

Rafting in the Antarctic springtail, *Gomphiocephalus hodgsoni*

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Abstract: Capture by water surfaces is a frequent but stochastic phenomenon for Antarctic collembolans (springtails), with implications for both the survival and dispersal of populations. This paper provides the first field description of the characteristics of rafting aggregations of the springtail *Gomphiocephalus hodgsoni* and provides the first observation of the inclusion of the mite, *Stereotydeus mollis*, within these aggregations. Field observations of aggregations in meltwater pools are used to develop a picture of the ecological implications of rafting for Antarctic springtails. The potential for marine capture was also demonstrated by additional observations of two springtails aerially deposited on to sea ice as well as springtails floating in the tidewater cracks between the sea ice and land.

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Introduction






The importance of passive dispersal to terrestrial invertebrates at both landscape and regional scales has long been of interest to biologists of Antarctic terrestrial fauna (Gressitt 1967). Although there is a consensus that the overall patterns of invertebrate distributions in Antarctica ice-free habitats reflect glacial isolation and endemism (Stevens *et al.* 2006, Convey & Stevens 2007, Convey *et al.* 2008, Pugh & Convey 2008), there is growing evidence to support the view that passive dispersal, both in terms of dispersal itself and as a distinct class of interactions with the abiotic environment, is not insignificant. With regard to the former, passive dispersal may contribute to both long and short-term transport of individuals and populations across the matrix of habitat that is not ice-free. Examination of the biogeographic signature of the Antarctic fairy shrimp, for example, makes it hard to come to any other conclusion, other than that phoresy (in particular, avian phoresy) is implicated in its current distribution on the Antarctic Peninsula (Hawes 2009). With regard to the latter, abiotic interactions have traditionally been viewed primarily in terms of physiological interactions with temperature and water availability. However, the physical manifestations of Antarctica's climate - wind, ice, meltwater - all represent distinct phenomena which challenge both the physical and physiological viability of individuals and populations. For example, some of the implications of wind and water capture have been examined in springtails already (Hawes *et al.* 2007, 2008). Although these experiments were limited to *Cryptopygus antarcticus* Willem, parallel work in the Arctic confirms that it is a generalized phenomenon in polar habitats (Coulson *et al.* 2002, Hawes 2007, 2008).

Gomphiocephalus hodgsoni Carpenter, is one of the most widespread springtails in continental Antarctica with a range that extends over most of southern Victoria Land

(Janetschek 1967, Stevens & Hogg 2002). Molecular phylogeography indicates high levels of genetic structure in populations consistent with the effects of isolation and glacial refugia on gene flow (Stevens & Hogg 2003, McGaughan *et al.* 2008, 2010). Studies of continental Antarctic springtails at fine spatial scales (Nolan *et al.* 2006, Hawes *et al.* 2010), in particular, have demonstrated that even small geographic barriers (e.g. streams, ridges, areas of permanent snow) may be effective mechanisms for genetic isolation. Two studies have also suggested, albeit inconclusively, that some aspects of the phylogeographic patterns identified, may be indicative of passive dispersal across such barriers: Stevens & Hogg (2003) found a shared haplotype between Cape Bird and Granite Harbour populations; likewise, Hawes *et al.* (2010) found a shared haplotype between two sites separated by a gully of ice.

Rafting on water surfaces is a well-known phenomenon in springtails and, in an Antarctic context, may have important ramifications for local, and occasionally long distance, dispersal (Hawes *et al.* 2008). Previous work (Hawes *et al.* 2008) has demonstrated the potential for long-term survival of individuals and even production of offspring. More recently McGaughan *et al.* (in press) have examined short-term survival of *Gomphiocephalus hodgsoni* floating on freshwater and seawater under laboratory conditions. However, although laboratory investigations permit a certain degree of inference about the significance of rafting, field observations have been wanting. The aim of the work described here, was to place these laboratory studies in a field context by examining their applicability to observations of *in situ* rafting. Thus, although physiological parameters are readily examined under controlled conditions, the actual occurrence of rafting aggregations may be associated with numerous factors that have not been replicated, or even recognized. This paper describes for the first time the

Table I. Comparison of pools and their raft aggregations.

