

Aerial dispersal of springtails on the Antarctic Peninsula: implications for local distribution and demography

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Abstract: Aerial dispersal has been frequently proposed as a potential mechanism by which polar terrestrial arthropods are transported to, and settle the ice free habitats of Antarctica, but to date there has been little substantive evidence in support of this hypothesis. Using water traps we investigated aerial deposition of arthropods on Lagoon Island, Ryder Bay, on the Antarctic Peninsula. Over a period of five weeks, trapping at three different altitudes, we captured a total of nine springtails, *Cryptopygus antarcticus*, all alive. This is the first study to demonstrate conclusively the survival of wind-borne native arthropods within Antarctica. By scaling the modest trapping area and success against island surface area, it is clear that hundreds, if not thousands, of springtails are regularly relocated by winds between the terrestrial habitats of Marguerite Bay. We use known desiccation rates of *C. antarcticus* and wind speeds to predict the likelihood of successful dispersal between the principal terrestrial habitats of the larger Marguerite Bay. Implications for local and long-range dispersal are discussed in relation to *C. antarcticus* and other polar arthropods.

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Introduction

Wind is a driving climatic force in Antarctica, influencing everything from patterns of snow accumulation to sea currents (Fogg 1998, Hansom & Gordon 1998). The effect of wind movements on Antarctic biota - particularly as a means of dispersing organisms or their propagules - has long excited the curiosity of polar biologists as a means of explaining dispersal between and to the isolated ice free terrestrial habitats of the continent (Gressitt 1967, Marshall 1996, Fogg 1998). These habitats are effectively islands, whether isolated by sea around the margins of the continent, or by ice inland, with the physical scale of isolation of individual habitat units varying between metres and thousands of kilometres.

Although Antarctica has for thousands of years been the recipient of biological particles from northern latitudes in the form of airborne propagules (e.g. bacteria, bryophyte and lichen propagules, microalgae, fungi, diatoms) (Marshall 1996, Chalmers *et al.* 1996, Fogg 1998), the importance of aerial dispersal to the establishment and colonisation of Antarctic terrestrial habitats by arthropods remains difficult to determine. In the late 1950s and early 1960s the Bishop Museum of Honolulu under the direction of J.L. Gressitt sampled the air over the Southern Ocean and Antarctic land surfaces, capturing insects from nine orders (Collembola, Thysanoptera, Psocoptera, Homoptera, Heteroptera, Lepidoptera, Diptera, Coleoptera, and Hymenoptera) as well as Acarina and Araneae (Gressitt *et al.* 1960, Yoshimoto *et al.* 1962, Yoshimoto & Gressitt 1963, Clagg 1966, Gressitt 1967). With the exception of the

Collembola, Acari, and Chironomidae (Diptera), none of these were indigenous to Antarctica or to the sub-Antarctic islands and, although two of the spiders 'may have been alive' on capture, none of the non-Antarctic species were believed capable of establishment (Gressitt 1967). Although Antarctic soil invertebrates capable of anhydrobiosis (tardigrades, nematodes) have been shown to survive aerial dispersal (Nkem *et al.* 2006), until now evidence of 'live' aerially dispersed arthropods (who are not capable of anhydrobiosis) has been lacking. Pugh (2003), for example, notes that all acarine records from aerial plankton caught over the Pacific and Southern Ocean are of dead individuals.

The harsh environment of continental Antarctica coupled with katabatic winds radiating from the centre of the continent and circumpolar coastal winds (circulating west to east) (Gressitt 1967) continue to make both the arrival and establishment of non-native arthropods, via aerial dispersal, unlikely. In contrast, the less remote and comparatively more benign habitats of the sub-Antarctic and parts of the maritime Antarctic - particularly in the context of contemporary climate warming - make future wind mediated introductions increasingly possible (Greenslade 1999, Convey 2005, Frenot *et al.* 2005). Recent observations of Lepidoptera on sub-Antarctic islands - the establishment of *Plutella xylostella* (Linn.) on Marion Island (Chown & Avenant 1992); the observations of migrants on Macquarie Island (*Agrotis ipsilon* (Hufnagel), *Dasypodia selenophora* Guenee, *Persectania ewingii* (Westwood), *Vanessa kershawi* (McCoy)) (Greenslade *et al.*

Table I. Evidence for the local aerial dispersal of Antarctic terrestrial arthropods.

