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Determinants of terrestrial arthropod community composition at Cape Hallett, Antarctica

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Abstract: The distribution and abundance of free-living arthropods from soil and under stones were surveyed at the Cape Hallett ice-free area (ASPA No. 106), North Victoria Land, Antarctica. A total of 327 samples from 67 plots yielded 11 species of arthropods comprised of three Collembola: *Cryptopygus cisantarcticus*, *Friesea grisea* and *Isotoma klovstadi* and eight mites: *Coccorhagidia gressitti, Eupodes wisei*, *Maudheimia petronia, Nanorchestes* sp., *Stereotydeus belli*, *S. punctatus*, *Tydeus setsukoae* and *T. wadei*. Arthropods were absent from areas occupied by the large Adélie penguin colony. There was some distinction among arthropod communities of different habitats, with water and a lichen species (indicative of scree slope habitats) ranking as significant community predictors alongside spatial variables in a Canonical Correspondence Analysis. Recent changes to the management plan for ASPA No. 106 may need to be revisited as the recommended campsite is close to the area of greatest arthropod diversity.

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Key words: Acari, Antarctic Specially Protected Area, Collembola, mites, spatial distribution, springtails

Introduction

The terrestrial arthropod fauna of the continental Antarctic region (*sensu* Smith 1984) is restricted to springtails (Hexapoda: Collembola) and mites (Arachnida: Acari) that are patchily distributed in coastal and inland ice-free habitats (Gressitt 1967a). Collembola and mites undoubtedly contribute significantly to soil ecosystem processes, although in continental habitats the function of even individual species remains to be quantified, and in many cases, described (but see Burn (1984) and Usher & Booth (1984) for examples of quantitative biology from maritime Antarctic Signy Island).

The continent-wide distribution of species was established in the 1960s (Gressitt 1967b), but the distribution of arthropods within ice-free areas has received less attention (Chown & Convey in press). Given that contemporary dispersal rates of microarthropods between ice-free areas are low (Kennedy 1999, Frati *et al.* 2001, Stevens & Hogg 2002), local population parameters are probably driven by local biotic and abiotic factors such as temperature, moisture and food availability. Anthropogenic effects on the abiotic environment are thus likely to influence the distribution of such arthropods, through changes in temperature (Kennedy 1995b, Convey *et al.* 2002, Doran *et al.* 2002, Sinclair 2002) or changes in habitat availability as a result of changes in precipitation, snow accumulation, water availability and glacial advance or recession (Ellis-Evans & Walton 1990). However, these processes operate on population parameters, species interactions, colonization and dispersal at a scale of hundreds to thousands of metres, and cannot be sensitively monitored at geographical distribution scales, nor simulated in small microcosms (Kennedy 1995a, 1995b, Convey *et al.* 2002). To comprehend and monitor the responses of the terrestrial Antarctic fauna to environmental change, it is therefore desirable to understand the factors that influence their distribution across a landscape as a baseline for future comparisons. Such knowledge is also important if informed decisions concerning the management and designation of protected areas are to be made (Pullin *et al.* 2004). This paper thus characterizes the identity and distribution of terrestrial arthropods at Cape Hallett, with respect to biotic and abiotic variables, and serves as a baseline for future monitoring.

Methods

Study site

Cape Hallett is a 72 ha coastal ice-free area in North Victoria Land (Fig. 1) that has a relatively diverse flora and fauna (Rudolph 1963, Wise & Shoup 1967, Logan & Bassett 1985). It was the site of Hallett Station from

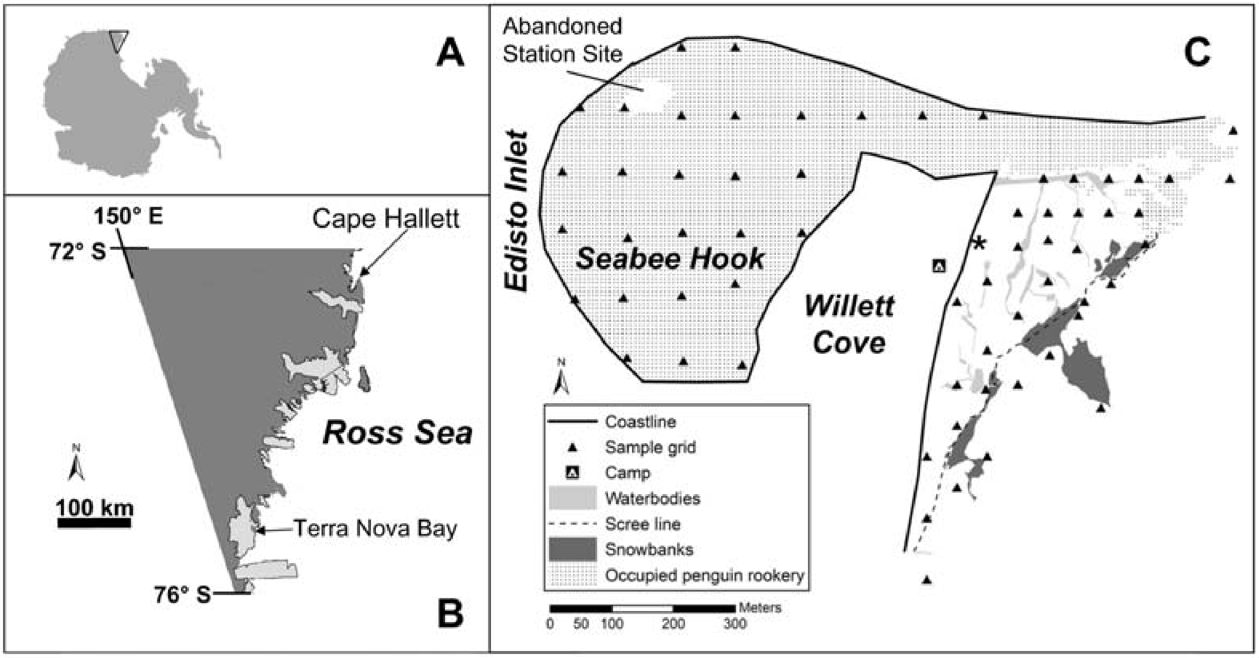

Fig. 1. a. Locator map for Cape Hallett on the Antarctic Continent, and **b.** within North Victoria Land, **c.** shows the layout of the lower ice-free area, including the sampling points for our survey. Of the three habitat types mentioned in the text, filled mid-grey areas are penguin rookery; the scree line indicates the base of the scree slope; the areas to the west (left) are 'algal flats' and the terrain to the south-east (right) of this line is significantly steeper and is the 'scree slope' habitat. The scree line continues through the penguin rookery, but data were not gathered to avoid disturbance to the birds. The asterisk indicates the approximate campsite position recommended by the revized management plan for ASPA No. 106.

