in early January most females of *N. antarcticus* contained one egg, and none carried four eggs. At this time of year each female at the Vestfold Hills carried an average of 2.64 eggs. At latitude 77° 53'S females of *N. antarcticus* probably lay a total of two or three larvae each summer. At 85° 32'S, in the southernmost part of the range of *N. antarcticus*, females may lay only one larva a year.

In the Vestfold Hills at least ten months of activity over a two-year period are required for the life-cycle of *N. antarcticus* to be completed. According to the length of the active period annually available for *N. antarcticus* at the other

places in Antarctica discussed above, the length of the life-cycle may range from one to five years, increasing with latitude. If five years are required before individuals of *N. antarcticus* reach maturity at the southernmost part of the range of the species, and females annually produce single progeny, then a mean life-span of about seven years is required for *N. antarcticus* to reproduce in a population at replacement level - assuming no mortality occurs. It is probable that population densities of *N. antarcticus* at 85° 32'S are low and individuals in these populations live for many years.

Janetschek (1970) considers that population densities of species of arthropods in the Chalikosystem are very low, but adds that there is insufficient quantitative information. *G. hodgsoni*, a species of collembolan which is characteristic of sites containing a mosaic of Bryosystem and Chalikosystem (Janetschek, 1967), reaches maximum population densities of the order of 100 collembolans per square metre in summer (Wise et al., 1964). Nevertheless, mean summer population densities for *G. hodgsoni* are in the order of twenty collembolans per square metre (Peterson, 1971).

Contrary to the above statements, this study has shown that population densities of *N. antarcticus* can be very large. The mean summer population density found during this study is considerably greater than the maximum population densities of other species of Nanorchestidae, and is often greater than the total population density for all species of the Acari in the Bryosystem of maritime Antarctica (Tilbrook, 1967b), Arctic tundra (Ryan, 1972), temperate grassland (Olivier and Ryke, 1965; Loots and Ryke, 1966; Wood, 1967b; Hutson, 1974; Lussenhop, 1976), temperate woodland (Den Heyer and Ryke, 1966) temperate forest (Van den Berg and Ryke, 1967), and desert sclerophyllous grassland and semi-arid woodland (Wood, 1971; Wallwork, 1972b).

Population densities of soil arthropods in Subantarctic ecosystems exceed those found in similar ecosystems in South America, but undergo large fluctuations (di Castri et al., 1967). In the Chalikosystem it is apparent, at least for *N. antarcticus*, that large population densities occur, and fluctuations of the order of more than fifty per cent, also take place annually.

The mean summer density of a population of *N. antarcticus* at the Vestfold Hills was $188.1 \pm 39.5 \times 10^3$ mites/m² from 21 November 1973 to 29 January 1974. The mean density of this population decreased to $60.6 \pm 8.0 \times 10^3$ mites/m² by 27 February 1974. This decrease coincided with a progressive desiccation of the habitat and it is assumed that the decrease in the density of mites during February was caused by mortality from desiccation. The desiccated carcasses of mites were frequently found, and seventy per cent of the mites present perished during that month. Peterson (1971) also observed severe mortality in a population of the Antarctic collembolan *Gomphiocephalus hodgsoni* as its habitat desiccated in late summer.

In the same population of *N. antarcticus*, a density of $94.1 \pm 18.7 \times 10^3$ mites/m² was measured at the end of the previous winter (2 October 1973). If the same mean summer density is assumed for the summer of 1972-1973 as for the summer of 1973-1974, then a mortality of fifty per cent may have occurred in the

population during February 1973. In the summer of 1973-1974 snowdrifts completely melted three weeks earlier than in the preceding and following summers. Desiccation of the habitat of *N. antarcticus* probably began earlier in the summer of 1973-1974 than in the other summers, and may account for the apparently higher mortality of *N. antarcticus* observed during February 1974.

Thus the availability of water at a site in the Chalikosystem during summer not only defines the habitat of *N. antarcticus*, but probably determines the limits to the abundance of the mites through mortality.

The biomass and the respiration rate of a population of *N. antarcticus* in the Chalikosystem, compared with the biomass and respiration rates of populations of other species of Acari in other terrestrial ecosystems, are alternative ways of comparing these ecosystems. The biomass of a population of *N. antarcticus* at the Vestfold Hills (Table 17) was calculated by summing the population biomass for each life stage; the product of mean individual live weight (Table 16) and the mean population density (Figure 13 and Appendix A) for each life stage. The respiration rate of a population of *N. antarcticus* at the Vestfold Hills (Table 17) was calculated similarly by summing the respiration rates contributed by each life stage in the population. In Table 16 the values for the mean live weights and respiration rates of the female, tritonymph and deutonymph of *N. antarcticus* are from Block (1976). The values for the remaining life stages given in Table 16 are assumed for the convenience of this discussion.