Pool	Aspect	Changes to pool status during observation period (15–26 Jan) ¹	Aggregation composition	Aggregation size (#individuals)	Escape? ³	Survival(%)	
						<i>G. hodgsoni</i>	<i>S. mollis</i>
Pool 1	North-facing; exposed		<i>G. hodgsoni</i> <i>S. mollis</i>	166 24	No	23.5	0
Pool 2	West-facing		<i>G. hodgsoni</i>	16	Yes	By escape	NA
Pool 3	West-facing		1st aggregation ² <i>G. hodgsoni</i> <i>S. mollis</i>	1st aggregation ² 363 1	Yes	By escape	By escape
			2nd aggregation <i>G. hodgsoni</i>	2nd aggregation 198			
Pool 4	West-facing		<i>G. hodgsoni</i> <i>S. mollis</i>	153 5	Yes	By escape	By escape
Pool 5	North-facing; surrounded by rock face		<i>G. hodgsoni</i>	14	No	21.4	NA

¹ = rings read clockwise where each slice represents one observation day; black = water, grey = frozen, white = dried out.

² = for pool 3 there were two aggregations, the second captured after the refilling of the pool on 21 Jan.

³ = assumes complete capture on pool surface; so 'escape' = where changes to pool conditions allow escape.

results of a series of continuous field observations of rafting aggregations of *Gomphicephalus hodgsoni* under natural conditions.

Methods

Research was carried out at meltwater pools in the vicinity of Granite Harbour, Victoria Land - the type locality for *G. hodgsoni* (Davidson & Broady 1996) from where



Fig. 1. Typical rafting aggregation. Note how extensive microscopic windblown detritus has been incorporated into the raft (body size = c. 1 mm).

samples were taken by the *Discovery* Expedition of 1901–04. Observations for this study were undertaken daily over a ten-day period during January 2009. Rafting aggregations were found in meltwater pools produced by the melting of ice and snow as a result of the warmer temperatures of the summer. The pools were produced by natural inclinations of topography and represented transient capture of free water depending on weather conditions (see Table I) - although not persistent, they would be expected to recur each summer given similar conditions. Five pools were identified within walking distance of the field camp and visited daily over the period. So as not to disturb the aggregations unnaturally, rafts were photographed daily and digital images used to count numbers of springtails and mites. At the end of the observation period, springtails and mites still remaining in pools were removed, checked for mortality, and counted to determine if escape had occurred. The status of each pool (wet, frozen, dry) was noted for each day. General observations were made to corroborate and/or augment previous descriptions of rafting. These included the size and composition of aggregations, their escape from surface capture, and survival at the end of the observation period. In addition to the pools visited daily, a c.1 km transect along the shoreline was walked, looking for evidence of dispersal to the marine environment either in terms of springtails floating in the tide cracks between sea ice and shore, or aerially deposited directly on to the sea ice. For safety reasons, the latter was confined to scanning sea ice which directly abutted the shore.



Fig. 2. Close-up of rafting aggregation highlighting moulting (coarse dash line circle), surfing on other springtails (solid line circle) and mite (fine dash line circle) (body size = *c.* 1 mm).

The results may be considered to be natural history observations that provide ecological context previously lacking in our understanding of rafting in Antarctic springtails. It is noted that no statistical comparisons were made between the pools because such comparisons, while potentially adding a quantitative veneer to observations

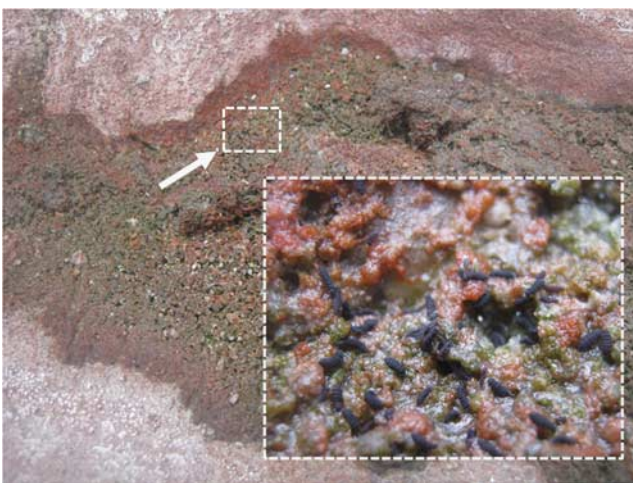


Fig. 3. Dried out pool with 'escaped' springtails released by the evaporation of the water (inset shows close-up of springtails; small white arrow and box indicates area magnified) (body size = *c.* 1 mm).