1957–1973, and has since been subject to increasing protection, such that the entire ice-free area is now designated Antarctic Specially Protected Area (ASPA) No. 106. Wise & Shoup (1967) and Gressitt & Shoup (1967) recorded three species of Collembola, and seven mite species from Cape Hallett, none of which are endemic to the area, but part of the wider North Victoria Land fauna (Gressitt 1967b, Frati *et al.* 1997).

Research on the terrestrial fauna at Cape Hallett has included physiological work on Collembola (Strong *et al.* 1970, Sinclair *et al.* 2006), examination of microclimate (Pryor 1962), life history studies on mites (Gressitt & Shoup 1967), and faunistic studies of Collembola and mites (Gressitt 1967a, Gressitt & Shoup 1967, Strandtmann 1967, Wise 1967, Wise & Shoup 1967). Pryor (1962) found no Collembola within the occupied penguin colony, but found that *Isotoma klovstadi* (Isotomidae) was widely distributed at Cape Hallett, particularly under stones and associated with moss. Gressitt & Shoup (1967) described the mites of North Victoria Land, including Cape Hallett and Possession Island. They found populations of mites in association with a penguin colony at Possession Island, but did not mention mites in such habitats at Cape Hallett.

The largest area of ice-free land on the 36 km long glaciated Hallett Peninsula is near the tip of the peninsula near Cape Hallett proper at Seabee Hook, which is a large, relatively recent beach deposit. The scree slopes near Seabee Hook are composed of medium sized blocks of mechanically weathered basalt (T.A. Rafter, personal communication 2004). Seabee Hook, and the adjacent moraines and scree slopes are collectively referred to as 'Cape Hallett' in this paper. Field work was conducted at Cape Hallett (72.318°S, 170.211°E) during the summer of 2002/2003 (9 November–27 January).

The habitats at Cape Hallett are poorly described (Pryor 1962, Rudolph 1963) but are of three main types:

1) Adélie (*Pygoscelis adeliae* (Hombron & Jacquinot)) penguin colony. This occupies about half the ice-free area (Fig. 1). The area is low-lying, and characterized by a compressed guano pavement, and a few highly eutrophic ponds. Apart from filamentous green algae (*Ulothrix* sp.) in the ponds, no macroscopic flora are visible.

2) Algal flats. These occur at the base of the scree slope and comprize an undulating moraine-covered area of flats and long-abandoned penguin mounds. South polar skuas (*Catharacta maccormicki* Saunders) breed in the area, and habitats include the tops of mounds (dry with loose gravel) and periodically inundated moss and algal flats, with sorted stones sitting in a single layer on a fine lithosol base (referred to as 'soil' throughout). The largest areas of vegetation are at the base of snowbanks at the bottom of the scree slope.

These snowbanks also provide the main source of water for streams, surface flooding and small ponds. In the wettest nutrient-rich microhabitats, the blue-green alga, *Nostoc commune* Vauchere, and the sheet-like green alga, *Prasiola crispa* (Lightf.) Menegh. form mats in seasonally inundated gravel beds and seeps south of the penguin colony. *Prasiola crispa* also occurs patchily in depressions, seasonal seeps and frost cracks, occasionally with the filamentous green alga, *Ulothrix* sp. The moss *Bryum argenteum* Hedwig forms a dense carpet along many seep margins. At the base of the scree slope, a matrix of *Bryum* spp., *P. crispa* and lichens such as *Xanthoria mawsonii* Dodge and *Buellia frigida* Darbish form patches below melting snowbanks. Permafrost underlies the area (*c.* 30 cm below the surface in mid-summer), and periglacial features include frost wedges and small sorted circles. This habitat is littered with debris from skua feeding (including penguin corpses, bones and eggshells), and also with rubbish from the abandoned station.

3) Scree slope. East of (and adjacent to) the algal flats, there is a steep, *c.* 200 m vertical scree slope, characterized by large blocks, good drainage (and therefore low water availability), and in many areas no soil within 50 cm of the surface. The stability of the slope is heterogeneous, but in more stable sections there is a crustose lichen flora including *X. mawsonii*, *B. frigida, Parmelia* sp., *Rinodina* sp., *Polycauliona* sp., *Umbilicaria* sp., *Lecidea* sp., *Lecanora* sp., and *Caloplaca* sp. (see also Rudolph 1963).

Cape Hallett has a continental Antarctic climate. Seabee Hook is surrounded by sea ice for > 8 months of the year. Prevailing winds are from the south, and may be very strong (> 50 $m\ s^{-1}$) (Gordon 2003). During the summer, daytime soil surface temperatures may be above freezing for periods of weeks (a maximum of 36.6°C reported by Sinclair *et al.* (2006)), allowing snow to melt quickly, although there is a strong diurnal cycle of temperature caused by shading from the Hallett Peninsula (Sinclair *et al.* 2003). Winter temperature data from 1959 indicate a typical continental Antarctic climate with a reported winter minimum of -47.8°C (Pryor 1962).

Although the most severe impacts of the station were in the penguin colony, a road was built at the edge of the algal flats, and several buildings were erected in the algal flats area (Gordon 2003). The bulk of the station was demolished in 1983–86 (Gordon 2003), and the remaining buildings removed since this fieldwork was conducted (S. Gordon & R. Roper-Gee, personal communication 2004). Specially Protected Area No. 7 was established in 1966 to protect the terrestrial flora and fauna, and this was expanded to include a greater area in 1985 (Logan & Bassett 1985) and again in 2002 (http://www.cep.aq/apa/aspa/sites/aspa106/index.html), such that the entire penguin colony and algal flats areas and a significant proportion of the scree slope habitats are now protected as ASPA 106.

Table I. Characters measured at each plot during the arthropod survey at Cape Hallett, Antarctica. Frequency of surface cover (number of 2.5 × 2.5 cm cells ($n = 100$) in which the character was present) was recorded for all characters except conductivity and water content.

Character	
Stones	All stone cover
Stones < 2 cm greatest diameter	
Stones 2–5 cm	
Stones 5–10 cm	
Stones 10–20 cm	
Stones >20 cm	
Sandy soil	All lithosol or mineral soil not covered by stones
Guano/ ornithogenic soil	All ornithogenic soil not covered by stones
Algae (*Prasiola*)	
Filamentous algae (*Ulothrix*)	
Cyanobacteria (*Nostoc*)	
Moss	All species combined
Rotting moss	Dead or decomposing moss; moss covered with cyanobacteria
Caloplaca sp.	
Umbilicaria spp	
Buellia frigida	
Buellia sp.	White and grey *Buellia* sp.
Litter	Includes eggshell debris and rubbish from old station
Penguin remains	
Conductivity (of 15:1 water:soil slurry)	$\mu S\ cm^{-1}$; 15:1 v/w water:soil slurry measured; available only for plots where soil samples were taken
Soil water content (g/g dw)	g water /g oven-dried soil; available only for plots where soil samples were taken

Site mapping

All distributions and maps are derived from a combination of aerial photographs taken in 1983 (available at http://www.anta.canterbury.ac.nz/gis/), a map of the penguin colony (Reid 1964), and uncorrected GPS measurements taken on the ground with a handheld GPS unit (Garmin E-Trex, Garmin International Inc., Kansas City, KS, USA), accurate to 6 m. All site position data and species locations were digitized and mapped using ArcView 3.3 (ESRI, Redlands, CA, USA), with a Lambert conformal conic projection with spheroid WGS84, a central meridian at 170.22ºE and standard parallels of 72.31ºS and 72.33ºS.