Taxon	Species <i>n</i>	Trapping method	Location	Source
Collembola				
<i>Friesea grisea</i> ?	1	Wind nets	Marble point, Victoria Land	Gressitt <i>et al.</i> (1960)
<i>Isotoma klovstadi</i>	2	Wind nets	Hallett Station	Pryor (1962)
	?	Observations of wind-deposited desiccated specimens	Sea ice 3 km SW of Hallett Station	
<i>Unidentified</i>	'many'	'Tanglefoot strips'	Hallett Station	
<i>Cryptopygus antarcticus</i>	6	Funnel + collection beaker with ethyl glycol solution	Rothera Point, Adelaide Island, Maritime Antarctic	Hayward (2001)
<i>Gomphiocephalus hodgsoni</i>	2	Wind nets	Cape Geology and Botany Bay, Granite Harbour, Southern Victoria Land	Mark Stevens, unpublished data
Acarina				
Unidentified	'a few'	'Tanglefoot strips'	Hallett Station	Pryor (1962)
Unidentified	1	Frisbee mounted on collection bottle with distilled water	Signy Island, Maritime Antarctic	Chalmers <i>et al.</i> (1996)
<i>Stereotydeus mollis</i>	3	Wind nets	Cape Geology and Botany Bay, Granite Harbour, Southern Victoria Land	Mark Stevens, unpublished data
Unidentified 'small arthropod'	1	Rotorod samplers and Tauber traps	Ross Island	Benninghoff & Benninghoff (1978)

* Gressitt *et al.* (1960) identify the collembolan they captured at Marble Point, as a 'podurid'. However, Wise (1967) notes that the identification of 'Family Poduridae' by Glance (1945) and Bryant (1945) – (the source for the Gressitt *et al.* (1960) identification?) – is in fact *Friesea grisea* (Schäffer).

1999) and South Georgia (*A. ipsilon*, *P. xylostella*, *Plodia interpunctella* (Hubner) [the last an introduction rather than a migrant]) (Convey 2005) - suggest that, for species capable of long-range dispersal, these latitudes may be less impregnable to settlement than ever before.

Within Antarctica, however, the role of winds in the local dispersal of arthropods between and within islands of terrestrial habitat has received scant attention (Table I). Nonetheless, aerial dispersal remains one of the most favoured explanations for the origins and local dispersal of arthropod populations (Gressitt 1967, Hogg & Stevens 2002). Although anecdotal observations of springtails captured on the surface film of water/oil barrels or ponds are well known, the problematic logistics of trapping insects in Antarctica (small return vs vast potential fallout space) are a deterrent to extensive aerial fallout surveys and the Bishop Museum's work remains to this day the most comprehensive study carried out on the continent. Here, we probe the ecological likelihood and implications of local aerial dispersal as a potential means of population recruitment and genetic desegregation.

Our aims in this study were two-fold: a) to identify whether arthropods could survive the natural process of aerial dislocation and transport, and b) if they could survive, to explore the implications of survival with regard to their dispersal to other ice free habitats. Although previous studies have documented aerial dispersal of Antarctic springtails and mites (Table I), the favoured capture method for these studies - wind nets and/or a killing solution - prevent an assessment of post-dispersal viability. To circumvent this problem, we used water traps. Polar springtails (numerically the most abundant arthropods in many Antarctic habitats) are capable of surviving extended

periods on the surface water film (Coulson *et al.* 2002, Hawes *et al.* unpublished data); while the most predominant mite of the study location, *Alaskozetes antarcticus* (Michael), can survive up to 55 days of saltwater submersion at 0°C (Strong 1967).

Methods

Site

Fieldwork was carried out at Lagoon Island c. 3–4 km from Rothera Research Station, Adelaide Island, off the west coast of the Antarctic Peninsula (Fig. 1). The island consists of two sections that are separated by a tidally inundated isthmus. Thirteen species of terrestrial arthropod are known from the island, including three species of Collembola (*Cryptopygus antarcticus* (Déharveng), *C. badasa* (Greenslade), and *Friesea grisea* Schäffer) (Convey & Lewis Smith 1997). *Cryptopygus antarcticus* are particularly abundant on the island - a survey of the islands of northern Marguerite Bay and Alexander Island found it to have densities of c. 1.5×10^6 m⁻² in debris extractions

Table II. Number of springtails caught in water traps on Lagoon Island.