Fig. 4. Springtail frozen into the ice of a pool (body size = *c.* 1 mm).

would, in essence, disguise the stochasticity and individuality of each rafting situation as it was observed. Indeed, any statistical differences identified would be invalidated by the fact that under natural conditions every variable - from source of springtails; to number of springtails; to pool size, topography, aspect and location - is unique.

Results and discussion

Rafting aggregations of *G. hodgsoni* are comprised of springtails, occasional mites (*Stereotydeus mollis*), microscopic windblown detritus, and moult exuviae (Table I, Figs 1 & 2). While Strong (1967) has shown the survival of mites after extended seawater immersion in the maritime Antarctic, it is noted that this represents the first recorded observation (although certainly not the first occurrence!) of rafting mites to my knowledge. It should be emphasized that the springtails, in particular, are not entirely passive on the water film. The provision of rafting materials such as moult exuviae and microscopic windblown detritus allows them to move around and considerably extends their survival ability. Also, in an aggregational context, these water traps stimulate intraspecific interactions geared toward improving survival. Moulting, for example, is cued by water availability as well as aggregation (Hopkin 1997). Other springtails may also be used as rafts, and the sight of springtails surfing on other

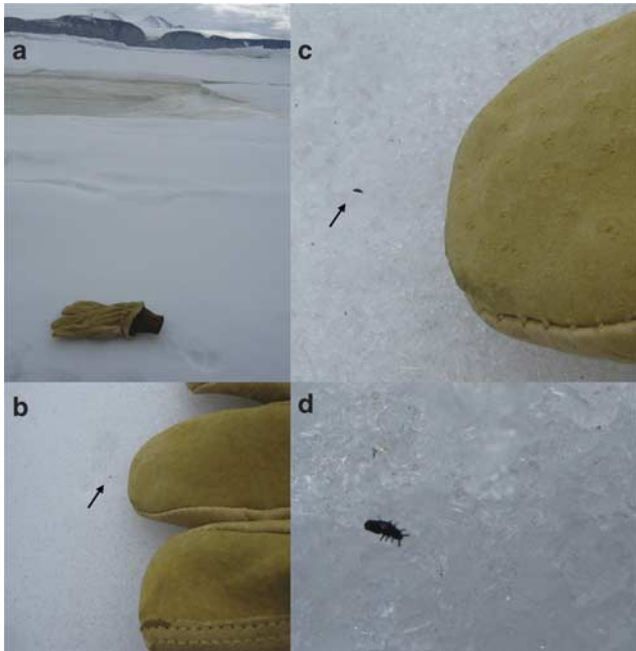


Fig. 5. Springtail aerielly deposited on the sea ice; glove shown for scale, with successive close-ups (a–d) showing the location of the springtail (body size = 1 mm).

springtails is a common observation in aggregations (Fig. 2). There are three main windows of escape for trapped animals: opportunistic drifting of aggregations or individuals to the edge of the pool, evaporation of the pool (e.g. Fig. 3) or freezing of the pool (Hawes *et al.* 2007). However, observations suggest that the last may be rarer, with animals as likely (or more likely) to be trapped by the freezing of surface water (e.g. Fig. 4).

Table I summarizes the results of the time series observations. The most obvious variable is the hydric status of the pools - water-filled, frozen or dried out - which in addition to being related to general meteorological conditions, may vary from pool to pool depending on their aspect and degree of exposure. Thus, for example, pool 1 was open and north facing and was the only pool to retain its status throughout the observation period, while pool 5, although also north facing, was closely surrounded by boulders, so that when it froze, it remained so for days at a time. In general, escape from water capture is shown to be a potentially regular (but localized) occurrence in this context, with the status of the temporary pools frequently changing. However, for those pools where no such change occurs, escape is unlikely and the probability of survival low.

