Body Water Content and Desiccation Resistance in Some Arthropods from Subantarctic South Georgia

R.A. Ring[1], W. Block[2], L. Sømme[3] and M.R. Worland[2]

[1]Department of Biology, University of Victoria, Victoria, BC V8W 2Y2, Canada
[2]British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 OET, UK
[3]Department of Biology, Division of Zoology, University of Oslo, P.O. Box 1050, Blindern, N-0316 Oslo 3, Norway

Summary. The body water content and resistance to desiccation were studied in two perimylopid beetles, *Perimylops antarcticus* and *Hydromedion sparsutum*, a chironomid midge, *Eretmoptera murphyi*, and two spiders, *Notiomaso australis* and *Perimaso grytvikensis* from the subantarctic island of South Georgia. Comparisons were made between different species, different life stages and, where possible, between a high and a low altitude. *Perimylops* is abundant at higher elevations and in more exposed habitats (fellfields). This may be accounted for by its feeding behaviour, high body water content (relative to *Hydromedion*) and low rate of water loss under desiccating conditions, particularly in the larval stages. *Hydromedion* is more abundant at the lower collection site. It is a more robust beetle than *Perimylops* and its feeding preference is for plants such as grasses and *Acaena*. Nevertheless, at the upper site adult *Hydromedion* are able to withstand desiccation to an even greater degree than *Perimylops*. Water loss rates for both beetles are significantly higher than those reported for related beetles from arid and semi-arid regions. The ability to regulate water loss is not as apparent in the polar perimylopids *Perimylops* and *Hydromedion* as in related species from other xeric habitats. These two species, in fact, resemble more closely carabid beetles in xeric habitats in rates of water loss under controlled conditions. Increased temperatures elevate the rate of water loss significantly. South Georgia spiders have a similar rate of water loss to several species of spiders that have been studied in the temperate zone. *Eretmoptera* is restricted to moist conditions and cannot survive desiccating conditions even for brief periods. It has the highest body water content (78% of fresh weight) of all of the South Georgian arthropods studied. Among the spiders, sufficient information could be obtained only for *Notiomaso*. This species is much less resistant to desiccation than the perimylopid beetles, and it has a relatively high body water content. It is quite numerous in the lower, warmer habitats where its insect prey is more abundant and diverse.

Introduction

The subantarctic island of South Georgia (54°S, 37°W) has a limited insect fauna (Gressitt 1970; Block 1988) which is adapted to a relatively severe environment. The climate of the maritime regions of the island is characterized by relatively mild winters (mean minimum for August = −15°C) and short, cool summers (Smith and Walton 1975). Such environments impose many constraints upon insects in terms of their behaviour, ecology and physiology. These constraints, in conjunction with the geographical isolation of South Georgia, are of considerable importance in accounting for the low level of species diversity in this region (Block 1984). Thus the species that inhabit such conditions are likely to exhibit profound adaptations to the cool, and often desiccating, conditions of an austral summer. Resistance to desiccation varies greatly among species from different habitats (Edney 1977). Leinaas and Sømme (1984) suggest that summer drought is an important limiting factor in lichen-dwelling insects on rocks, requiring special adaptations in order to survive. In addition, dehydration plays an integral part in the freezing avoidance in overwintering insects (Ring 1980; Storey and Storey 1988). Although dehydration is a common feature in hibernating insects, Cannon and Block (1988) point out that the relative water content can remain constant during the dehydration process through tissue weight loss and metabolic adjustments.

The purpose of this study, therefore, was to determine the body water content and resistance to desiccation among a variety of arthropods living in the Husvik area on the north-east coast of South Georgia. The species were selected for their altitudinal habitat range as well as their population density and availability. Although the ice-free mountains surrounding the Husvik area rise steeply to around 800 m above sea level (a.s.l.), insects and spiders are rarely found above 300 m altitude. Such a short altitudinal gradient allows a comparative approach to the study of the physiology of a few selected species. Two species of spiders, *Notiomaso australis* Banks and *Perimaso grytvikensis* Tambs-Lyche, a larval chironomid midge, *Eretmoptera*

murphyi Schaeffer, together with the adults and larvae of the perimylopid beetles *Perimylops antarcticus* Müller and *Hydromedion sparsutum* (Müller) were tested for their tolerance to dehydration. The five taxa will hence-forth be referred to by their generic names. An upper study site was established at just under 300 m a.s.l. in alpine fellfield with very sparse vegetation (scattered mosses and lichens) and a lowland site in a *Festuca* grassland community at c. 20 m a.s.l. A microclimate monitoring station was operated for 2 months at each site, since this study formed part of a larger investigation on the adaptations of terrestrial arthropods to the subantarctic environment (Block et al. 1988).