Date	Altitude		
	10 m	25 m	50 m
27/01/2005	1	0	0
05/02/2005	2	0	0
14/02/2005	4	0	0
22/02/2005	0	0	0
02/03/2005	1	0	1
Total	8	0	1
Mean	1.6	0	0.2

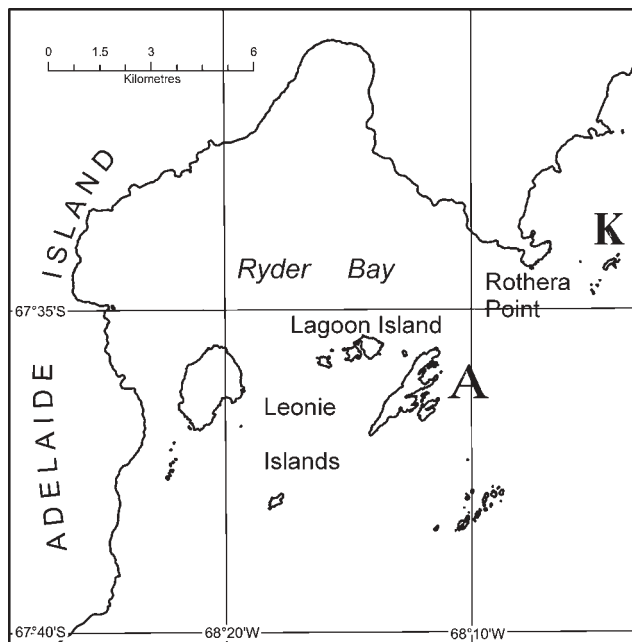
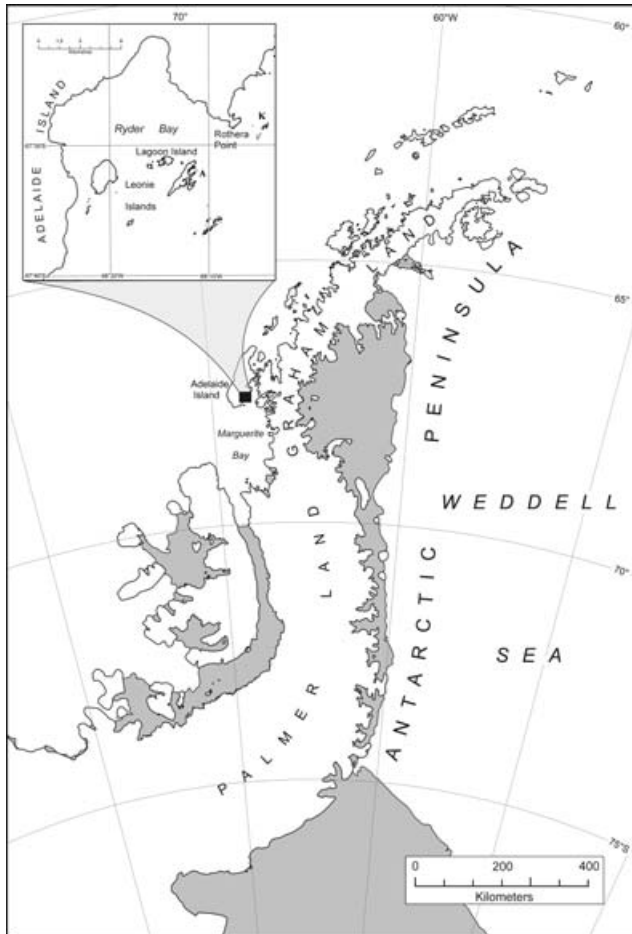


Fig. 1. a. Map showing study area (Ryder Bay) (inset) in relation to rest of the Antarctic peninsula, **b.** Map of Ryder Bay (northern Marguerite Bay) (A = Anchorage Island, K = Killingbeck Islands, all other terrestrial habitats labelled).

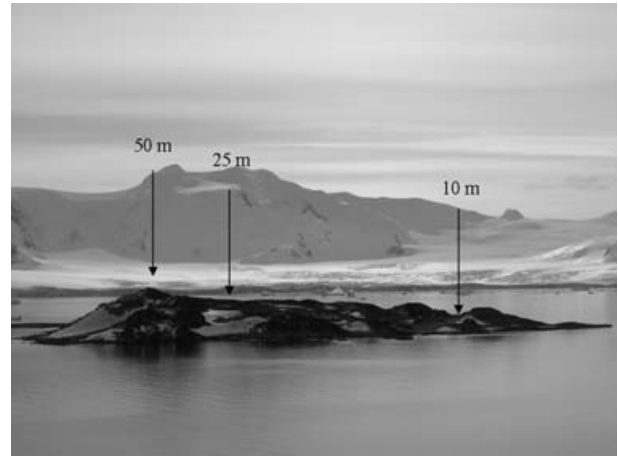


Fig. 2. Northern Lagoon Island viewed in profile from Anchorage Island with trapping locii indicated (10, 25, and 50 m) (Photo: TCH).

