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Microhabitats occupied by terrestrial arthropods in the Stillwell Hills, Kemp Land, East Antarctica

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Abstract: A fine-scale survey of the distribution of free-living terrestrial arthropods in the Stillwell Hills region of Kemp Land, East Antarctica, was carried out between 22 December 1996 and 27 January 1997. Three species, all Acari, were recorded: *Protereunetes maudae* Strandtmann, *Nanorchestes triclivatus* Booth and *N. lalae* Strandtmann. Population densities varied from 0 to 6802 ind. m^{-2} with a mean of 954 ind. m^{-2}. The favoured microhabitat was found to be beneath stones in damp locations on north- and west-facing slopes. Sites with microalgal growth supported more microarthropods than sites with mosses, lichens and macroalgae. Arid and saline habitats, including such sites as wind-swept ridges and the seashore, were found to lack microarthropods. Thermal and humidity profiles above and below the ground surface were recorded to investigate the microenvironments of Acari. Special attention was focused upon the moderating role of snow thickness, vegetation cover, aspect and vertical depth in the soil profile. These microclimate data suggest that Acari are able to avoid the extremes of low temperature experienced at macroclimate level but that heat stress and desiccation may play important limiting roles.

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Key words: Acari, heat stress, limiting factors, moisture availability, operating environments, spatial pattern

Introduction

The major groups of invertebrates known to occur in Antarctica are the Rotifera, Tardigrada, Nematoda, Acarina, Collembola and Diptera (Block 1984). The first three groups are generally referred to as meiofauna and the last three groups as microarthropods. Considerable data exist on the distribution of these taxa from West Antarctica, including the Antarctic Peninsula, South Orkney Islands and South Shetland Islands, where many biological collections have been made over the last 100 years (e.g. Trouessart 1912, Strong 1967, Tilbrook 1967, Lippert 1971, Richard *et al.* 1994, Convey & Smith 1997). Relatively little is known about the species composition of the East Antarctic fauna with the exception of Dronning Maud Land (e.g. Boström 1995, Ohyama & Hiruta 1995, Sohlenius *et al.* 1995, 1996), Victoria Land (e.g. Janetschek 1963, Gressitt & Shoup 1967, Janetschek 1970, Freckman & Virginia 1991) and those areas immediately adjacent to research stations (e.g. Rounsevell 1977, Matsuda 1977, Rounsevell & Horne 1986, Sugawara *et al.* 1995).

During the period 22 December 1996 to 27 January 1997 a series of plant and invertebrate collections was undertaken in the Stillwell Hills region (67°22'S, 59°25'E) of Kemp Land, East Antarctica, as part of the 50th Australian National Antarctic Research Expedition (ANARE). This locality lies within the Coastal Phytogeographic Region of East Antarctica (cf. Pickard & Seppelt 1984). No information on the terrestrial biology of the Stillwell Hills has previously been published. The nearest comprehensive biological information is for the region surrounding Mawson Station, 160 km farther east, where limited studies of vegetation characteristics (Seppelt & Ashton 1978, Broady 1982) and Tardigrada (Gardiner & Pidgeon 1987, Miller & Heatwole 1995) have been made. Farther west, isolated invertebrate collections have been taken from the vicinity of Molodezhnaya Station (Meyer *et al.* 1967, Sitnikova 1968).

The Stillwell Hills comprise a series of ice-exposed ridges and islands covering an area of *c.* 100 km^2 on the edge of the Antarctic polar plateau. The region is bounded by the waters of Stefansson Bay to the west, William Scoresby Archipelago to the east and by Dovers Glacier to the south. A wide variety of terrestrial habitats exist within this region including bare rock outcrops, coastal cliffs, raised beaches, montane plateau, meltwater stream and lake shores, moss carpets, lichen beds and ornithogenic sites such as penguin rookeries and skua roosts. The geology of the region has been discussed by Trail (1970), Grew *et al.* (1988), Clarke (1988) and by White & Clarke (1993). The dominant substratum is unstable glacial scree strewn with frost-shattered boulders of quartz-feldspar gneiss and hornblende-pyroxene-plagioclase. Soils vary from lithosols in areas recently exposed by ice retreat to ornithogenic soils at sites frequented by penguins, skuas and storm petrels. The lithosols are coarse-textured and covered by a surface stone layer and may be characterized as ahumic lithosols with low moisture content. At localized ornithogenic sites, the organic component of the soil is increased by the addition of bird feathers and guano as well as occasional carcasses in near-shore areas.

The objectives of the present study were two-fold: (1) to determine whether or not free-living invertebrates are present in the Stillwell Hills, and (2) to survey the fine-scale distribution of any microarthropods encountered to gain insight into their microhabitat utilization. Detailed microclimate monitoring was also carried out to investigate the environmental conditions experienced a short distance above and below the ground surface. In this paper, these biological and environmental data are integrated to address the question "what physical conditions do Antarctic invertebrates actually experience?" The outcome is considered to have value for interpreting the relative importance of temperature and moisture supply as limiting factors.

Materials and methods

Two sites were occupied during the ANARE expedition (Fig.1). The first camp, known as Ledingham's Depot, (67°22.05'S, 59°27.64'E) lies on a flat tidal plain in the central Stillwell Hills and was occupied for two periods, between 23 December 1996 and 9 January 1997 and between 18–27 January 1997. The second camp, known as the Kemp Peak Depot, (67°25.14'S, 59°26.49'E) lies in a small basin of glacial boulders beneath a prominent mountain in the southern Stillwell Hills and was occupied between 10–17 January 1997.