Materials and Methods

The study was carried out at Husvik between 20 January and 23 February, 1988, a time period which encompasses mid- to late summer in South Georgia. Mean air temperatures for the warmest months (January, February, and March) were 4.6°, 5.3° and 4.5°C respectively and for the coldest months (June, July, and August) only −1.1°, −1.3° and −1.5°C (Smith and Walton 1975). However, snow cover was more or less permanent from May to October, with mean monthly wind velocities ranging from 14.1 to 17.6 km/h throughout the year. Total monthly precipitation for January and February (the study period) was 102 and 124 mm respectively (data from a meteorological station at King Edward Point, 17 km SE of Husvik) (Smith and Walton 1975; Headland 1984).

Collections of arthropods were made at regular intervals from both a lowland (lower) and high fellfield (upper) site for all experimental work. Only the adults and larvae of *Perimylops* and *Hydromedion* at both sites, the larvae of *Eretmoptera* at the upper site, and the adults and sub-adults (differentiation among the late juvenile instars could not be made) of the spiders *Notiomaso* and *Perimaso* at the lower site were collected in sufficient numbers to undertake the experiments.

Specimens were placed individually in glass vials within humidity chambers in which the relative humidity was maintained at approx. 5% by the use of silica gel. The relative humidity was monitored by both a hair hygrometer and a Vaisala humidity probe. The chambers were then placed within an insulated cabinet where the temperature was controlled at $15° \pm 1°C$, simulating temperature conditions on a warm summer day (Worland et al., in press). Two preliminary experiments were undertaken at 22°C. Individual specimens were weighed at regular intervals (8–12 h) to determine rate of water loss, and this was continued until the last specimen of the sample was either moribund or dead, thus allowing calculation of the times to 50% mortality (LT_{50}) and 100% mortality (LT_{100}) of the sample population. Body water content was determined by drying to constant weight in an oven regulated at 60°C. All weighings were carried out on a battery-operated Cahn electrobalance (sensitivity $\pm 1 \mu g$). Since data expressed as percentages are not normally distributed, each percentage was first arcsine transformed (Zar 1984).

In order to summarize the maximum weight loss sustained by individuals during these desiccation experiments, we defined maximum weight loss as the percent of the initial fresh weight lost up to, and including, the measurement immediately prior to that at which the individual was either moribund or dead. Individuals that were moribund or dead at the first measurement after the experiment was initiated were not included. We calculated the mean and standard deviation of maximum weight loss for each stage of each species in each of the fourteen experiments. Experiments were subsequently pooled to permit comparisons between sites, stages and species. In a similar fashion, we calculated the mean and standard deviation of the time to maximum weight loss. Rate of weight loss (percent of fresh weight loss divided by time (h) to maximum weight loss) was calculated for each individual and, as above, we calculated the mean and standard deviation. The latter two measures (time to maximum weight loss and rate of weight loss) should be treated with caution because the interval between measurement times was variable.

We compared two means using Student's t-test for independent samples. Prior to analysis, each value of maximum weight loss (percent of fresh weight loss) was arcsine transformed. Three or more means were compared simultaneously using analysis of variance, and multiple comparisons of each pair of means were conducted using the Student-Newman-Keuls procedure.

During the earliest of these experiments it was noted that in certain individuals, especially the beetle larvae, defaecation often occurred during the initial phase of exposure to desiccating conditions. Being cognizant of the fact that faeces can form an important source of water loss (Salt 1961; Cannon and Block 1988), the extent to which faeces contributed to body weight loss was calculated, and since this weight loss was minimal (<0.5%) it was excluded from further calculations.

Results

Body Water Content

Mean body water content (WC) for the different species and life stages are presented in Table 1.

Individuals of *Perimylops* exhibited considerable variation in mean body water content ranging from 70% −83% of fresh weight. Both larvae and adults had higher mean body water content at the lower site than at the upper site, but only larval water content differed significantly in terms of the elevation of the collection site. *Perimylops* from both the upper and lower sites contained a higher proportion of water as larvae than as adults, but the observed differences were not significant. *Hydromedion* adults were more homogeneous than *Perimylops* with respect to body water content throughout the trial period although the trend in WC loss was similar. The adults of both species at the upper site had lower WC than those at

Table 1. Summary of mean water content (as % of fresh weight). *indicates a significant difference between means ($P < 0.05$, t-test). Each entry is mean $\pm$ SD (n)

	Larva		Adult	
	Lower collection site	Upper collection site	Lower collection site	Upper collection site
Perimylops	$77.90 \pm 2.48(8)$ *	$74.49 \pm 3.75(11)$	$75.04 \pm 4.98(18)$	$73.47 \pm 4.04(45)$
Hydromedion	$73.58 \pm 3.20(12)$	—	$71.55 \pm 3.82(41)$	$68.61 \pm 2.90(6)$
Eretmoptera	—	$77.97 \pm 2.46(9)$	—	—
Notiomaso	—	—	$76.32 \pm 3.16(19)$ *	$71.48 \pm 4.00(7)$
Perimaso	—	—	$77.64 \pm 5.20(3)$	—

the lower site, and the adults at the lower site had lower WC than larvae from the same habitat, although the differences were *not* significant in either case. In the spider *Notiomaso*, individuals from the lower site contained a higher proportion of water than those from the upper site and the difference was significant.