Sampling design and methods

Survey sampling was conducted between 13 December 2002 and 17 January 2003 at sites indicated in Fig. 1. The ice-free area was blocked into a 50 m grid, and alternating grid squares were selected in a checkerboard pattern, such that in the penguin colony any 100 × 100 m area contained at least one site. In the more heterogeneous algal flats, we selected more sites, such that any 100 × 100 m area contained between 2 and 4 sites. Because of the instability of the scree slope habitat, only two sites were located in this habitat, although we also conducted some *ad hoc* sampling in this habitat. The sampling point for each site was the centre of the 50 × 50 m area, and was selected using pre-determined GPS coordinates. If a sampling point fell onto snow, the nearest snow-free ground was used for sampling. If a sampling point fell onto an incubating penguin or skua, a nearby patch of ground was selected. Several samples were taken from occupied penguin mounds, and at least one recently abandoned penguin nest was sampled. A total of 63 sites were fully sampled, and soil samples only taken from a further four sites.

At each site, five plots were randomly selected by direction and distance within a 2 m radius of the central point. Using a 25 × 25 cm quadrat divided into 100 equal-sized cells, frequency of occurrence (number of cells in which a character occurred) and percent cover of physical and biological characters (Table I) were recorded. At each plot, the stone > 2 cm minimum diameter closest to the central point was selected, arthropods and debris washed off the surface with warm water into a plastic container, which was then sealed and returned to the laboratory tent, and the stone's dimensions recorded. At the first, third and fifth plots for each site, a small (*c*. 50 g) soil sample was collected into a plastic ziplock bag with a clean teaspoon. The soil sample did not include any stones > 2 cm minimum diameter, and if a plot was covered with stones, the soil sample was taken from beneath a different stone to that washed for arthropod sampling. If no stones occurred in the plot, the nearest stone was washed. If no soil occurred in a plot, even underneath surface stones (this was the case for plots on the scree slope), then no sample was taken for the site. In total, 195 soil and 315 stone samples were included in this study.

Samples were kept at tent temperature (usually between -5 and +10°C) until sorted within five days of collection. Soil samples were weighed, poured into a container of water and scanned (Sinclair 2001), and all arthropods were removed and preserved as above. Stone washings and soil samples were scanned under a dissecting microscope, and all arthropods removed, counted and preserved in ethanol. Nematodes were then extracted from the soil sample using a Baermann funnel (Sinclair & Sjursen 2001) (results to be reported elsewhere), and thereafter the soil was dried and weighed to give a dry weight. Soil subsamples were mixed with water in a 15:1 ratio by mass, and specific conductivity of the solution was measured (YSI model 33 conductivity meter, Yellow Springs, Ohio, USA).

Ad hoc sampling was also conducted around Cape Hallett, in conjunction with physiological studies (Sinclair *et al.* 2003, 2006) and used in analyses as appropriate. In most cases, the presence or absence and identity of Collembola were noted, accompanied by a GPS position. On one occasion, an ice-free ridge at the top of the scree slope (*c*. 300 m a.s.l.) was visited, and soil, but no stone, samples were collected.

Identification of arthropods

Voucher specimens of mites and Collembola are deposited at Iziko Museums of Cape Town, South Africa. Collembola were identified after Wise (1967), and in comparison with mounted specimens at the Auckland Museum. In practice, the three species present were sufficiently different to allow ready discrimination using a hand lens, or by eye.

Mites were mounted in Hoyer's medium and identified using Strandtmann (1967) and Wallwork (1962), as well as type material loaned from the Bishop Museum (Hawaii). The *Stereotydeus* specimens of both species collected differed from the generic description by the presence of one pair of lateroventral hysterosomal pore slits, in addition to the given three other dorsal pairs. The pores are homologous with cupules and lyrifissures, in the Astigmata and Oribatida, respectively, and their usual occurrence in four or more pairs suggests that the ventral pair was overlooked in the description. Furthermore, the collected specimens of *S. punctatus* differed from Strandtmann's (1967) description in having a ventral, rather than a dorsal anal opening. At least one of the type specimens examined also had a ventral anal opening, suggesting that this may be a variable character of this species. All the other large prostigmatid mite species considered here were consistent with Strandtman's descriptions.

Data analysis

Stone axis measurements were converted into area using the formula of Sinclair *et al*. (2001). Abundance of arthropods is expressed as density (per g dry weight of soil for soil samples, per cm^2 of sampled surface for stone samples). GPS positions were normalized around zero (at the centre of the site) and a third-order polynomial of the form $E+S+ES+E^2+S^2+E^2S+ES^2+E^3+S^3$ (where E is positions east and S is positions south) was included in the dataset to account for the most commonly encountered spatial patterns in distribution (Legendre & Legendre 1998). Pearson's correlation coefficients were calculated between spatial and environmental variables and subjected to a table-wide step-up false discovery rate correction for significance at $\alpha = 0.05$ (García 2004). The relationships between invertebrate density and environmental (including spatial) characters were examined using Canonical Correspondence Analysis (CCA) with biplot scaling (ter Braak & Smilauer 1998). Species that were present in fewer than three sites were omitted, and densities were $\log_{10}(x+1)$ transformed before analysis. Because spatial variables were incorporated in the