(Convey & Lewis Smith 1997). Trapping was carried out at the northern side of the island at three altitudes: 10, 25 and 50 m (Fig. 2).

Aerial trapping

The deposition and survival of aerially transported springtails was monitored using water traps. Seawater was used to decrease the probability of capture surfaces freezing during freeze-thaw cycles. Five cylindrical metal water traps ($h = 17$ cm, circumference = 36 cm, trapping surface area = 17.3 cm²) were placed at each of the three sites (i.e. insects were sampled 17 cm above ground level at each elevation along the altitudinal transect). To exclude non-aerial matter (e.g. climbing arthropods) a 15 cm wide ring of Vaseline grease was smeared around the top lip of each trap. To deter wind dislodgement and vandalism from skuas (*Catharacta maccormicki* Saunders), traps were weighed down with stones pre-washed in seawater to prevent contamination (this method was successful at the 10 and 50 m sites, but skuas nesting near the traps at 25 m still managed to damage the traps). Traps were surveyed every 5–10 days for evidence of wind deposited arthropods. Captured animals were noted as alive (active) or dead, then removed for identification and preserved in alcohol.

Meteorological data

Wind speed and direction data for the summer field season were taken from a BAS long-term monitoring micro-meteorological dataset collected on neighbouring Anchorage Island (c. 2 km from the Lagoon Island study sites).

Table III. Frequency of wind speed thresholds during the summer of 2004–2005

	Number of days wind speeds (ms^{-1}) reached threshold values			
	< 6	6–12	12–18	> 18
October	11	8	10	1
November	7	10	13	0
December	13	15	3	0
January	16	14	1	0
February	6	17	5	0
March	10	12	9	0

Dispersal predictions

Predicted survival of airborne springtails in the airstream was calculated from the relationship between wind speed, distance between habitats isolated by sea, and the known desiccation resistance of *Cryptopygus antarcticus* (time to

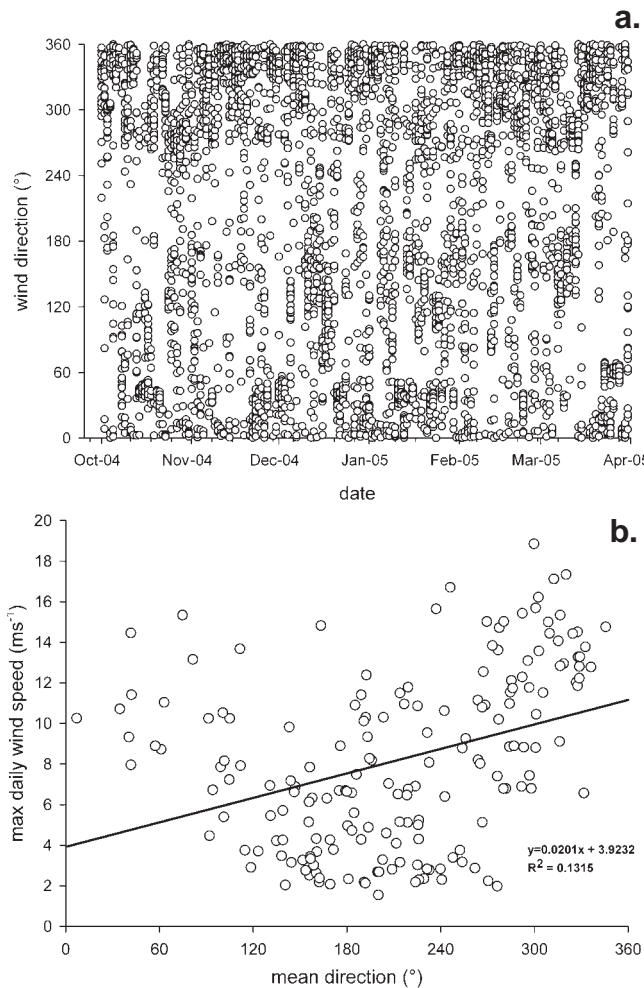


Fig. 3. a. Wind direction ($^{\circ}$) and **b.** the relationship between mean wind direction ($^{\circ}$) and max daily wind speeds (ms^{-1}) during the summer of 2004–2005 (Anchorage Island micro-met station, British Antarctic Survey) (0° = north, 90° = east, 180° = south, 270° = west).