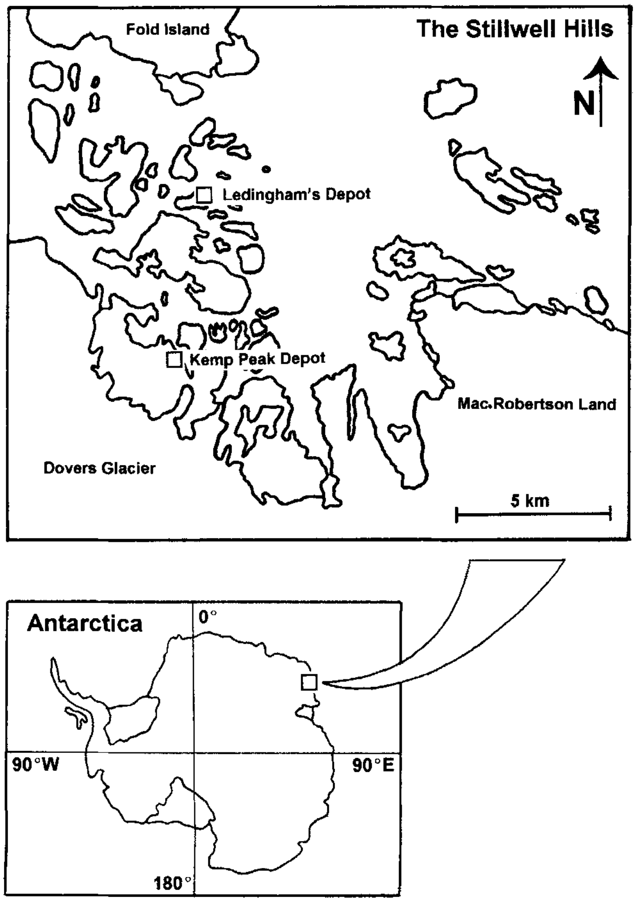

Fig. 1. Map showing the Stillwell Hills region of Kemp Land, East Antarctica. The two field camps occupied during this study, Ledingham's Depot and Kemp Peak Depot, are marked.

Habitat characteristics

A comprehensive variety of terrestrial habitats was explored. Macrohabitat notes were made for each of the sites at which biological material was encountered. The key variables recorded were: (1) general site description, (2) altitude, (3) aspect, (4) angle of slope, (5) substratum type, (6) substratum stability, (7) vegetation, (8) hydrology, (9) marine influence, (10) snow input, (11) ornithogenic input, (12) exposure to wind, (13) distance to shore, (14) direction to shore. These habitat descriptions, although mostly subjective in nature, provide a basis from which to interpret the factors controlling the distribution of plants and invertebrates in the Stillwell Hills.

Temperature and relative humidity profiles were recorded at a variety of sites in the Stillwell Hills using an SQ32-12K/2L/2V and an SQ80-16K Eltek Grant Squirrel meter/logger (Eltek Ltd, Haslingfield, Cambridge, CB3 7LL, UK). Ten microthermistor probes (Type K: Ni Cr^+, Ni Al^-) and two relative humidity sensors (Type HMP 31 UT, Vaisala Ltd, Finland) were carefully positioned either on the surface of the soil profile or at different depths above and beneath the ground surface. The thermistor probes were shielded from direct solar radiation.

Microarthropod collection

An initial survey was carried out of the broad-scale distribution of terrestrial invertebrates. In the case of substrata that could be collected (e.g. mineral fines, coarse sand, algal mats, foliose lichen thalli, moss cushions) small quantities of the material were placed in petri dishes and teased apart with forceps while searching for invertebrates. A modified Tullgren apparatus (Macfadyen 1961) was then used to induce any remaining invertebrates to migrate downwards through a heat and humidity gradient into a series of collecting pots. Where substrata could not be collected (e.g. boulders, stones frozen into the soil by permafrost, crustose lichens attached to rock outcrops, fissures in bedrock) the microhabitats were examined *in situ* with a magnifying glass.

The above techniques provided qualitative information on the composition and distribution of microarthropod assemblages in the Stillwell Hills. To gain quantitative data on the factors influencing their relative abundance a more detailed study was carried out across a wide variety of sites containing stones resting on underlying substrata. Such habitats varied from bryophyte- and algae-dominated sites in well-irrigated locations to bare, exposed sites at the top of ridges and along the sea shore. At each of these sites, 20 stones were selected, overturned and examined for a uniform period of two minutes. Any microarthropods present were collected using an aspirator and then fixed and preserved in a solution of 70% ethanol, 29% water and 1% glycerol for return to Australia. The dimensions of the stones (length x breadth) were recorded, together with the depth at which their undersurface had rested below the soil surface. A subjective measure of the texture, colour, angularity, fracture and percentage cover by wetness (as indicated by the proportion of surface area that glistened) was made on a 1 to 5 scale. If microalgae were visible as a green stain on the stone the spatial area and distribution of the stain were recorded. An estimate of where the majority of microarthropods occurred on the stone was also made.

Microscopy

The preserved microarthropods were examined with a Jeol JSEM840 scanning electron microscope using a 10 kv electron beam operating through a 1 x 10^{-10} amp probe size. Sample preparation involved an ethanol dehydration series followed by two steps of 100% dry acetone. Critical point drying was then applied using liquid CO_2. The dehydrated animals were mounted onto brass stubs with silver conducting paint. Finally, the surface of the animals was sputter-coated with gold to a depth of 21 nm.

Results

A summary of those Stillwell Hills microhabitats in which intensive microarthropod collecting was undertaken is presented in Table I.

Microclimate characteristics

At the start of the expedition it had been hypothesized that aspect, soil depth, snow cover and vegetation architecture would play an important role in modifying microclimate characteristics. Consequently, special attention was focused on these four factors. Replicate 24 hour recording runs were made under a variety of soil, snow and vegetation conditions for use in interpreting the fine-scale microhabitat preferences of terrestrial arthropods.