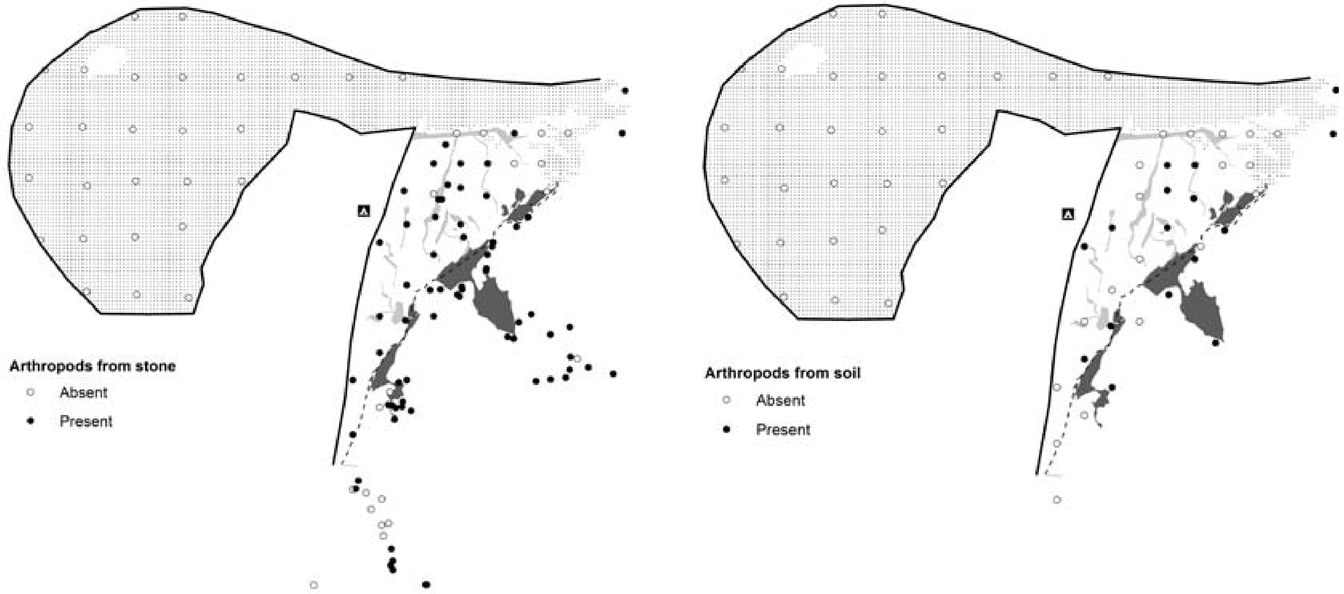

Fig. 2. Presence/absence of arthropods from stones (left) and in soil (right) at Cape Hallett. Stone samples include *ad hoc* sampling and systematic survey; soil samples are just from the systematic survey.

model, nested or split-plot designs were not used to distinguish between plots within sites. CANOCO's forward-selection procedure on all variables was used to initially determine significant explanatory variables. The model was then re-run with only significant explanatory variables. Any candidate explanatory variables that were non-significant in this model were also discarded, before a final model was run, and the scores on the first two

Table II. Density (individuals cm^{-2} for stone samples, individuals per gram dry soil for soil samples), abundance and occupancy of arthropods collected from stone surfaces and soil samples at Cape Hallett. Means for each species were calculated only from occupied samples. Sites refer to the 67 sampling sites across the area, while plots refers to the 5 (stone) or 3 (soil) samples taken at each site.

	Max. density in soil	Mean ± s.e.(m) density in soil	Total no. of individuals from soil samples	Max. density on stones	Mean ± s.e.(m) density on stones	Total no. of individuals from stone samples	Occupancy (out of 327 plots)	Occupancy (out of 67 sites)
Acari								
Cryptostigmata								
SCHELORIBATIDAE								
Maudheimia petronia Wallwork	-	-	0	0.951	0.533 ± 0.136	110	5	1
Prostigmata								
RHAGIDIDAE								
Coccorhagidia gressitti Womersley & Strandtmann	0.500	0.319 ± 0.101	4	-	-	0	3	3
EUPODIDAE								
Eupodes wisei Womersley & Strandtmann	0.615	-	2	0.956	0.335 ± 0.083	35	10	7
PACHYGNATHIDAE								
Nanorchestes sp.	0.649	0.331 ± 0.082	40	0.873	0.577 ± 0.161	22	7	2
PENTHALODIDAE								
Stereotydeus belli Trouessart	0.915	0.547 ± 0.060	34	0.969	0.345 ± 0.052	254	34	15
Stereotydeus punctatus Strandtmann	0.744	0.410 ± 0.085	23	0.242	-	2	8	4
TYDEIDAE								
Tydeus setsukoae Strandtmann	0.744	0.337 ± 0.200	5	0.867	0.408 ± 0.051	75	23	13
Tydeus wadei Strandtmann	-	-	0	0.672	-	2	2	1
Collembola								
ISOTOMIDAE								
Cryptopygus cisantarcticus Wise	29.784	3.078 ± 0.957	990	6.546	0.891 ± 0.220	1726	61	21
Isotoma klovstadi Carpenter	2.162	0.524 ± 0.119	166	2.789	0.528 ± 0.104	670	46	15
NEANURIDAE								
Friesea grisea (Schäffer)	0.936	0.599 ± 0.071	59	1.949	0.565 ± 0.164	104	25	14

canonical axes plotted for each arthropod species, with vectors representing the correlation of the axes to environmental or spatial variables. Soil and stone samples from the survey were run separately, and had slightly different sets of species.

Results

Eight species of free-living mite and three species of springtail were identified from soil and beneath stones at Cape Hallett (Table II). In addition, a single astigmatid feather mite (excluded from analyses, but deposited with voucher specimens) was collected at an algal flats site. A full list of positions and densities of arthropods collected during the survey is available from the corresponding author upon request, and has been lodged with Antarctica New Zealand and in hard copy form at Iziko Museums of Cape Town. The distribution of these species was extremely patchy: only 112 of 327 plots were occupied by any arthropods, and the most frequently encountered species, *C. cisantarcticus,* was present at only 21 of 67 sites. No arthropods were found in samples collected from areas occupied by the penguin colony (Fig. 2).

In addition to the grid sampling and recorded observations on Seabee Hook and the associated areas, soil samples were collected from a ridge at the summit of the scree slope (*c.* 300 m a.s.l.), where the lichen flora is dominated by *Usnea antarctica* Du Rietz and *Umbilicaria* sp. At this site, all three Collembola species were present, as well as *Coccorhagidia gressitti, Nanorchestes* sp. and *Stereotydeus punctatus.*

Of the Collembola, *Cryptopygus cisantarcticus* was found in both scree margin and algal flats, although it was most abundant, and showed the highest occupancy in the wet algal flats (dominated by *Prasiola crispa*) close to the penguin rookery. *Friesea grisea* was not abundant at any sites, but was present in both algal flat and scree slope habitats. *Isotoma klovstadi* was dominant on the margins of the scree slope, and was present at many locations on the scree slope itself. Collembola were generally found in both soil and stone samples, with the exception of dry, blocky scree slopes, where soil was not present. *Isotoma klovstadi* and *C. cisantarcticus* satisfied the assumptions of χ^2 for a comparison of soil and stone presence-absence, but presence in soil and stone samples were not significantly associated in either case (*I. klovstadi* $\chi^2 = 5.538$, df = 2, $P = 0.063$; *C. cisantarcticus* $\chi^2 = 2.968$, df = 2, $P = 0.227$).