lose 50% of body water (T_{50}) = 44.9 mins; Block *et al.* 1990). The likelihood of the successful dispersal of *C. antarcticus* in Marguerite Bay was calculated for wind speeds of 2–18 ms^{-1} (representing the spectrum of speeds observed during the summer of 2004–2005 (Table III)), for transport between each of the principal arthropod habitats in the Bay: Léonie Island, Lagoon Island, Anchorage Island, Rothera Point, and Killingbeck Island (Fig. 1).

Results and discussion

Table II shows the results of aerial trapping. A total of nine springtails (*C. antarcticus*) were captured, all alive. The total surface area of the northern and southern halves of Lagoon Island is 383 987 m^2 (Peter Fretwell, personal communication 2006) and the total trapping area was 259.5 cm^2 . Scaling trapping success ($n = 9$) up to total island surface area gives an estimate of *c.* 150 000 individuals being aerially dispersed on the island during the study period. Given the complexities of atmospheric behaviour and the stochastic nature of aerial capture, this is, of course, an overly simplified estimate. Nonetheless, it is clear that the numbers of Maritime Antarctic springtails regularly re-located by winds during the summer are in the hundreds, if not thousands. The ability of springtails to survive for extended periods on water films (Coulson *et al.* 2002, Hawes *et al.* unpublished data), also allows for the possibility of interactions between aerial dispersal and melt- and seawater dispersal i.e. deposition on water surfaces and carriage to ice free habitats. The origins of aerially deposited animals cannot, of course, be determined. Traps were

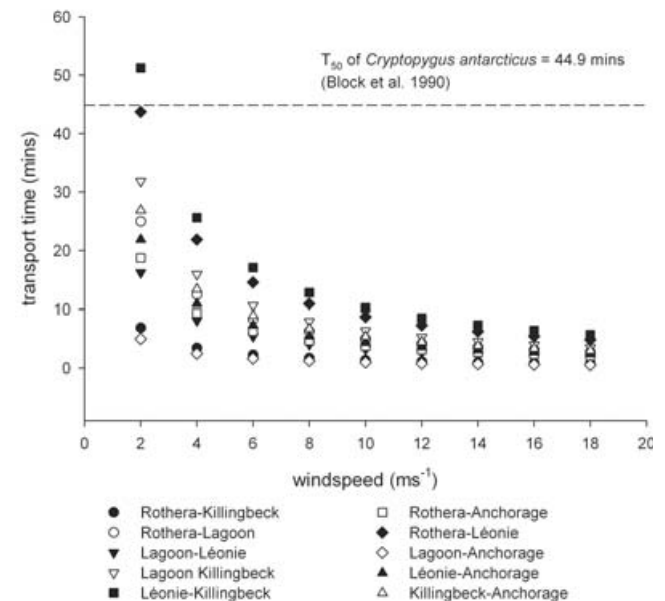


Fig. 4. The relationship between wind speed and transport time of aerially dispersed *Cryptopygus antarcticus* between each of the principle terrestrial arthropod habitats on Marguerite Bay.

Table IV. Comparative desiccation resistance in Antarctic arthropods.