Life Stage	Mean ind. wt. (μg)	Respiration rate at 5°C	
		($\times 10^{-3}$ μ litre $\text{O}_2/\text{ind.}/\text{hr}$)	(μ litre $\text{O}_2/\text{gm}/\text{hr}$)
Male	3.371+	1.05+	311
Female	3.371*	1.05*	311
Tritonymph	3.590*	1.13*	316
Deutonymph	1.590*	0.15*	94
Protonymph	1.000+	0.10+	100
Larva	0.500+	0.50+	100

(* after Block (1976); + assumed)

Table 16. Mean individual live weight and mean respiration rate for life stages of *N. antarcticus*.

DATE	MEAN DENSITY* (mites/m ² x 10 ⁻³)	BIOMASS (µg/m ²)	RESPIRATION (µ litre O ₂ /m ² /hr)	RATE (cal/m ² /hr) *
Summer average	29 Nov. 1973 188.1 ± 39.5	432.5 ± 90.9	114.7 ± 24.1	0.55 ± 0.11
Summer maximum	4 Dec. 1973 209.6 ± 48.0	460.9 ± 105.5	122.2 ± 27.9	0.58 ± 0.13
Summer minimum	29 Jan. 1974 163.8 ± 39.3	360.3 ± 86.5	93.1 ± 22.3	0.44 ± 0.10
Late winter	2 Oct. 1973 94.1 ± 18.7	270.3 ± 53.7	78.4 ± 15.6	n.a.
Early winter	27 Feb. 1974 60.6 ± 8.0	148.9 ± 19.7	40.3 ± 5.3	n.a.

(* Assuming 4.8 kcal/l Oxygen consumed)

Table 17. Biomass and respiration rate of a population of *N. antarticus* in the Vestfold Hills derived from mean densities of mites given in Section 5.5.

Respiration rates for the population of *N. antarcticus* at Site B in the Vestfold Hills (Table 17) are calculated for a temperature of 5°C. The upper one centimetre of substrate at Site B reached a maximum diurnal temperature of 5°C or greater in the period 21 November 1973 to 29 January 1974 (Table 3). The respiration rate of the population probably reached 114.7 ± 24.1 litres of Oxygen per square metre per hour or 0.55 ± 0.11 cal/m²/hr at some time each day over this period of seventy days.

On 2 October and 27 February, the maximum temperatures of the top one centimetre of substrate were about 0°C (Section 5.1; Table 3). Respiration rates calculated for these occasions (Table 17) probably are overestimated because the substrate temperature remained below 5°C. Regardless of the effect of lower temperatures, these estimates of respiration rates are substantially lower than on occasions in mid-summer because of the reduced mite densities (Table 17).

The mean summer biomass of the population of *N. antarcticus* studied was 432.5 ± 90.0 mg/m² (Table 17). This figure is within the range 300 to 5400 mg/m² for the mean annual biomass of different species of oribatid mites in other soil ecosystems (Harding and Stuttard, 1974), despite the relatively small size of individuals of *N. antarcticus*.

The rate of respiration in *N. antarcticus* is greater than in temperate species of oribatid mites (Block, 1976), and similar to that of some other species of prostigmatic mites in temperate deciduous woodland (Wood and Lawton, 1973). On days when the mean temperature of the substrate is 5°C during summer, the respiration rate of the population of *N. antarcticus* at the Vestfold Hills (0.55 ± 0.11 cal/m²/hr) is of the same order as that recorded for all species of Acari in a blanket bog (2.28 cal/m²/hr) at Moor House, England (Heal, 1968), and for forty-six species of oribatid mites (2.45 cal/m²/hr) in forest soil in Belgium (Berthet, 1963).

Engelmann (1966) found the following relationship between caloric respiration and net productivity in poikilotherms:

$$\text{Log } R = 0.62 + 0.86 \text{ Log } p,$$

where R represents the respiration of a population and p represents the net productivity (both measured in kcal/m²/year). A value of 1.18 kcal/m²/yr is obtained for net productivity in the population of *N. antarcticus* by substituting the value of R equivalent to the above respiration rate at 5°C during seventy days of the austral summer. However, production in the population occurred mainly during the seventy days and not during the rest of the year when temperatures were low; therefore net productivity would be 0.22 kcal/m² per seventy days which probably amounts to the total annual net productivity of the population. This net productivity is of the same order as that found by Engelmann (1961) for all species of oribatid mites (0.43 kcal/m²/yr) in abandoned pastures or "old fields".