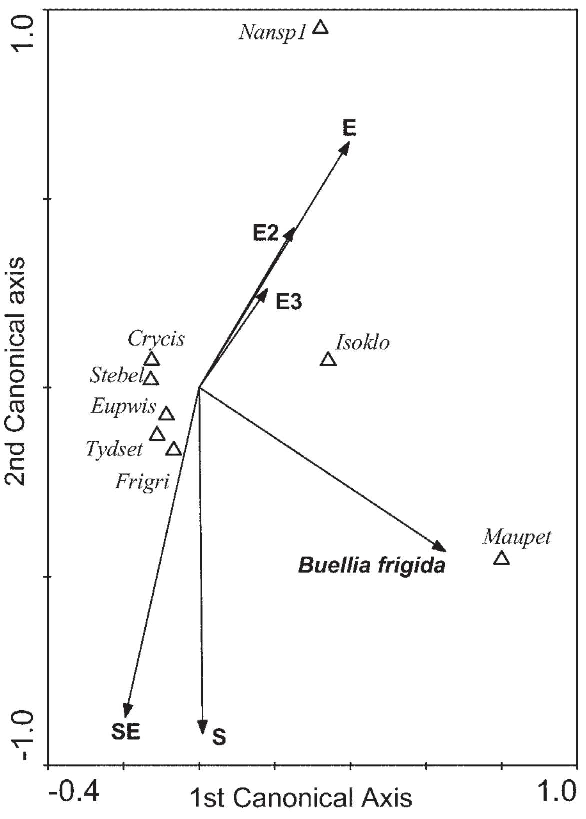

Fig. 3. Species-environment biplot generated by Canonical Correspondence analysis (CCA) of stone arthropod densities and plot-level characteristics. Arrows indicate the direction and magnitude of significant explanatory environmental variables; E, E^2, E^3, SE and S refer to transformations of the south and east spatial position at the site (normalised about the site centre; see text for further details of spatial analysis). Species are: *Crycis* = *Cryptopygus cisantarcticus*, *Eupwis* = *Eupodes wisei*, *Frigri* = *Friesea grisea*, *Isoklo* = *Isotoma klovstadi*, *Maupet* = *Maudheimia petronia*, *Nansp1* = *Nanorchestes* sp., *Stebel* = *Stereotydeus punctatus*, *Tydset* = *Tydeus setsukoae*. First axis eigenvalue 0.529, F = 13.803, $P = 0.0001$, all axes trace 1.18 F = 6.783 $P = 0.0001$. The first axis explains 16.5% of species variation and 44.8% of the species-environment relationship, while the first two axes combined explain 26.1% of species variation and 71% of the species-environment relationship. The first canonical axis is significantly correlated with E ($P < 0.001$), E^2 ($P < 0.05$) and lichsp1 ($P < 0.001$). The second canonical axis is significantly correlated with all environmental variables shown. Thus, the first axis represents variation in an easterly direction across the site, and also an increase in the abundance of the lichen *Buellia frigida*, while the second axis represents the general spatial characteristics of the site. See Table III for correlations between spatial variables and environmental characteristics.

Stereotydeus belli was the most abundant mite, and was present largely on the algal flats (Table II). By contrast, *S. punctatus* was present at only four sites (including the ridge site). *Tydeus setsukoae* was also widely distributed, ranging from algal flats to dry scree slopes, although its congener, *T. wadei* was found at only a single site high on the scree slope, and once in a transect on the algal flats (Sinclair *et al.* unpublished data). *Eupodes wisei* was present largely in dry parts of the algal flats. The sole oribatid mite at Cape Hallett, *Maudheimia petronia*, was present at a single location on a dry scree slope at the top of a snow bank (*c.* 100 m a.s.l.). *Nanorchestes, Tydeus* and *Stereotydeus* spp. were found largely in soil, while *E. wisei*

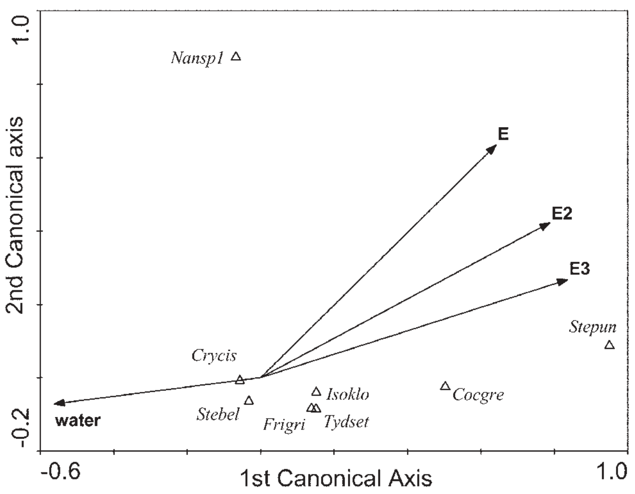

Fig. 4. Species-environment biplot generated by Canonical Correspondence analysis (CCA) of soil arthropods and plot-level characteristics. Arrows indicate the direction and magnitude of significant explanatory environmental variables; E, E^2 and E^3, refer to transformations of the easterly spatial axis of the site (normalised about the site centre, see text for details). Water refers to soil water content. Species are *Crycis = Cryptopygus cisantarcticus, Cocgre = Coccorhagidia gressitti, Frigri = Friesea grisea, Isoklo = Isotoma klovstadi, Maupet = Maudheimia petronia, Nansp1 = Nanorchestes* sp., *Stebel = Stereotydeus belli, Stepun = Stereotydeus punctatus, Tydset = Tydeus setsukoae*. First axis eigenvalue 0.51, F = 8.333, P = 0.0029, all axes trace 1.057 F = 5.275 P = 0.0001. The first axis explains 14.5% of species variation and 48.3% of the species-environment relationship, while the first two axes combined explain 22.3% of species variation and 74% of the species-environment relationship. The first canonical axis is significantly correlated with E ($P < 0.001$), E^2 ($P < 0.001$), E^3 ($P < 0.001$) and water ($P < 0.001$). The second canonical axis is significantly correlated with E ($P < 0.001$) and E^2 ($P < 0.01$). Thus, the first axis represents variation in an easterly direction across the site, and also variation in soil water, while the second axis represents spatial variability on the east-west axis of the site. See Table III for correlations between spatial variables and environmental characteristics.

and *M. petronia* were only found under stones (Table II). *Stereotydeus belli* satisfied the assumptions of χ^2 for a comparison of soil and stone presence-absence, but presence in soil and stone samples were not significantly associated ($\chi^2 = 5.857$, df = 2, $P = 0.053$).