Order	Species	Location	Dehydration resistance (mean (\pm SD) % water loss h ⁻¹)	Method	Reference
Acari	<i>Alaskozetes antarcticus</i>	Maritime Antarctic	< 0.5	0°C and 5% RH	Worland & Block (1986)
	<i>Halozetes belgicae</i>	Maritime Antarctic	0.7 \pm 0.9	As above	Worland & Block (1986)
	<i>Gamasellus racovitzai</i>	Maritime Antarctic	2.1 \pm 0.6	As above	Worland & Block (1986)
	<i>Stereotydeus villosus</i>	Maritime Antarctic	4.1 \pm 0.8	As above	Worland & Block (1986)
Collembola	<i>Archisotoma brucei</i>	Maritime Antarctic	24.6 \pm 2.1	As above	Worland & Block (1986)
	<i>Cryptopygus antarcticus</i>	Maritime Antarctic	44.9	0% RH with temperature ramped from 5 to 34°C at 0.5 min ⁻¹	Block <i>et al.</i> (1990)
	<i>Parisotoma octooculata</i>	Maritime Antarctic	35.4	As above	Block <i>et al.</i> (1990)
	<i>Friesea grisea</i>	Maritime and Continental Antarctic	112.5	c. 5% RH at 20°C with silica gel	Sinclair <i>et al.</i> (2006)
	<i>Cryptopygus cisantarcticus</i>	Continental Antarctic	45	As above	Sinclair <i>et al.</i> (2006)
	<i>Isotoma klovestadi</i>	Continental Antarctic	105	As above	Sinclair <i>et al.</i> (2006)
			Time to 50% water loss (T ₅₀)		
			Time to 50% mortality		

situated in a habitat matrix known to have relatively low densities of soil arthropods (rock scree) (personal observation), nonetheless animals could have originated locally or from further afield.

Mean wind direction during the summer was 213.6 (\pm 1.89) (SSW) (Fig. 3a). Wind speeds over the summer ranged between 0–18 ms⁻¹ (Table III), with a mean wind velocity during the trapping period of 4.5 ms⁻¹ (\pm 0.11). There was a significant linear relationship between mean wind direction and wind speed (df = 1, F = 27.24, R² = 13.1, P = < 0.001) with faster winds blowing in a north-westerly direction (Fig. 3b). However, it is clear that insects could potentially have been dispersed to any of the non-viable or viable ocean or land surfaces at varying rates.

Plotting transport time against wind speeds shows that only animals travelling the greatest distance of c. 8 km between Killingbeck and Léonie islands, and at wind speeds of 2 ms⁻¹ or less, would be at risk of losing more than 50% of their body water (Fig. 4). Comparisons with the desiccation resistance of other Antarctic collembolans (Table IV) suggests that they too will be capable of travelling similar distances at wind speeds of 4 ms⁻¹ or greater and with only the distances between Léonie and Killingbeck islands, and Léonie Island and Rothera Point having the potential to cause difficulties at slower wind speeds.

Although passive dispersal by winds over large distances is unlikely in Antarctic Collembola (Gressitt *et al.* 1960, Hogg & Stevens 2002, Sinclair & Stevens 2006) as cuticular permeability makes them prone to rapid desiccation (Hopkin 1997) – this is not the case for short-range dispersal: either between local habitat micro-‘islands’ (e.g. nutrient flushes of bryophytes within a matrix of scree habitat), or between isolated but proximal ice free habitats such as the island networks of Marguerite Bay. The trapping results from this study and the projections of dispersal feasibility obtained by comparing wind speeds and

predicted transport times within Marguerite Bay, suggest that as a local dispersal mechanism, aerial transport is certainly viable. Although Collembola vary in their cuticular permeability and desiccation resistance according to the degree to which their lifestyles are edaphic (Kaersgaard *et al.* 2004), it is probable that other Antarctic species are also capable of surviving short-range dispersal events (Table IV). Indeed, the other predominant collembolan on the Antarctic peninsula, *Friesea grisea*, (Convey & Lewis Smith 1997) has been found to prefer drier habitats and show less intense behavioural stress responses to low humidity (Hayward *et al.* 2004).

Mites, the other principal component of terrestrial arthropod communities in Antarctica, may, from a physiological point of view, have even greater dispersal capabilities given that sclerotisation provides a greater barrier to desiccation. The oribatids, *Alaskozetes antarcticus* and *Halozetes belgicae* (Michael), in particular, are ‘mesic’ (*sensu* Eisenbeis 1983) species (Worland & Block 1986) (Table I). Indeed at temperatures below -2°C – a realistic scenario in Antarctica for both air and ground temperatures – *A. antarcticus*, loses virtually no water (Worland & Block 2003). However, there is little evidence that long-range dispersal has occurred in the past (Pugh 2003), while the likelihood of short-range dispersal may be diminished by other factors. The life history strategies of the oribatids, in particular, involve long periods as aggregations on rocks – where they moult, reproduce, and oviposit – indeed, when moulting they are physically cemented to the lithic surface.