In a comparison of all species by ANOVA, *Hydromedion* had significantly lower percent water content than the other four species; *Perimylops* was significantly lower than *Eretmoptera*; but all other comparisons between species did not show any significant differences. For sites and sampling periods combined, *Perimylops* contained a higher proportion of water than *Hydromedion*. The difference was significant in comparisons of (a) adults only and (b) adults and larvae combined, but not in comparisons of (c) larvae only.

Adults from the upper site showed a significant decrease in WC during the sampling period from 20 January to 23 February (Table 2).

Desiccation Resistance

Table 3 summarizes the results of the fourteen desiccation experiments conducted between 24 January and 19 February, 1988. *Perimylops* showed little evidence of differences in weight loss between adults from lower and upper sites (Table 4, Fig. 1). However, larvae of this species from the lower site appeared to lose water at a faster rate than those at the upper site, and, consequently, died earlier in the experiments. For lower and upper sites combined, larvae were able to sustain significantly greater weight loss (42% fresh weight) prior to death than adults (34% fresh weight). Larval *Perimylops* also lost water at a rate three times slower than adults, resulting in longer survival times for larvae compared with adults (Fig. 1).

Table 2. Differences in percent body water content between sampling dates

A *Perimylops* — adults, upper site

	20 Jan 88	28 Jan 88	14 Feb 88	23 Feb 88
n	6	15	12	12
$\bar{x}$	73.98a, b	76.32a	72.35b	70.77b
SD	2.91	3.56	1.59	4.71

$(F = 6.31, df = 3, 41, P < 0.01)$
$* = 0.21\%/day$

B *Hydromedion* — adults, lower site

	25 Jan 88	9 Feb 88	19 Feb 88
n	11	6	24
$\bar{x}$	73.53a	72.13a	70.49a
SD	2.50	1.73	4.35

$(F = 267, df = 2, 38, P > 0.05)$
$* = 0.12\%/day$

In each series, means followed by the same letter are NOT significantly different $(P > 0.05$, Student Newman-Keuls multiple comparisons)
$* =$ rate of weight loss over the sampling period

In *Hydromedion* adults, the results of experiments with individuals from lower versus upper sites were not significantly different (Table 5, Fig. 1). In comparisons of larval versus adult *Hydromedion* (upper and lower sites combined), no significant differences were found in the amount or rate of water loss prior to death (Table 5). On the other hand, adult and subadult *Notiomaso* from the lower site were able to withstand a higher water loss for longer periods than those from the upper site (Table 6). It is interesting to note that the spiders collected at the upper site had a higher proportion of larger individuals (weight range from 1.25–3.03 mg) than those collected at the lower site (weight range from 0.72–1.75 mg).

In a comparison of all species, the desiccation resistance of the spider *Notiomaso* was well below that of both coleopterans, *Perimylops* and *Hydromedion* (Fig. 1). *Notiomaso* lost water relatively quickly and approached death faster than the other two species. More formal comparisons between *Perimylops* and *Hydromedion* (Table 7) revealed that, as larvae, *Perimylops* was able to withstand desiccating conditions for longer periods than *Hydromedion*, possibly due to their slightly lower rate of water
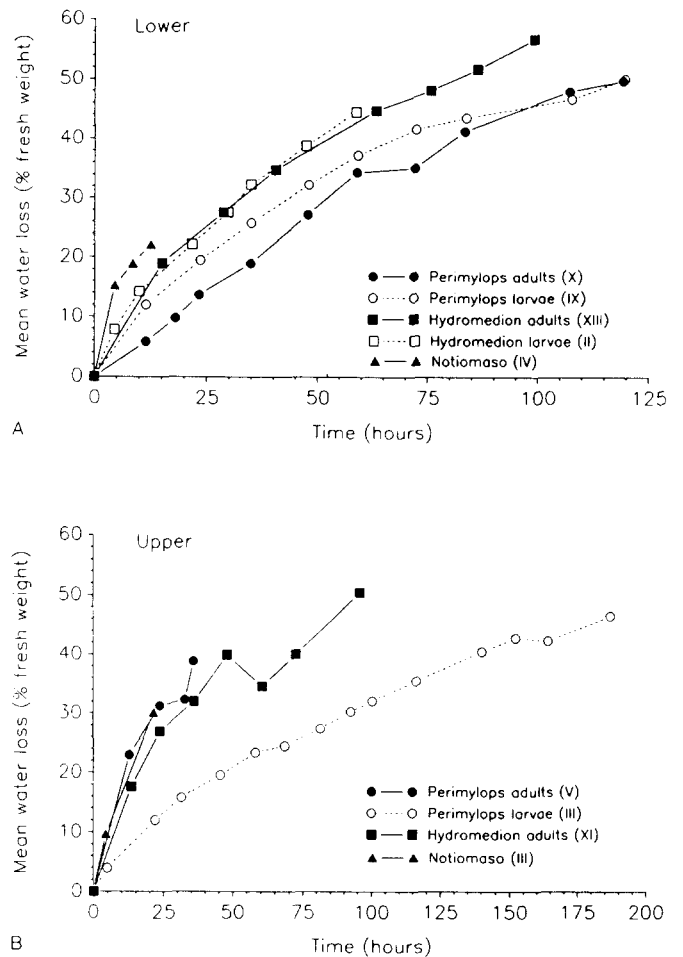