Determinants of distribution

Canonical Correspondence Analysis (CCA) was used to examine habitat and spatial variables associated with the species distributions. Spatial characters were significant descriptors of arthropod distributions from both stones (Fig. 3) and soil samples (Fig. 4). Table III shows the correlations between the significant spatial variables in the CCA and the other environmental variables. In the CCA of stone samples (Fig. 3), there is a set of species (*C. cisantarcticus, F. grisea, S. belli, E. wisei* and *T. setsukoae*) which are found in similar habitats on the algal flats, reflecting the qualitative observations made above. These species are clustered on Axis 1, but spread along Axis 2. Axis 2, as well as reflecting the spatial arrangement of the algal flats, represents a gradient from drier, nutrient poor habitats with larger stones and a plant community dominated by lichens (*Caloplaca* spp., *B. frigida*) (negative values on Axis 2; *F. grisea, T. setsukoae and E. wisei*), to one that still has large stones, but with predominantly algal vegetation (positive values on Axis 2; *C. cisantarcticus* and *S. belli*). *Isotoma klovstadi* and *M. petronia* were found on the scree slope, and this is reflected in their positions along Axis 1; which represents larger stones and algae (in the easterly spatial variables) as well as the lichen *B. frigida*. The position of *Nanorchestes* sp. at the extreme end of Axis 2 probably reflects its location: at Cape Hallett, it was only found in the northernmost plots examined. Water and easterly spatial variables are the main predictors of distribution of arthropods from soil samples (Fig. 4). *Stereotydeus punctatus* shows a strong spatial separation from *S. belli.*

Discussion

The arthropod fauna of Cape Hallett

Eleven species of free-living arthropods were recorded at Cape Hallett. Of these, two (*Coccorhagidia gressitti* and *Eupodes wisei*) have their type localities at Cape Hallett (Strandtmann 1967). This is the first record of *Nanorchestes* sp. at Hallett, although it has been recorded elsewhere in North Victoria Land (Womersley & Strandtmann 1963, Gressitt & Shoup 1967, Strandtmann 1967). In terms of species richness, Cape Hallett is therefore at present the most diverse arthropod community known in the Ross Sea region (Gressitt 1967a), although extensive surveys have not been conducted at other potentially important locations, for example Cape Adare and Possession Island.

The major difference between our data and that of earlier workers is a possible reversal in the relative abundance of the two congeneric *Stereotydeus* species, which could indicate a recent change in community-level processes. Although Gressitt & Shoup's (1967) work is subjective, both they and Strandtmann (1967) are clear in stating that *S. punctatus* is more abundant than *S. belli*. This is unlikely to be a result of misidentification, but could reflect differences in sampling, or chance biases in the collections that were examined by Strandtmann.

No terrestrial arthropods were found in the Adélie penguin colony at Cape Hallett. This is in contrast to other Antarctic habitats, including the Antarctic Peninsula (Tilbrook 1967), Dronning Maud Land Nunataks (Ryan & Watkins 1989) and possibly the Possession Islands near

Table III. Correlation matrix of spatial variables and plot characteristics at Cape Hallett, Antarctica. Pearson's correlation coefficients are presented. Coefficients in bold type and marked with an asterisk remained significant ($P < 0.05$) after table-wide step-up False Discovery Rate correction. Correlations with soil water and conductivity were conducted as a separate analysis including only plots for which soil samples were available ($n = 186$), correlations with other environmental variables included stone and soil plots ($n = 315$). Spatial variables are derived from the site GPS positions south and east, standardized about the centre of the site and combined into a 3rd order polynomial of the form $S + E + SE + S^2 + E^2 + SE^2 + S^2E + S^3 + E^3$. Correlations with S^3 are not shown because none were significant ($P > 0.05$). Environmental variables not shown because they showed no significant correlations ($P > 0.05$) were stones < 2 cm and 2–5 cm; moss; *Buellia* sp.; filamentous algae (*Ulothrix* sp.); *Nostoc*, rotting moss and penguin remains.

Environmental variables	Spatial variables							
	S	E	SE	E^2	S^2	SE^2	S^2E	E^3
Soil water	**-0.168***	0.065	-0.055	-0.057	**-0.237***	0.052	0.058	-0.056
All stones	**0.167***	0.127	-0.006	0.037	**0.171***	-0.074	0.058	0.066
Stones 5–10 cm	**0.356***	**0.270***	-0.055	-0.115	0.132	-0.019	0.107	0.066
Stones 10–20 cm	**0.273***	**0.144***	0.007	-0.005	0.097	0.001	0.088	0.031
Stones > 20 cm	0.107	**0.168***	**-0.170***	**0.185***	**0.178***	**-0.191***	**0.181***	**0.184***
Sandy soil	**-0.359***	**-0.399***	-0.025	-0.018	-0.140	0.040	-0.074	-0.106
Guano/ornithogenic soil	**-0.299***	**-0.305***	0.073	-0.079	**-0.233***	0.113	-0.128	-0.1011
Algae (*Prasiola*)	0.013	**0.205***	-0.018	-0.077	**-0.156***	0.071	-0.006	-0.042
Caloplaca sp.	**0.303***	0.077	0.080	-0.058	**0.172***	0.056	0.035	-0.027
Litter	-0.021	**-0.191***	**0.156***	-0.067	-0.105	0.095	-0.126	-0.088

Cape Hallett (Gressitt & Shoup 1967), where ornithogenic soils and/or penguin colonies are sites of high arthropod abundance. However, at Cape Bird, on Ross Island, Sinclair (2001) did not find arthropods in the penguin colonies. The probable reason for this absence at Hallett is because the substrate of hard-packed guano, with few stones, provides little soil or shelter for arthropods. The area of the former station is also highly compacted and is probably unsuitable.

Outside the penguin colony, the distributions of individual species were qualitatively similar to those reported previously (Gressitt & Shoup 1967, Wise & Shoup 1967). With the exception of *S. belli*, Collembola were more abundant than mites, and occurred in both soil and on stones in densities 2–3 orders of magnitude greater than the mites. Given the much larger size of Collembola, it seems that Collembola contribute the bulk of arthropod biomass at Cape Hallett.

Several species were probably undersampled in our survey. In particular, *C. gressitti* was regularly observed on the undersides of stones, but was not collected in a single stone sample (probably because of its speed). *Isotoma klovstadi* was extremely abundant in select locations at the base of the scree slope (see also Sinclair *et al*. 2003 and Strong *et al*. 1970), but none of these sites fell into our systematic samples.

Abiotic determinants of arthropod distribution at Cape Hallett

A few *ad hoc* samples were taken from the ridge at the top of the scree slope. This habitat differs from the scree slope in having a lichen vegetation dominated by the fruticose *Usnea antarctica* that is similar to the vegetation of high ice-free areas elsewhere in North Victoria Land (Sinclair & Scott, unpublished observation, J.A. MacDonald, personal communication 2002). The species composition of the soil fauna (particularly the Collembola) in the ridge habitat is similar to that of the lower areas of Cape Hallett in spite of the more exposed habitat at the edge of the permanent snowcap at 300 m a.s.l., possibly because the ridge habitat is relatively stable and has a high water input from nearby snowmelt. The ridge habitat is not currently included in the protected area. Stable patches in the scree slope only occur around protruding bedrock and areas of low gradient. High drainage in the scree slope also means that water availability is probably very low away from snowfield margins. Nevertheless, in areas of moderate stability near snowfield margins, there are abundant *X. mawsonii* and *B. frigidia* lichens, as well as an oribatid mite, *M. petronia,* found only on the slope among the habitats at Cape Hallett, and *I. klovstadi* and *Tydeus* spp., which are present in a number of habitats around the site. Of interest here is that *M. petronia* was not found in association with fruticose lichens, which had been assumed to be its main food source and habitat by Gressitt & Shoup (1967), although Marshall & Convey (1999) found that *M. wilsoni* density was positively correlated with foliose lichens in Dronning Maud Land.