Vertical depth in the soil profile was shown to exert a buffering effect upon temperature. Changes at four vertical levels in a dry sand substratum during two days in early January 1997 are presented in Fig. 2a. The highest temperature experienced during this period, 26.2°C, occurred at the ground surface level. The lowest temperature, -5.6°C, also occurred at ground surface level. Conversely, at 100 mm depth, maximum and minimum temperatures of only 10.2°C and 1.5°C were experienced. The relative magnitude of these two temperature ranges, 31.8°C versus 9.7°C, demonstrates how organisms may potentially avoid extremes of temperature by positioning themselves at a particular depth in the soil profile. Of special significance for frost-sensitive species is the observation that, at depths below 50 mm, sub-freezing temperatures are unlikely to be experienced at this time of year.

A distinct lag in the time at which temperature maxima and minima occur is apparent at this site. On 6 January the highest temperature at soil surface level occurred at 15h30 while at 10 mm depth it occurred at 17h15, at 50 mm depth at 17h45

Table I. Characteristics of Stillwell Hills microhabitats surveyed for microarthropod abundance.

No	Site	Altitude (m)	Aspect	Substratum	Stability	Vegetation	Hydrology	Bird input	Distance to shore (m)
1	snow bank - side	50	20°, NE-facing	gravel & rocks	moderate	crustose lichens, mosses	moist	low	2000
2	snow seepage area	10	35°, N-facing	coarse sand & gravel	high	lichens, algal cushions	moist	high	50
3	glacial meltwater	40	15°, W-facing	fine gravel	moderate	none	wet	low	150
4	stream shore	50	20°, W-facing	shale on mineral soil	moderate	lichens & sublithic algae	wet	low	350
5	moss bed	250	35°, N-facing	scree with mineral soil	moderate	moss cushions	moist	low	3000
6	base of snow bank	48	20°, NE-facing	gravel & rocks some fines	moderate	cushion mosses, lichens	wet	low	2000
7	foot of glacier	5	10°, SE-facing	gravel & stones	moderate	sublithic microalgae	wet	low	50
8	algal cushions	10	10°, E-facing	sand, gravel & shale	moderate	large algal cushions	wet	moderate	600
9	recently ice-exposed	50	10°, S-facing	frost shattered stones & rocks	moderate	sublithic microalgae	moist	low	2500
10	snow bank – top	52	20°, NE-facing	gravel & rocks	moderate	crustose lichens	arid	low	2000
11	lichen bed	240	15°, N-facing	scree & pebbles	moderate	foliose & crustose lichens	arid	low	3000
12	ornithogenic site	35	15°, W-facing	sand	high	crustose lichens	arid	high	150
13	lake shore	5	10°, SE-facing	gravel on mineral fines	moderate	aquatic algae	wet	none	750
14	rock outcrop	60	20°, W-facing	sand between boulders	high	mosses & crustose lichens	arid	moderate	100
15	frost boils	40	flat	mixed – fines to shale	low	lichens on larger stones	moist	none	40
16	sea shore	1	10°, E-facing	sand & fine gravel	high	none	arid	moderate	10
17	saline flats	3	5°, E-facing	gravel & coarse sand	moderate	none	arid	moderate	100
18	ridge	150	45°, N-facing	rock scree	low	crustose lichens, mosses	arid	low	200
19	summit	100	30°, S-facing	rocks & stones	low	none	arid	low	50
20	shaded site	20	20°, E-facing	mineral sand	moderate	none	arid	low	40

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and at 100 mm depth at 19h00. The timing of the lowest temperatures also shows a staggered pattern, occurring at 03h45, 04h45, 05h30 and 06h45 respectively. This lag period in the downwards propagation of the thermal wave is caused by the imperfect conductivity of the soil and by the large amount of energy required to overcome the soils's high specific heat capacity. Potentially it allows invertebrates to maximise the period of time that they spend in a favourable thermal environment by migrating through the soil profile in synchrony with the thermal wave.

Relative humidity was monitored on the upper and lower surface of a stone between 6–7 January 1997. The stone was located on a scree slope of approximately 35° angle and NW-facing aspect. The substratum underlying the stone was a mixture of small pebbles and sand. Moisture was sporadically available at the site from a nearby snowbank.

Relative humidity both above and below the stone fluctuated widely with slightly greater variation on the upper than on the lower surface. A diel cycle is apparent with lower humidities experienced by day than by night (Fig. 2b). The minimum values experienced on the upper and lower surfaces of the stone were 17.5% and 50.0% respectively at 21h00 and 14h15. The maximum values were 60.0% and 87% respectively at 03h00 and 01h30. Relative humidity on the lower surface of the stone was consistently greater than on the upper surface throughout the two-day period. The range of elevation was between 20% and 50% depending upon the time of day. The maximum difference occurred during the late afternoon when solar radiation incident on the slope was greatest. Minimum elevation occurred at night.