One of the most pressing questions raised by previous experimental work on rafting by Hawes *et al.* (2008) was the extent to which they successfully translate into the field ecology of springtails under Antarctic conditions. Thus although the *potential* for survival, reproduction, and, therefore, dispersal, has been demonstrated; the extent to which such projections are realistic merits further

consideration. The conditions of continental Antarctica are considerably more challenging than those of maritime Antarctica, so the case of *G. hodgsoni* is different to that of *Cryptopygus antarcticus* (see Hawes *et al.* 2008). In particular, *G. hodgsoni* experiences lower temperatures and reduced water availability (flushes of vegetation which are not uncommon on the Antarctic Peninsula are extremely rare and through most of its range, it occupies what are effectively polar desert landscapes). Aggregations, likewise, at least in terms of rafting - compare for example typical raft aggregations shown here and in Hawes *et al.* (2008) - are considerably smaller and probably generally reflective of smaller populations. Certainly, for example, some variation in tolerance and motility might be expected between families like Hypogastruridae (*G. hodgsoni*) and Isotomidae (*C. antarcticus*) as a result of body-shape and the degree of furca reduction. However, although the observations described here concern one species, the broad findings remain relevant to springtails throughout Antarctica. Indeed, unpublished pilot experiments (TCH) have found short-term survival of rafting in *Friesea grisea* (Schäffer) in the maritime Antarctic and *Gressittacantha terranova* Wise at Terra Nova Bay. While Pryor (1962) noted the presence of *Isotoma klovstadi* Carpenter floating on temporary pools produced by meltwater runoff. It is also worth noting, that Coulson *et al.* (2002) demonstrated the potential for oceanic rafting in a range of representative species (including isotomids and hypogastrurids) in the high Arctic.

In addition to the springtails observed in meltwater pools, examinations of the tidewater cracks of seawater that existed between the land and sea ice, revealed a number of springtails floating on the surface. Although there was nowhere for them to go - the sea ice blocked further carriage elsewhere and the area is enclosed within a bay - the potential for marine dispersal was evident. Inspection of the sea ice surface along the same observational transect - looking at sea ice which directly touched the land (without tidewater cracks in between) revealed two instances of springtails that had been aerielly deposited on to the sea ice from the land (Fig. 5). It has been previously noted that aerial dispersal of Antarctic springtails may also be an important interacting factor with water capture (Hawes *et al.* 2007). Of course, realistically, even for springtails that are less isolated - such as in the maritime Antarctica - the word to emphasize is 'potential'. This potentiality is a product of numerous factors, many of them stochastic (such as topography, distance to suitable habitat etc) - although it does increase with time. For the moment, it must be noted that although none of the observations presented here represent movements of significance to populations, they do contribute to our understanding and characterization of the factors that make such events so stochastic.

The present study also emphasizes the extent to which water capture is a class of environmental interaction in its own right for Antarctic springtails. Even our understanding of its

physiological implications remains incomplete. In this context, it is worth noting that the observations of rafting aggregations also suggested an additional previously unrecognized (Hawes *et al.* 2008) influence on the viability of rafting springtails: the recognition that the physiological challenge of survival may not only be determined by responses to water and temperature, but also by continuous direct exposure to sunlight with the concomitant danger of extended exposure to ultraviolet radiation (UV-R). A separate paper (Hawes *et al.* unpublished data) will examine the potential for UV-R damage in *G. hodgsoni*; but for now it is sufficient to note, that capture on the water surface effectively prevents access to mitigating cover, so that springtails on the water surface may be directly exposed for days at a time to 24 h UV-R. Given the variability of Antarctic weather, such exposure may be intermittent and unpredictable, but it is nonetheless recurrent and unavoidable for such captured springtails.

The significance of rafting to springtails, to dispersal in particular, has been previously highlighted (Hawes *et al.* 2008). Continuous field observations of rafting in *G. hodgsoni* agree with these findings but also show the ways in which the size and composition of rafts are dependent on (or perhaps reflective of) the local faunal assemblage. They also emphasize two additional ecological parameters - the stochasticity of the raft environment and potential for extended exposure to UV-R. Thus, although water capture is an accidental phenomenon, it is a recurring and widespread component of springtail ecology in Antarctica and, irrespective of its implications to dispersal, should be considered as a common and distinct class of ecological interaction with the Antarctic abiotic environment.

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