The CCA indicated that spatial variables were more frequent predictors of arthropod communities than most of the environmental variables we measured. These spatial variables seem to reflect both substrate (for example, stones larger than 20 cm indicate the scree slope habitat) and primary productivity (perhaps indicated by water and lichen species). Given the spatial segregation of the four main habitat types, the spatial variables at Cape Hallett may be surrogates for relevant environmental variables.

Sinclair (2001) found that macroscopic vegetation was a poor predictor of arthropod distribution at Cape Bird. Since we did not have facilities to measure soil organic content or chlorophyll *a*, quantifying only macroscopic vegetation as we did at Hallett may not be an adequate surrogate for arthropod food resources. Similarly, although measurements of soil water content are used in analyses, water availability can be influenced by several factors, often related to the position and extent of winter snow cover, and the pattern and the melting rate of this snow cover over the summer season (Janetschek 1970, Kennedy 1993, Frati *et al.* 1997, Sinclair 2001, Gooseff *et al.* 2003). Thus, spot measurements provide a poor proxy of actual water availability. Factors that are likely to be important to arthropod communities, but were not measured at all, include the stability of the habitat, the moisture/relative humidity and temperature conditions, as well as the daily and seasonal variation in these factors (Sømme 1986, Sinclair *et al.* 2003). Microclimate temperature records indicate that there are significant differences in summer cooling rates and freeze-thaw cycles between scree and algal flats habitats only tens of metres apart at Cape Hallett (Sinclair *et al.* 2006). Physiological data for the Collembola suggest that the restriction of *C. cisantarcticus* to the algal flat habitat may be a consequence of its physiological tolerance to thermal stress (Sinclair *et al.* 2006), a variable we could not quantify at the appropriate resolution for this analysis.

Implications

In this study we have presented a detailed baseline survey of the arthropod fauna of Cape Hallett which can be used in future work to detect changes at the site. We have also shown that the arthropod species are spatially segregated, and that no arthropods are present in the penguin colony. Finally, we have demonstrated a significant influence of the environment on the density and distribution of arthropods at Cape Hallett. The influence of the abiotic environment on arthropod distribution suggests that the arthropod fauna at Cape Hallett may be affected by changes to the abiotic environment, either through direct disturbance from human activities, or via the broader effects of climatic change. In addition, because the distribution of arthropods is mutually exclusive with the distribution of penguin colony, measures to protect Adélie penguins from disturbance will not necessarily protect the arthropod fauna.

However, recent changes to the protected area at Cape Hallett have moved the emphasis to protection of breeding birds at the site (http://www.cep.aq/apa/aspa/sites/aspa106/index.html). The revized management plan has also shifted the recommended campsite to a new location on the edge of the algal flats (Fig. 1). Although protection for the terrestrial habitat remains in force, designated campsites are often associated with significant peripheral disturbance to soil (Campbell *et al.* 1993) and introductions of non-native species (Frenot *et al.* 2005). Given that the site has the highest arthropod diversity in the Ross Sea Region, we suggest that such disturbance (particularly if the use of Cape Hallett as an LGP site results in long-term use or high traffic over a period of years) will not only contradict the original purpose for a protected area at Cape Hallett (Logan & Bassett 1985), but that extensive human disturbance undermines any use of the site for monitoring long-term changes to the arthropod community due to climate. We therefore strongly recommend that the management plan be revisited with a view to providing increased protection for the terrestrial ecosystem at Cape Hallett.

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References

BURN, A.J. 1984. Energy partitioning in the Antarctic collembolan *Cryptopygus antarcticus*. *Ecological Entomology*, **9**, 11–21.

CAMPBELL, I.B., BALKS, M.R. & CLARIDGE, G.G.C. 1993. A simple visual technique for estimating the impact of fieldwork on the terrestrial environment in ice-free areas of Antarctica. *Polar Record*, **29**, 321–328.

CHOWN, S.L. & CONVEY, P. In press. Spatial and temporal variability across life's hierarchies in the terrestrial Antarctic. *Philosophical Transactions of the Royal Society of London Series B*.

CONVEY, P., PUGH, P.J.A., JACKSON, C., MURRAY, A.W., RUHLAND, C.T., XIONG, F.S. & DAY, T.A. 2002. Response of Antarctic terrestrial microarthropods to long-term climate manipulations. *Ecology*, **83**, 3130–3140.

DORAN, P.T., PRISCU, J.C., LYONS, W.B., WALSH, J.E., FOUNTAIN, A.G., MCKNIGHT, D.M., MOORHEAD, D.L., VIRGINIA, R.A., WALL, D.H., CLOW, G.D., FRITSEN, C.H., MCKAY, C.P. & PARSONS, A.N. 2002. Antarctic climate cooling and terrestrial ecosystem response. *Nature*, **415**, 517–520.

ELLIS-EVANS, J.C. & WALTON, D. 1990. The process of colonization in Antarctic terrestrial and freshwater ecosystems. *Proceedings of the NIPR Symposium on Polar Biology*, **3**, 151–163.

FRATI, F., FANCIULLI, P.P., CARAPELLI, A. & DALLAI, R. 1997. The Collembola of northern Victoria Land (Antarctica): distribution and ecological remarks. *Pedobiologia*, **41**, 50–55.

FRATI, F., SPINSANTI, G., & DALLAI, R. 2001. Genetic variation of mtCOII gene sequences in the collembolan *Isotoma klovstadi* from Victoria Land, Antarctica: evidence for population differentiation. *Polar Biology*, **24**, 934–940.

FRENOT, Y., CHOWN, S.L., WHINAM, J., SELKIRK, P.M., CONVEY, P., SKOTNICKI, M. & BERGSTROM, D.M. 2005. Biological invasions in the Antarctic: extent, impacts and implications. *Biological Reviews*, **80**, 45–72.

GARCÍA, L.V. 2004. Escaping the Bonferroni iron claw in ecological studies. *Oikos*, **105**, 657–663.

GOOSEFF, M.N., BARRETT, J.E., DORAN, P.T., FOUNTAIN, A.G., LYONS, W.B., PARSONS, A.N., PORAZINSKA, D.L., VIRGINIA, R.A. & WALL, D.H. 2003. Snow-patch influence on soil biogeochemical processes and invertebrate distribution in the McMurdo Dry Valleys, Antarctica. *Arctic Antarctic and Alpine Research*, **35**, 91–99.