The nature of thermal amelioration caused by snow cover is illustrated in Fig. 2c. This graph shows temperature variation at ground surface level during two sunny days in late December 1996. One microthermistor probe was carefully inserted beneath a 10 cm layer of snow so that it rested on the ground surface; the other probe was placed on an adjacent area of exposed ground a short distance away. A third probe was elevated to 1.5 m above the ground to record ambient air

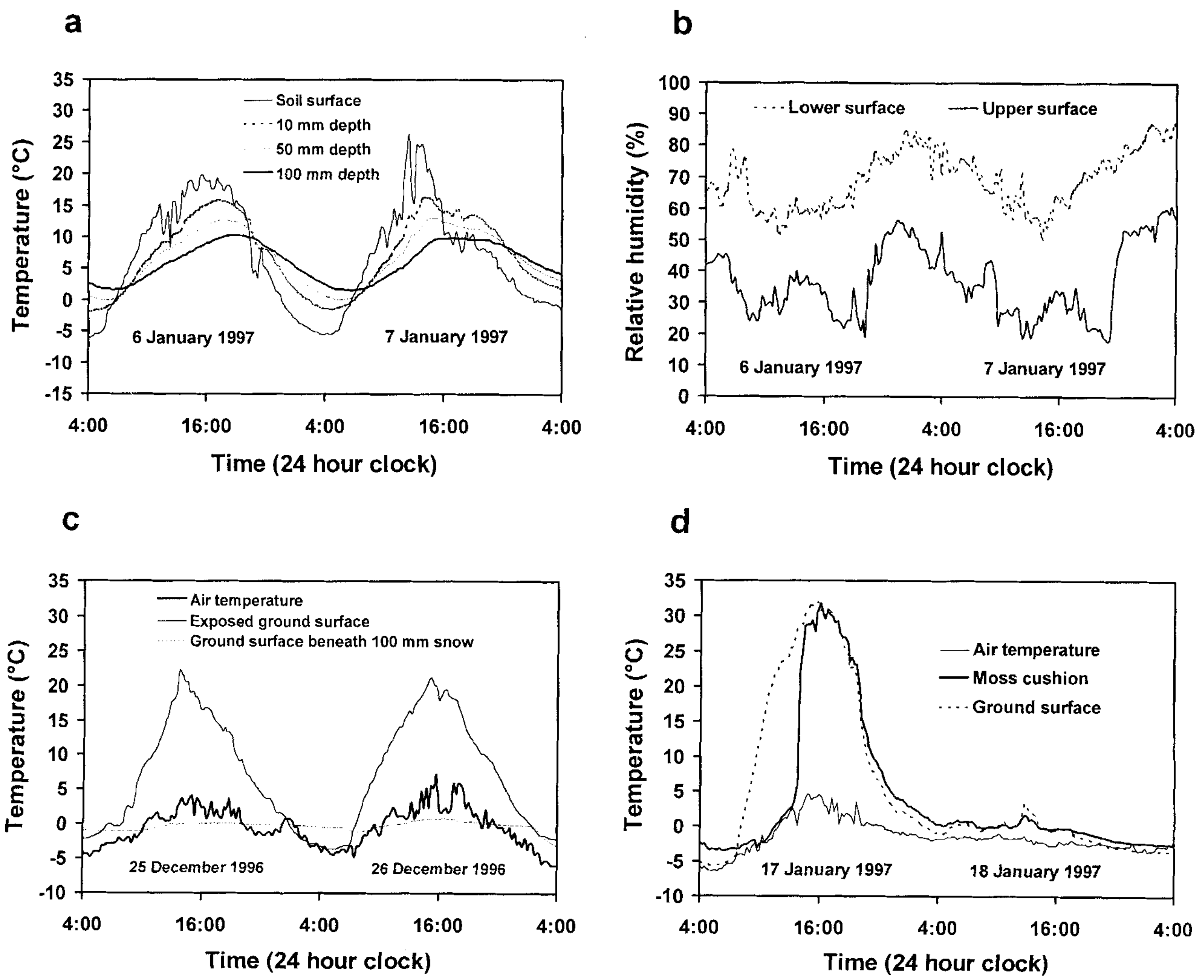

Fig. 2. A selection of microclimate data recorded from the Stillwell Hills. **a.** Temperature variation in relation to soil depth, **b.** relative humidity in relation to position on stone, **c.** temperature variation in relation to snow cover, **d.** temperature variation in relation to vegetation cover.

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temperature.

Considerably more stable thermal conditions were experienced beneath snow cover than at the exposed ground surface. Minimum and maximum temperatures over the two day period were -3.5°C and 22.2°C on the exposed ground surface relative to only -2.9°C and 0.9°C beneath snow, a difference in diurnal range of 21.9°C. During the day time the temperature beneath the snow was consistently lower than on exposed soil while at night time the order was reversed. This provides the potential for organisms to avoid extremes of high and low temperature by migrating between exposed soil and snow patches. Snow cover thicker than 10 cm is expected to have even greater thermal buffering effect.

The buffering role of vegetation architecture is illustrated in Fig.2d. This demonstrates diel temperature variation at three vertical levels in a Grimmia-dominated site. One microthermistor probe was placed at 1.5 m height in the air column, a second probe was placed at 10 mm depth within a moss cushion and a third probe was placed on the ground surface. The graph shows temperature variation between 04h00 on 17 January 1997 and 04h00 on 19 January 1997. The first day was characterized by bright sunshine and still conditions while the second day was overcast with 40 knot easterly winds and blown snow.

Air temperature differs significantly from the thermal environment in both the moss cushion and at ground surface level. Minimum and maximum values of -6.4 °C and 4.7 °C were recorded in the air column relative to -5.7 °C and 32.0 °C at ground surface level. Within the moss cushion, minimum and maximum temperatures of -3.5°C and 31.8°C were experienced. The moss took longer to warm up in the mornings but retained heat until later in the evenings. These differences suggest that the complex 3-D structure of moss cushions may act to trap warmth during the day and to retain it into the night, so providing a relatively favourable microhabitat in which invertebrates can avoid low temperature extremes.