The desiccation-dispersal distance model employed here is, of course, a simplification. Our understanding of desiccation tolerance of Antarctic arthropods (Table I) is based on static techniques, not on the dynamic form of water loss aerially dispersed arthropods are likely to experience. Firstly, in contrast to the fully hydrated animals used in desiccation experiments, arthropods captured by winds will be in varying states of hydration when they begin

their 'journey'. Secondly, heterogeneity of the air column in terms of humidity, wind speed, and temperature means that the rate of water loss will not be constant. The picture is also further complicated by the subtleties of other macro- and micro-atmospheric processes, heterogeneity in local topography and the large areas of inhospitable landing sites like the ocean and ice (ice free areas comprise less than 0.3% of the 14 million km² continent (British Antarctic Survey 2004)).

Comparisons with high Arctic observations of arthropod aerial dispersal emphasise the importance of wind speeds to these events. Thus, although winds contribute to the transoceanic dispersal of arthropods to Svalbard (Coulson 2000, Coulson *et al.* 2002), at local scales evidence for the passive dispersal of Collembola and mites (Coulson *et al.* 2003, Hawes 2003) and ballooning linyphiid spiders (Coulson *et al.* 2003, Hawes *in press*) is meagre. Likewise, trapping of insects at Point Barrow, Alaska, for three months (July–August) with a total trapping area (900 cm²) three times that described here, captured only seven Collembola (Gressitt & Yoshimoto 1974). Although aerial dispersal no doubt occurs - on Svalbard, the establishment of arthropod communities on islands isolated from the mainland for *c.* 150 years testifies to this (Hodkinson *et al.* 2004, Hodkinson 2005) - its occurrence is probably more infrequent than in Antarctic habitats. Wind velocity during the summer at Kongsfjorden, West Spitsbergen, for example, when terrestrial habitats are snow- and ice free, typically ranges between 2–3 ms⁻¹ (Coulson *et al.* 2003, Hawes *in press*) - in comparison to Marguerite Bay where mean wind speeds ranged between 2–18 and 2–6 ms⁻¹ during the summer and study period, respectively. Higher wind speeds both increase the likelihood of passive aerial capture (and of dislodgement into the air column in the first place) and reduce the transport time to deposition sites (Greenslade *et al.* 1999). Data for wind direction and speeds from this study suggest that meteorological processes are conducive to random, but not consistent, successful dispersal. In short, the numbers of aeolian hitchhikers may be many, but the numbers arriving at suitable habitats could be few.

To date, available genetic evidence supports this view, at least on continental Antarctica. Studies on variation in Victorian Land arthropod populations isolated by glaciation have largely confirmed the genetic segregation of *Gressitacantha terranova* (Fanciulli *et al.* 2001), *Isotoma klovstadi* (Frati *et al.* 2001) *Gomphiocephalus hodgsoni* (Stevens & Hogg 2003, 2006), and *Stereotydeus mollis* (Stevens & Hogg 2006). Studies of *G. hodgsoni*, while confirming genetic vicariance in geographically isolated populations, have found limited mixing of haplotypes in populations separated by McMurdo Sound (Stevens & Hogg 2003). The distance between these populations - *c.* 100 km - is too great for arthropods to survive desiccation at normal wind speeds (although perhaps not for rare

meteorological events?). The observed connections between populations have been attributed therefore, at least speculatively, to other passive dispersal agencies such as humans or avian phoresy (Stevens & Hogg 2003).

Within the context examined here, however, the potential for contributions to settlement and genetic mixing is much more realistic - with maximum distances between isolates of *c.* 8 km (Rothera to Léonie Island). Indeed, as desiccation is probably the principle obstacle to successful dispersal, the comparatively more humid environment of the Maritime Antarctica may also make aerial dispersal more feasible than in continental habitats (Marshall & Pugh 1996, Pugh 2003, 2004).

At the landscape scale, Marguerite Bay is structurally a natural model of metapopulation geography (*sensu* Levins 1969, 1970) - in which the favourable habitat consists, literally, of islands (plus one shoreline - Rothera Point), surrounded by the unfavourable, non-viable, habitat matrix of seawater (Marguerite Bay itself). At the microhabitat level, each of these islands have their own local population dynamics with patch networks of favourable and unfavourable micro-habitats (e.g. moss vs rock scree). The extent to which these fragmented populations - at either spatial scale - conform to the extinction-recolonization scenarios of metapopulation theory, *sensu strictu*, is uncertain, but certainly aerial dispersal processes may be implicated in maintaining contiguity between such populations.

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