N. antarcticus is the dominant (and possibly the only) consumer of soil algae at the sites studied during the present work. If an ecological efficiency of ten per cent is assumed (Whittaker, 1974) for the utilization of energy in soil algae eaten by the population of *N. antarcticus*, then a net

productivity of soil algae of at least two kcal/m²/yr supported the population of mites.

The abundance and rates of production and respiration of populations of *N. antarcticus* in the Chalikosystem are similar to those found in populations of other species of Acari in soil ecosystems generally. Nevertheless, populations of *N. antarcticus* occur in the Chalikosystem only where water is available, and grow only during the short Antarctic summer. A large proportion of the Chalikosystem cannot support *N. antarcticus*, and some of it does not support any living organisms (Boyd et al., 1966).

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APPENDIX A

RESULTS OF CORE ANALYSES

Date	Total Counted	M	F	Life Stage				Total Unidentified	Total* Lost
				T	D	P	L		
16 Aug.	252	60	71	26	12	8	6	18	51
16 Aug.	804	154	136	81	38	43	29	96	227
19 Sept.	518	107	142	28	7	12	7	44	171
2 Oct.	430	73	66	38	33	11	14	32	163
2 Nov.	538+	65	72	39	43	17	63	47	-
21 Nov.	898	106	160	96	77	68	51	37	303
4 Dec.	1337	154	165	195	115	149	158	48	443
2 Jan.	901+	237	340	74	51	29	16	154	-
2 Jan.	1131	168	116	122	150	173	86	100	216
16 Jan.	1562	184	116	147	189	172	139	105	510
29 Jan.	1045	106	109	95	127	109	103	125	271
13 Feb.	627	86	92	70	73	41	40	83	142
27 Feb.	475	71	68	53	62	43	35	48	95

* See Section 4.5 for explanation of these categories

Table 1. Summary of the numbers of mites counted and identified in quantitative and non-quantitative+ samples of substrate from Site B.

Coordinate	Totals																											Mean No. mites/ cm ²
	47	32	02	19	62	56	36	34	88	10	76	95	39	87	28	45	78	04	*	**								
Males	4	1	14	2	13	2	2	8	11	5	2	15	6	5	13	19	16	16	154	257	2.91							
Females	3	1	8	2	4	8	10	16	3	6	1	7	6	5	11	25	12	8	136	227	2.57							
Tritonymphs	5	3	7	2	1	3	2	7	8	1	4	4	7	2	6	6	6	7	81	135	1.53							
Deutonymphs	4	2	4	1	0	0	2	2	2	5	2	1	0	2	4	4	1	2	38	64	0.73							
Protonymphs	2	1	2	0	0	3	0	6	11	1	0	0	2	1	2	5	0	7	43	72	0.49							
Larvae	5	2	4	0	1	0	0	4	4	1	0	0	2	2	1	1	0	2	29	49	0.33							
Unidentified	7	4	4	0	16	4	3	11	2	5	9	2	2	3	5	12	5	2	96									
Lost	27	6	13	3	6	18	1	6	31	10	13	4	14	15	14	15	12	19	227									
Total	57	20	56	10	41	38	20	60	72	34	31	33	39	35	56	87	52	63	804	804	9.11 ± 1.24							

Mean no. of mites/core = 44.15 No. of Cores = 18 Core area = 3.5 cm² * Actual
 ** Corrected

Table 2. Core analysis 16 August 1973, Site B Quadrat.

Core length (cm)	5.0 5.5 4.0 3.5 4.0 3.5 4.0 3.5 4.0 3.5 4.0 3.5 4.0 3.5 4.0 3.5 4.0 - 3.5																	Totals	Mean no. mites/cm ²
	22 ϕ	22	20	18	16	14	12	10	8	7	6	5	4	2 ϕ	2 *	**			
Males	-	2	1	1	2	2	0	13	24	10	7	8	0	-	3	73	134	2.94	
Females	-	2	2	1	4	4	0	10	5	10	16	5	0	-	7	66	121	2.65	
Tritonymphs	-	1	1	0	2	0	1	2	8	7	3	9	0	-	4	38	69	1.51	
Deutonymphs	-	0	1	0	3	0	0	7	7	4	3	7	0	-	1	33	60	1.31	
Protonymphs	-	1	0	0	1	0	0	2	0	2	1	1	3	-	0	11	20	0.43	
Larvae	-	2	0	0	2	2	0	1	0	0	1	2	1	-	3	14	26	0.57	
Unidentified	-	3	1	0	0	2	1	1	9	2	11	1	1	-	0	32			
Lost	-	8	3	1	7	14	0	22	30	36	18	9	2	-	13	163			
Total	(26)	19	9	3	21	24	2	58	83	71	60	42	7	(38)	31	430	430	9.41 \pm 1.87	