Microarthropod distributions

Three species of free-living terrestrial Acari were recorded during this survey: *Protereunetes maudae* Strandtmann 1967 (Eupodidae), *Nanorchestes triclivatus* Booth 1984 (Nanorchestidae) and *Nanorchestes lalae* Strandtmann 1982 (Nanorchestidae). No Collembola, Diptera or other microarthropod taxa were encountered in the Stillwell Hills.

The mean density of Acari recorded across all of the sites was 954 ind. m^{-2}. All but four of the sites supported fewer than 1000 ind. m^{-2} while Acari were completely absent from five of the sites (Table II). Two of the depauperate sites occurred at relatively high altitude (a mountain summit and an exposed ridge), two sites had high salinity (the intertidal zone and an area of salt-encrusted rocks adjacent to Ledingham's Depot) while the fifth was in perpetual shade, being hidden behind the crest of a ridge. The greatest overall microarthropod density was 6802 ind. m^{-2} from beneath stones beside a snow bank on a north-east facing slope at 50 m altitude. This site had a sparse vegetation cover, primarily of crustose lichens with occasional shallow moss cushions. High densities were also found at sites near meltwater streams, glacier-fed tarns and in the vicinity of snowbanks that provided a reliable supply of moisture.

The microarthropod abundances recorded on individual stones showed significant variation both within and between sites. Of the 400 stones examined in detail, 69.3% supported no microarthropods while 12.1% had only one microarthropod on their surface (Fig. 3a). The greatest number of Acari recorded on a single stone was 71 from an area of snow seepage. This was also the only site at which every stone

Table II. Abundance of terrestrial Acari at sites around the Stillwell Hills.

Rank	Site description	Mean abundance ± s e (ind. m^{-2})	Range (ind. m^{-2})	% stones occupied	Mean stone area (cm^{-2})
1	side of snow bank	6802 ± 1759	0–32432	80	14.1
2	snow seepage area	6658 ± 1468	0–22152	100	48.1
3	glacial meltwater	1182 ± 379	0–6048	65	34.6
4	stream shore	1079 ± 308	0–4523	65	44.2
5	moss bed	798 ± 343	0–5983	40	24.4
6	base of snow bank	702 ± 171	0–2459	60	15.2
7	foot of glacier	535 ± 113	366–1382	60	31.9
8	algal cushions	482 ± 187	0–2521	35	18.3
9	recently ice-exposed soil	325 ± 131	0–2381	35	18.5
10	top of snow bank	186 ± 91	0–1282	20	14.2
11	lichen bed	121 ± 62	0–909	20	24.0
12	ornithogenic site	120 ± 62	215–1010	20	30.4
13	lake shore	38 ± 38	0–752	5	51.0
14	rock outcrop	28 ± 28	0–550	5	27.6
15	frost boils	14 ± 14	0–273	5	38.2
16=	sea shore	0	0–0	0	67.2
16=	saline flats	0	0–0	0	22.5
16=	ridge	0	0–0	0	33.2
16=	summit	0	0–0	0	37.3
16=	shaded site	0	0–0	0	25.2

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examined supported at least one microarthropod. The greatest overall density on any single stone was equivalent to 32 432 ind. m^{-2}. An indication of the variability, and hence patchiness, associated with microarthropod distributions is expressed by the large standard errors attached to the population means. This suggests that the distribution of terrestrial Acari in Antarctica shows a high degree of small-scale clustering.

The vertical distribution of microarthropods showed distinct zonation (Fig. 3b). On picking up stones, most of the invertebrates were found congregated in a relatively shallow zone between 5 mm and 30 mm below the ground surface. This corresponded to the depth at which a distinct boundary occurred between parts of the rock surface that were of matt appearance and parts that were dark and glossy, reflecting an ecotone between dry and damp conditions. Most microarthropods were found in the damp, shiny portion of the stone surface with relatively few on the dry, matt part. However, microarthropods did not occur at depth in extremely wet habitats, such as beside lakes or in the splash-zone of meltwater streams, where waterlogging is likely to occur.

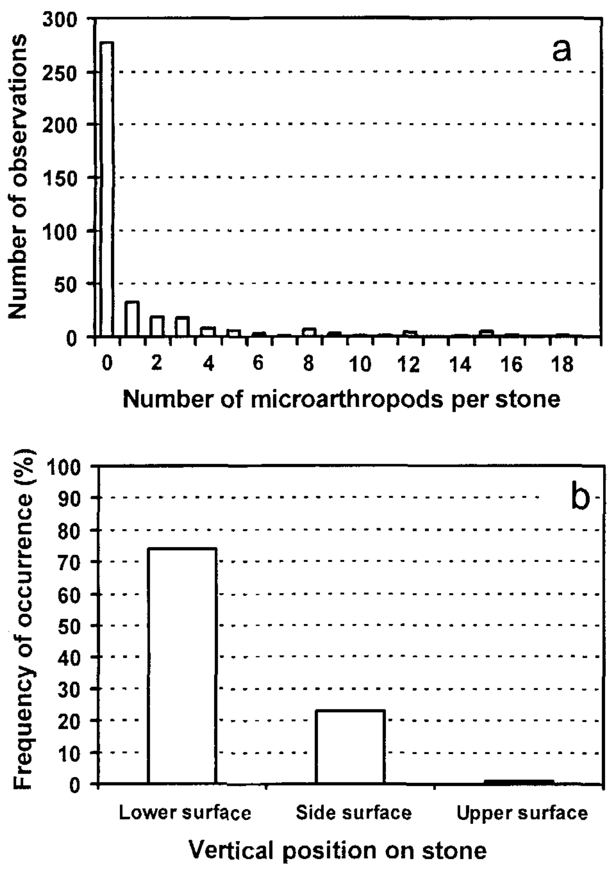

Fig. 3. a. Frequency with which between 0 and 20 Acari were recorded on individual stones from 20 sites in the Stillwell Hills. **b.** Vertical distribution of microarthropods in the Stillwell Hills. The graph shows the frequency with which terrestrial Acari were recorded at three vertical positions (upper surface, side surface, lower surface) on stones from 20 different sites, expressed as percentage of the total number of observations.