GORDON, S. 2003. *Site description and literature review of Cape Hallett and surrounding areas*. Christchurch: Antarctica New Zealand, 18 pp.

GRESSITT, J.L. 1967a. Introduction. *Antarctic Research Series*, **10**, 1–33.

GRESSITT, J.L., *ed.* 1967b. Entomology of Antarctica. *Antarctic Research Series*, **10**, 1–395.

GRESSITT, J.L. & SHOUP, J. 1967. Ecological notes on free-living mites in North Victoria Land. *Antarctic Research Series*, **10**, 307–320.

JANETSCHEK, H. 1970. Environments and ecology of terrestrial arthropods in the high Antarctic. *In* HOLDGATE, M.W., *ed. Antarctic Ecology*, vol. 2. London: Academic Press, 871–885.

KENNEDY, A.D. 1993. Water as a limiting factor in the Antarctic terrestrial environment: a biogeographical synthesis. *Arctic and Alpine Research*, **25**, 308–315.

KENNEDY, A.D. 1995a. Simulated climate change: are passive greenhouses a valid microcosm for testing the biological effects of environmental perturbations. *Global Change Biology*, **1**, 29–42.

KENNEDY, A.D. 1995b. Antarctic terrestrial ecosystem response to global environmental change. *Annual Review of Ecology and Systematics*, **26**, 683–704.

KENNEDY, A.D. 1999. Modelling the determinants of species distributions in Antarctica. *Arctic, Antarctic and Alpine Research*, **31**, 230–241.

LEGENDRE, L. & LEGENDRE, P., *eds.* 1998. *Numerical ecology*. Amsterdam: Elsevier, 853 pp.

LOGAN, L.A. & BASSETT, J.A. 1985. Survey of Specially Protected Area No. 7 Cape Hallett, Northern Victoria Land. *New Zealand Antarctic Record*, **6**, 47–50.

MARSHALL, D.J. & CONVEY, P. 1999. Compact aggregation and life-history strategy in a continental Antarctic mite. *In* BRUIN, J., VAN DER GEEST, L.P.S. & SABELIS, M.W., *eds*. *Ecology and evolution of the Acari*. Amsterdam: Kluwer, 557–567.

PRYOR, M.E. 1962. Some environmental features of Hallett Station, Antarctica, with special reference to soil arthropods. *Pacific Insects*, **4**, 681–728.

PULLIN, A.S., KNIGHT, T.M., STONE, D.A. & CHARMAN, K. 2004. Do conservation managers use scientific evidence to support their decision-making? *Biological Conservation*, **119**, 245–252.

REID, B. 1964. *Adélie penguin rookery, Seabee Spit Cape Hallett, Antarctica, 1:1800*. Wellington, New Zealand: DSIR.

RUDOLPH, E.D. 1963. Vegetation of Hallett Station, Victoria Land, Antarctica. *Ecology*, **44**, 585–586.

RYAN, P.G. & WATKINS, B.P. 1989. The influence of physical factors and ornithogenic products on plant and arthropod abundance at an inland Nunatak group in Antarctica. *Polar Biology*, **10**, 151–160.

SINCLAIR, B.J. 2001. On the distribution of terrestrial invertebrates at Cape Bird, Ross Island, Antarctica. *Polar Biology*, **24**, 394–400.

SINCLAIR, B.J., LORD, J.M. & THOMPSON, C.M. 2001. Microhabitat selection and seasonality of alpine invertebrates. *Pedobiologia*, **45**, 107–120.

SINCLAIR, B.J. & SJURSEN, H. 2001. Terrestrial invertebrate abundance across a habitat transect in Keble Valley, Ross Island, Antarctica. *Pedobiologia*, **45**, 134–145.

SINCLAIR, B.J. 2002. Effects of increased temperatures simulating climate change on terrestrial invertebrates on Ross Island, Antarctica. *Pedobiologia*, **46**, 150–160.

SINCLAIR, B.J., KLOK, C.J., SCOTT, M.B., TERBLANCHE, J.S. & CHOWN, S.L. 2003. Diurnal variation in supercooling points of three species of Collembola from Cape Hallett, Antarctica. *Journal of Insect Physiology*, **49**, 1049–1061.

SINCLAIR, B.J., TERBLANCHE, J.S., SCOTT, M.B., BLATCH, G., KLOK, C.J. & CHOWN, S.L. 2006. Environmental physiology of three species of Collembola at Cape Hallett, North Victoria Land, Antarctica. *Journal of Insect Physiology*, **52**, 29–50.

SMITH, R.I.L. 1984. Terrestrial plant biology of the sub-Antarctic and Antarctic. *In* LAWS, R.M., *ed. Antarctic ecology,* vol. 1. London: Academic Press, 61–162.

SØMME, L. 1986. Ecology of *Cryptopygus sverdrupi* (Insecta: Collembola) from Dronning Maud Land, Antarctica. *Polar Biology*, **6**, 179–184.

STEVENS, M.I. & HOGG, I.D. 2002. Expanded distributional records of Collembola and Acari in southern Victoria Land, Antarctica. *Pedobiologia*, **46**, 485–495.

STRANDTMANN, R.W. 1967. Terrestrial Prostigmata (Trombidiform mites). *Antarctic Research Series*, **10**, 51–80.

STRONG, F.E., DUNKLE, R.L. & DUNN, R.L. 1970. Low-temperature physiology of Antarctic arthropods. *Antarctic Journal of the United States*, **5**(4), 123.

TER BRAAK, C.J.F. & SMILAUER, P. 1998. *Canoco Reference Manual and User's Guide to Canoco for Windows.* Wageningen: Centre for Biometry, 351 pp.

TILBROOK, P.J. 1967. Arthropod ecology in the Maritime Antarctic. *Antarctic Research Series*, **10**, 331–356.

USHER, M.B. & BOOTH, R.G. 1984. Arthropod communities in a maritime Antarctic moss-turf habitat: three-dimensional distribution of mites and Collembola. *Journal of Animal Ecology*, **53**, 427–441.

WALLWORK, J.A. 1962. *Maudheimia petronia* n. sp. (Acari: Oribatida), an oribatid mite from Antarctica. *Pacific Insects*, **4**, 865–868.

WISE, K.A.J. 1967. Collembola (Springtails). *Antarctic Research Series*, **10**, 123–148.

WISE, K.A.J. & SHOUP, J. 1967. Distribution of Collembola at Cape Hallett. *Antarctic Research Series*, **10**, 325–330.

WOMERSLEY, H. & STRANDTMANN, R.W. 1963. On some free living prostigmatid mites of Antarctica. *Pacific Insects*, **5**, 451–472.