Mean no. of mites/Core = 32.93 No. of Cores = 13 Core area = 3.5 cm²

(ϕ indicates cores used to determine the vertical distribution of mites)

* Actual
** Corrected

Table 3. Core analysis 2 October 1973, Site B traverse.

Core length (cm)	7.0	7.0	4.0	5.0	4.0	3.5	4.0	4.0	3.5	4.0	3.5	Totals		Mean no. mites/cm ²
	Position (m)	22	20	18φ	16	14	10	8	6	4φ	2	0	*	
Males	0	30	-	8	9	16	4	23	-	15	1	106	171	3.87
Females	3	58	-	2	9	28	6	32	-	18	4	160	258	5.85
Tritonymphs	0	37	-	10	9	10	3	12	-	14	1	96	154	3.49
Deutonymphs	2	16	-	12	15	11	0	9	-	11	1	77	124	2.81
Protonymphs	4	23	-	8	8	13	2	5	-	5	0	68	109	2.47
Larvae	2	19	-	9	7	3	1	4	-	6	0	51	82	1.86
Unidentified	0	14	-	9	2	6	0	5	-	0	1	37		
Lost	29	41	-	28	28	22	24	39	-	83	9	303		
Total	40	238	(43)	86	87	109	40	129	(62)	152	17	898	898	20.35 ± 3.93

Mean no. of mites/Core = 91.18 No. of Cores = 11 Core area = 3.5 cm² * Actual
 ** Corrected

(φ indicates cores used to determine the vertical distribution of mites)

Table 4. Core analysis 21 November 1973, Site B traverse.

Core length (cm)	5.0	4.0	4.0	4.0	3.5	3.5	3.5	3.5	4.0	3.5	4.0	3.5	4.0	3.5	4.0	Totals	Mean no. mites/cm ²
Position (m)	24	22	20	18	16	14	12	10	8	6	4	0	-2	*	**		
Males	13	14	12	17	7	1	14	9	19	18	23	2	5	154	243	3.81	
Females	22	21	8	23	3	4	12	5	26	13	21	1	6	165	261	4.09	
Tritonymphs	15	9	16	9	3	2	0	9	8	8	14	1	11	105	166	2.60	
Deutonymphs	23	22	12	12	3	1	1	14	5	7	12	0	3	115	182	2.85	
Protonymphs	20	53	8	13	3	2	2	9	4	3	28	1	3	149	235	3.69	
Larvae	5	99	3	22	2	3	0	3	1	5	15	0	0	158	250	3.92	
Unidentified	7	17	1	3	1	0	4	0	0	1	8	2	4	48			
Lost	23	86	23	40	30	1	3	29	72	31	78	9	18	443			
Total	128	521	83	139	52	14	36	78	135	86	199	16	50	1337	1337	20.96 ± 4.80	

Mean no. of mites/Core = 102.85 No. of cores = 13 Core area 4.9 cm² * Actual
 ** Corrected

Table 5. Core analysis 4 December 1973, Site B traverse.

Core length (cm)	Core length																	Totals		Mean no. mites/cm ²
	6.8	6.8	7.0	7.0	8.1	6.9	7.1	7.2	7.2	7.0	7.0	7.0	7.4	6.9	5.8	7.0	*	**		
Position (m)	24	22	20	18	18	16	14	12	10	8	6	4	4	2	0	-2	*	**		
Males	5	4	1	3	3	18	5	32	10	27	51	5	6	2	6	6	184	304	3.87	
Females	12	5	0	3	1	10	4	17	11	24	14	3	6	2	1	3	116	191	2.43	
Tritonympha	18	9	7	5	1	7	7	19	14	20	22	2	3	2	3	8	147	242	3.08	
Deutonymphs	20	21	14	5	2	8	5	24	13	31	37	1	6	1	0	1	189	312	3.98	
Protonymphs	18	26	9	10	1	8	1	23	19	22	26	3	4	2	0	0	172	284	3.62	
Larvae	11	39	19	5	1	5	0	16	14	3	16	3	6	0	0	1	139	229	2.92	
Unidentified	6	11	12	3	0	11	4	12	12	7	20	1	1	0	3	2	105			
Lost	42	41	12	12	11	6	4	68	49	56	131	10	44	7	4	13	510			
Total	132	156	74	46	20	73	30	211	142	190	317	28	76	16	17	34	1562	1562	19.90 ± 4.43	