Aspect appeared to play a significant role in determining microarthropod distributions. South-facing slopes lacked high densities of Acari while partially north- or west-facing slopes supported the greatest abundances (Tables I, II). Sites that were flat were not particularly populated. It is impossible to separate the influence of aspect on temperature and moisture because both the warmest and wettest conditions in the Stillwell Hills are experienced on north- and west-facing slopes, particularly during midday and early afternoon. On south-facing slopes the ground remained frozen as permafrost throughout the five-week visit.

Microarthropod abundance did not show any clear correlation with stone texture, fracture, angularity and colour. Rocks that were rough, split, sharp or composed of dark hornblende-pyroxene-plagioclase minerals did not support greater Acari populations than stones that were smooth, unfractured, round or composed of light-coloured quartz-feldspar gneiss (Fig. 4). On the basis of these observations, microhabitat selection at the scale of individual stone properties does not appear to take place.

Ornithogenic influence did not play a strong role in the distribution of microarthropods. Many sites in the northern portion of the Stillwell Hills contained substantial accumulations of feathers, guano and occasional bird carcasses, usually confined to restricted areas. These were indicative either of penguin moulting sites (feathers, guano) or skua observation points (carcasses). At these locations the upper layers of the soil was usually baked dry to form a hard crust beneath which lay a layer of moister, nutrient-rich soil with a high content of decomposing feathers. However, detailed examination of this habitat revealed that neither the crust nor the underlying soil supported high densities of Acari.

Microarthropods did not show any particular affinity for vegetated sites. Of the three macrophyte-dominated areas examined during this survey the *Bryum* moss bank supported the highest density of Acari at 798 ind. m^{-2}. Macroalgal cushions contained nearly half this number, at 482 ind. m^{-2}, while lichens supported the fewest invertebrates at 121 ind. m^{-2}. In contrast, stones supporting microalgal growth were populated by high densities of Acari. Accumulations of mites were concentrated around green patches of microalgae adhering to the undersurface of the stones. Often the microarthropods' vertical depth below the ground surface appeared to be set by the vertical depth at which the microalgae occurred.

A synthesis of the data collected during this survey indicates that the preferred habitat of free-living terrestrial Acari in the Stillwell Hills is beneath rocks and stones overlying a layer of moist sand in areas irrigated by meltwater from nearby snowbanks. They also occupy the splash zone alongside meltwater streams and those portions of slopes dampened by water seepage. Although difficult to test empirically, personal observations suggest that sites bordered by deep snowbanks, where water was available for much of the summer, supported

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greater microarthropod abundances than sites bordered by transient snow banks, that melted early in the spring, where moisture supply was only ephemeral.

Discussion

Microclimate characteristics

The results of the current study complement earlier research into the operating environments of Antarctic invertebrates (e.g. Pryor 1962, Janetschek 1967, Tilbrook 1967, Walton 1982, Davey *et al.* 1992, Marshall *et al.* 1995) and extend microclimate cover to a geographical vicinity that has previously received little attention (see MacNamara (1973) for a summary of conditions at Molodezhnaya Oasis, the nearest site for which comprehensive microclimate data exist).

On clear summer days in the Stillwell Hills, temperatures as high as 32.0°C are experienced at ground surface level while air temperatures remain below 5.0°C. Similar values have been reported from the Bunger Hills and Mirny areas of Queen Mary Land and from Bailey Peninsula in Wilkes Land (Grigoriev 1959, Rubin 1965, Smith 1988, Bölter 1992), implying that Antarctic invertebrates dwelling at ground surface level experience markedly warmer summer temperatures than meteorological data suggest. This is significant since the locomotor activities of Antarctic Acari are temperature-dependent and suppressed below freezing (Marshall *et al.* 1995). The elevated thermal regime experienced at ground surface level thus extends the period of time during which feeding, reproduction and other activities may occur.

The effect of depth beneath the soil surface is considered to have special significance for microarthropods. These may avoid extremes of temperature and desiccation by positioning themselves on the sides or undersurfaces of rocks or within soil interstitial matrices (Worland & Block 1986). In the Stillwell Hills a maximum temperature of 26.2°C was experienced at soil surface level between 6–7 January 1997 while a maximum temperature of only 10.2°C occurred at 100 mm depth. The minimum temperatures for the same positions were -5.6°C and 1.5°C respectively. The rate at which this thermal buffering occurs depends on a variety of factors, the most important being the soil particle size and moisture content. Consequently, appropriate choice of substratum and correct positioning within the soil profile may be critical for invertebrate survival.

Little information has previously been published on the rate of temperature change experienced at different levels within the soil profile, despite this being a significant determinant of organism survival. Rapid temperature changes may inflict tissue damage more readily than slow temperature changes,

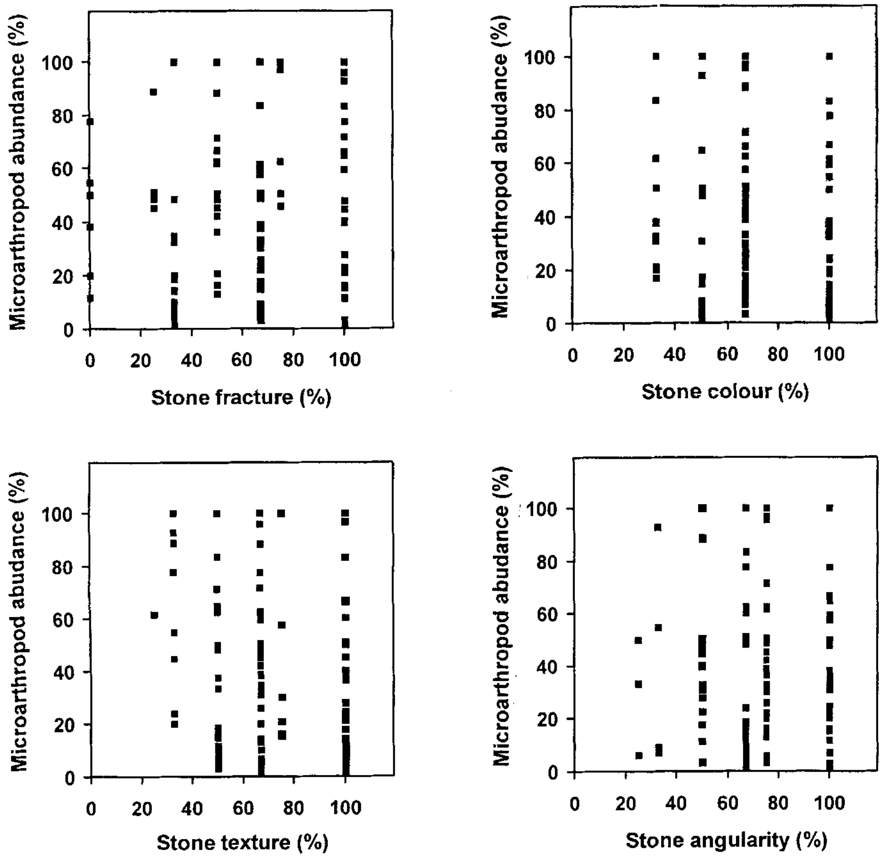

Fig. 4. Relationship between microarthropod abundance and four facets of stone morphology: fracture, colour, texture and angularity. Faunal values expressed as the percentage of total microarthropods occurring at each site. Stone values expressed as percentage of maximum facet value occurring at each site. The absence of a linear relationship demonstrates that Acari do not occur more frequently on stones of any particular type.

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particularly if they occur across a phase-change boundary such as 0°C (Burke *et al.* 1976, Sakai & Larcher 1987, Steponkus 1990). In the Stillwell Hills rates of temperature change are much faster at ground surface level than either above or below the ground surface. Between 05h00 and 12h00 on 7 January 1997 a rate of temperature increase of 3.6°C hr^{-1} was recorded at soil surface level while at 10 cm depth the rate of change was only 0.5°C hr^{-1}. At in intermediate depth of 5 cm the rate of change over the same period was 1.1 °C hr^{-1}. These figures compare with maximum rates of 7.5°C hr^{-1} and 1.5°C hr^{-1} recorded by Pryor (1962) at ground surface level and 3 cm depth near Hallett Station. Invertebrates living at ground surface level are thus more vulnerable to rapid temperature fluctuations than organisms inhabiting the soil profile. Migrating downwards into the soil provides one method by which they may avoid such stressful conditions.

Snow plays an important role in mediating the climate experienced at ground surface level (Billings & Bliss 1959, Weller & Holmgren 1974, Longton 1988, Davey *et al.* 1992, Coulson *et al.* 1995). Snow cover protects underlying organisms from temperature extremes and also buffers against rates of change. At the same time it maintains a relatively constant humidity in the sub-nival zone and provides a source of meltwater when it melts. During the current study minimum and maximum temperatures of -2.9°C and 0.9°C were experienced beneath 10 cm snowcover during a two day period in December when equivalent ground surface temperatures were -3.5°C and 22.2°C.

The presence of vegetation at a site can significantly alter the thermal regime experienced at the underlying soil surface (Oke 1978). Mosses, lichens and algal mats act to shield the ground from incident solar radiation and to insulate it from air movements, so acting as a barrier to heat and moisture exchange. This reduces the maximum temperature experienced during the day and increases the minimum temperature experienced at night. The degree of protection depends upon the growth form, colour and texture of the plants, with thick, convoluted or pubescent species of high moisture content achieving significantly greater thermal buffering than thin, sparse plants with only minimal water content. Shallow cryptogamic mats with low surface albedo may actually warm the underlying soil during day time (Gold 1998). In the Stillwell Hills, where little free water is available and the growth form of mosses is limited to cushions 2–3 cm thick, only a limited buffering effect of vegetation was recorded. The most significant difference occurred at night when a minimum temperature of -3.5°C was recorded within a moss cushion relative to a minimum of -5.7°C at the adjacent ground surface.

Microarthropod abundance

The microarthropod population densities recorded in the Stillwell Hills are comparable with those reported from other sites around the Antarctic continent. The maximum population density was 6802 ind. m^{-2} with a mean of 954 ind. m^{-2} from the 20 microhabitats studied. This compares with published microarthropod densities of between 100 to 6000 ind. m^{-2} elsewhere (e.g. Wise & Spain 1967, Ryan *et al.* 1989, Sugawara *et al.* 1995). The exception to these figures is work by Rounsevell (1981) who described a population of *Nanorchestes antarcticus* with a density of 160 000 mites m^{-2} from the Vestfold Hills, the highest abundance ever recorded for this species.