Mean no. of mites/Core = 97.63 No. of cores = 16 Core area = 4.9 cm² * Actual
 ** Corrected

Table 7. Core analysis 16 January 1974, Site B traverse.

Core length (cm)	7.6	7.4	7.4	8.0	8.0	8.1	8.3	8.3	8.3	8.0	7.9	8.1	8.2	8.3	Totals		Mean no. mites/cm ²
Position (m)	24	22	20	20	16	12	10	8	8	6	4	4	0	-2	*	**	
Males	2	0	2	1	0	35	4	17	19	10	4	4	0	12	106	171	2.68
Females	2	4	2	6	0	25	2	28	18	9	4	4	1	8	109	176	2.76
Tritonymphs	4	1	5	6	3	20	5	10	12	15	4	4	0	10	95	153	2.40
Deutonymphs	10	2	6	5	1	42	6	5	18	19	5	5	3	5	127	204	3.20
Protonymphs	7	4	1	3	2	19	10	5	16	32	5	2	2	3	109	175	2.74
Larvae	2	2	3	3	3	25	8	10	18	16	10	2	2	1	103	166	2.60
Unidentified	12	1	7	1	18	17	9	6	28	12	3	2	2	9	125		
Lost	15	5	3	19	11	21	13	10	103	29	13	6	6	23	271		
Total	54	19	29	44	38	204	57	91	230	144	48	16	16	71	1045	1045	16.38 ± 3.93

Mean no. of mites/Core = 80.38 No. of cores = 13 Core area = 4.9 cm²

* Actual
** Corrected

Table 8. Core analysis 29 January 1974, Site B traverse.

Core length (cm)	Position (m)																	Totals		Mean no. mites/cm ²
	3.0	3.3	5.0	3.0	3.8	4.2	5.6	6.3	5.6	6.0	6.5	7.3	6.7	4.8	5.8	*	**			
Males	0	2	10	1	1	7	6	21	5	2	4	4	6	7	10	86	134	1.82		
Females	0	7	24	0	0	7	5	25	2	1	5	0	5	5	6	92	144	1.96		
Tritonymphs	1	4	12	0	1	3	3	17	2	2	9	3	3	8	2	70	108	1.48		
Deutonymphs	1	9	16	1	0	3	12	12	2	4	6	1	1	2	3	73	114	1.55		
Protonymphs	1	1	2	2	0	3	8	9	4	2	6	2	0	0	1	41	64	0.87		
Larvae	0	0	4	1	0	6	7	5	1	1	8	4	1	2	0	40	62	0.84		
Unidentified	4	4	6	6	4	11	17	10	0	4	4	2	5	2	4	83				
Lost	0	9	24	0	10	7	16	24	4	7	22	7	5	4	3	142				
Total	7	36	98	11	16	47	74	123	20	23	64	23	26	30	29	627	627	8.52 ± 1.78		

Mean no. of mites/core = 41.80 No. of cores = 15 Core area = 4.9 cm²

* Actual
** Corrected

Table 9. Core analysis 13 February 1974, Site B traverse.

Core length (cm)	6.2	4.3	5.0	3.9	4.0	5.0	5.9	5.7	4.8	6.0	6.1	5.7	6.0	4.8	4.8	5.7	Totals	Mean no. mites/cm ²	
Position (m)	24	22	22	20	18	16	14	12	10	8	6	4	4	2	0	-2	*	**	
Males	2	0	3	8	4	4	3	6	5	8	9	1	3	1	2	12	71	102	1.30
Females	3	3	1	5	6	3	4	9	7	3	12	2	2	0	1	7	68	97	1.23
Tritonymphs	3	1	2	2	5	4	2	10	1	3	5	1	6	4	1	3	53	76	0.97
Deutonymphs	3	6	4	5	7	3	1	10	6	0	2	0	7	1	4	3	62	89	1.13
Protonymphs	4	3	1	1	0	1	0	11	5	4	4	2	5	2	0	0	43	62	0.79
Larvae	1	4	0	2	2	5	3	7	8	2	1	0	0	0	0	0	35	50	0.64
Unidentified	1	3	4	3	3	2	0	5	4	2	12	0	1	4	1	3	48		
Lost	2	6	3	7	7	8	0	2	18	17	1	0	12	4	0	8	95		
Total	19	26	18	33	34	30	13	60	54	39	46	6	36	16	9	36	475	476	6.06 ± 0.80

Mean no. of mites/Core = 29.69 No. of cores = 16 Core area = 4.9 cm² * Actual
 ** Corrected

Table 10. Core analysis 27 February 1974, Site B traverse.

APPENDIX B
RESULTS OF SITE ANALYSIS

SITE	A	B	C	D	E	F	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Substrate	2	2	3	3	2	2	3	2	2,3	2	2	3	2	3	2	3	2	1	2	2	3	1,2	2,3
Metres above mean sea level	4	4	15	10	25	25	4	10	15	5	20	18	1	11	10	5	5	50	-20	25	120	50	25
Moss	+			+	+																		
Algae	1,2	1,2		1	1,3		1	3	1,3	2,5	2,5		3	2,5	5	5		4					
Lichens	4,5	4,5		1,2	1,2		1,2		1							2,3	4,5						2
Microfauna	4	3,4		2	1,2		2	1,2												3			
Vertebrates			2		1																		
SITE	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	35	37	38	39	40	41	42
Substrate	3	1	2	2	2	2	3	2	3	2	3	3	2	2	3	2	2	4	2	2	3	3	2
Metres above mean sea level	25	50	20	2	25	25	5	0	55	50	15	3	-40	-40	22	60	22	2	5	5	25	40	150
Moss	+														+							+	+
Algae	4			3,4	3,4		2,4	2,4	5	5	5	2,3	2,3	4,5	4,5	1,2	1,2	3,4	1,2	2	5	1,2	
Lichens	2,3																					2,4	5,6
Microfauna					3		2					2				4	3,4	3,5	4			1	
Vertebrates					4		2			2								4				1	

KEY: Substrate: * = *N. antarcticus* present + = Avian nest flea
 1 silt, 2 sand, 3 grit, 4 water
 Algae: 1 *Nostoe*, 2 *Oscillatoria*, 3 *Prasiola*, 4 diatoms, 5 coccoid (blue-green).
 Lichen: 1 *P. citrina*, 2 *B. frigidida*, 3 *A. gwynii*, 4 *P. coryi*, 5 *C. elegans*, 6 *B. antarctica*
 Microfauna: + 1 *G. antarcticus*, 2 *T. erebus*, 3 rotifers, 4 nematodes, 5 tardigrades
 Vertebrates: 1 *P. nivea*, 2 *D. capense*, 3 *S. macormacki*, 4 *P. adeliae*

Table 1. Plants, animals and types of substrate found at Sites A - F and 1 - 42.

SITE	A	B	C	D	E	F	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	
FUNGI																								
<i>C. pannorum</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
F8	+	+																						
<i>T. microsporus</i>	+																							
<i>D. salina</i>																								
<i>P. melinii</i>																								
<i>A. strictum</i>																								
<i>C. cladosporoides</i>																								
PP																								
ACTINOMYCETES																								
<i>Streptomyces sp.1</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Streptomyces sp.2</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
BACTERIA																								
White bacilli	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Lemon bacilli	+	+																						
Yellow bacilli	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Orange bacilli	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Pink cocci	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
YEAST																								

+

Table 2. Microorganisms found at Sites A - F and 1 - 42.

* = *N. antarcticus* present + = Avian nest flea

SITE	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	35	37	38	39	40	41	42
FUNGI																							
<i>C. pannorum</i>			+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
F8																							
<i>T. microsporus</i>			+	+	+	+	+	+	+	+	+	+	+	+	+	+							
<i>D. salina</i>																							
<i>P. melinii</i>																							
<i>A. strictum</i>																							
<i>C. cladosporoides</i>																							
PP																							
ACTINOMYCETES																							
<i>Streptomyces</i> sp.1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Streptomyces</i> sp.2			+																				
BACTERIA																							
White bacilli	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Lemon bacilli																							
Yellow bacilli	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Orange bacilli																							
Pink cocci	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+

* = *N. antarcticus* present + = Avian nest flea

Table 2. (Continued) Microorganisms found at Sites A - F and 1 - 42.