Few published data exist describing microarthropod abundance in the sublithic habitat. Richard *et al.* (1994) carried out a survey of Acari and Collembola beneath stones in the South Shetland Islands, off the tip of the Antarctic Peninsula, and found that arthropods were present at 24 of the 25 stone sites sampled. Of the 270 stones examined, 76% were occupied by at least one species of arthropod and the maximum count per stone was 1057 individuals. These figures are significantly greater than those recorded in the Stillwell Hills where arthropods were absent from five of the 20 stones sites sampled and only 30.7% of the 400 stones examined supported any arthropods at all. The maximum count beneath any single stone was 71 individuals. The differences probably reflect the relative severity of the continental Antarctic environment and possibly also the aggregatory habits of many maritime Antarctic microarthropod species (Usher & Booth 1984).

Microarthropod habitat preferences

The favoured microhabitat of Acari was found to be the undersurface of small stones. The microenvironment at this level is influenced by two main characteristics. First, the type of stone on which the microarthropods are located (shape, size, colour, texture, angularity etc) and second the type of soil on which that stone is lying (particle size, nutrient status, moisture content etc). A related factor is the separation between these two zones.

In the Stillwell Hills the type of soil on which stones were located was seen to play the primary role in determining invertebrate abundance. Microarthropods were only found on stones that lay upon a layer of damp sand or mineral fines. They were never found on stones in contact with dry shale or glacial scree, particularly where individual rock fragments were separated by large air spaces. This finding supports earlier research that has shown microarthropods to favour the undersurfaces of stones in contact with damp moss or soil substrata (Strong 1967, Rounsevell 1977, Convey & Smith 1997). The explanation is likely to relate to the need for retention of moisture and to the thermal buffering provided by soil with a high water content.

The physical characteristics of the stone surface itself appeared not to influence the population abundance of microarthropods. It had been expected that a positive, linear relationship would be obtained as microarthropods favoured the coarsest and most fractured stones available at any site (indicative of degree of protection, shelter and habitat heterogeneity) as well as the darkest material with the lowest albedo which would be the warmest stones present at each site. However, on the basis of the current observations such stone-selection does not appear to take place. Surface texture, fracture, angularity and colour showed little correlation with invertebrate density. This finding suggests that stone properties, as measured here, play little role in ameliorating extremes of temperature, moisture, irradiance and freeze-thaw cycles.

Ornithogenic input did not play a strong role in controlling the distribution of microarthropods. Sites with a significant component of feathers and guano sometimes supported Acari and sometimes lacked them. This observation contrasts with sites on the Antarctic Peninsula where collembolan densities as high as 1.5 x 10 6 ind. m^{-2} have been recorded from Adélie penguin moulting sites (Convey & Smith 1997). In the Stillwell Hills the bulk of ornithogenic material is associated with skua roosts which tend to be located on patches of elevated ground that are usually dry. Thus, although nutrient conditions may be favourable for microarthropods, water conditions are likely to be limiting. An alternative explanation for the low abundance is the different microarthropod species encountered in the maritime Antarctic and in the Stillwell Hills.

Microarthropod distribution in relation to vegetation

A surprising observation was the low number of microarthropods that occurred at sites with moss beds, algal cushions and foliose lichen thalli. These microhabitats were ranked 5th, 8th and 11th in terms of Acari abundance respectively. Conversely, substantially higher microarthropod densities were encountered at sites with a high sublithic microalgal content.

It had been anticipated that habitats characterized by plant growth would support the highest microarthropod abundances. This assumption was based on data from the maritime Antarctic (Usher & Booth 1984, Usher & Edwards 1984, Richard *et al.* 1994) where maximum invertebrate abundance is found at vegetated sites. However, the current data suggest that this relationship does not apply to the Antarctic continent: densities of only 798, 482 and 121 ind. m^{-2} were recorded in each of the moss, algae and lichen habitats examined in the Stillwell Hills.

The likely explanation for this difference is that the maritime Antarctic is dominated by Collembola while continental Antarctica tends to support large numbers of Acari, as found in the Stillwell Hills. The favoured habitat of Collembola may be different to that of Acari. It has been reported (Tilbrook 1967, Heatwole *et al.* 1989) that members of the Nanorchestidae prefer a barren, rocky habitat while *Cryptopygus antarcticus* favours damp, vegetated situations, a consequence of its hydrophobic cuticle (Strong 1967). The predatory mesostigmatid *Gamasellus racoviztai* was reported by Richard *et al.* (1994) as being the only mite species regularly found in vegetated habitats. If these habitat preferences are mirrored by other species of Collembola and Acari it could explain the low number of microarthropods recorded at vegetated sites in the Stillwell Hills.

Conclusions

The microarthropod distributions recorded during this study support the hypothesis that, in Antarctica, water is the primary factor limiting the distribution of terrestrial life. The occurrence of *Protereunetes maudae*, *Nanorchestes triclivatus* and *N. lalae* around the Stillwell Hills correlated closely with gradients in moisture availability. Meltwater zones around glaciers and snowbanks, as well as areas of seepage and upwelling, supported the highest Acari abundances. Conversely, no invertebrates were recorded at xeric sites even when these provided favourable thermal conditions. This moisture-dependent distribution supports the results of earlier research into the role of limiting factors (Llano 1956, Strong 1967, Light & Heywood 1975, Kennedy 1993).

The temperature profiles recorded from the Stillwell Hills suggest that, during summer, microarthropods rarely encounter low temperatures outside their ecophysiological tolerances (Block 1982, Block & Sømme 1982, Cannon & Block 1988). Instead, incident solar radiation causes soil warming and an elevated thermal regime at ground surface level. This heat passes downwards through the soil profile as a thermal wave and is retained sufficiently long after nightfall to keep the ground warm until the sun reappears the next day. During winter the insulating role of snow cover probably prevents extremes of low temperature from exceeding thresholds of survival, even during the coldest months. Consequently, low temperatures may not play aa important a role in limiting the fine-scale distribution of terrestrial biota as has hitherto been supposed.

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