Fig. 1. Desiccation curves for three species of South Georgian arthropods from lower (**A**) and upper (**B**) sites. Points are mean water loss for living individuals only, and experiment number (see Table 3) in Roman numerals is in parentheses. All experiments were conducted at 15°C and 5% RH; refer to Table 3 for starting sample sizes.

Table 3. The results of fourteen desiccation experiments on four species of South Georgian arthropods

Expt.		Stage	Site	Date	Conditions (°C/%RH)	n	Max weight loss (% FW)	Time to max weight loss (h)	Rate of weight loss (%FW/h)	Time to 50% mortality (h:min)	Time to 100% mortality (h:min)
I	Perimylops	Adult	Upper	24.1.88	22°/5%	6	28.84± 5.51 (21.09 − 36.91)	7.25± 0.00 (7.25 − 7.25)	3.98±0.76 (2.91 − 5.09)	—	<17:40
	Hydromedion	Adult	Upper	24.1.88	22°/5%	3	28.73± 0.93 (27.73±29.57)	7.25± 0.00 (7.25 − 7.25)	3.96±0.13 (3.82 − 4.08)	7:15	<17:40
II	Perimylops	Adult	Lower	26.1.88	15°/5%	5	26.66± 6.05 (17.83 − 31.64)	24.43± 8.78 (9.92 − 30.00)	1.18±0.34 (1.00 − 1.80)	30:00	<47:15
	Hydromedion	Adult	Lower	26.1.88	15°/5%	2	23.19± 5.26 (19.47 − 26.91)	9.92± 0.00 (9.92 − 9.92)	2.34±0.53 (1.96 − 2.71)	9:55	<22:15
	Hydromedion	Larva	Lower	26.1.88	15°/5%	11	33.11±11.92 (12.65 − 47.43)	39.21± 20.03 (10.00 − 58.92)	1.01±0.42 (0.73 − 2.05)	47:25+	<72:00
III	Perimylops	Larva	Upper	28.1.88	15°/5%	11	41.99± 4.04 (34.47 − 46.30)	41.59± 37.74 (45.50 − 187.50)	0.33±0.15 (0.25 − 0.76)	152:30	<195:00
	Notiomaso	Adult	Upper	28.1.88	15°/5%	8	9.65± 3.02 (5.90 − 14.80)	4.50± 0.00 (4.50 − 4.50)	2.14±0.67 (1.31 − 3.23)	—	<21:30
IV	Notiomaso	Adult	Lower	30.1.88	15°/5%	8	20.47± 4.00 (15.28 − 25.88)	8.00± 3.34 (4.50 − 12.50)	2.92±1.08 (1.46 − 4.23)	8:30+	<23:30
V	Perimylops	Adult	Upper	28.1.88	15°/5%	11	32.02± 6.23 (18.95 − 38.89)	20.93± 8.98 (12.75 − 35.75)	1.72±0.63 (1.08 − 2.97)	23:45+	<47:45
VI	Eretmoptera	Larva	Upper	4.2.88	15°/5%	9	—	—	—	—	—
VII	Notiomaso	Adult	Lower	30.1.88	15°/5%	5	20.02± 5.02 (14.43 − 27.59)	17.00± 4.11 (12.50 − 20.00)	1.25±0.55 (0.84 − 2.21)	20:00+	<37:30
VIII	Hydromedion	Adult	Lower	9.2.88	15°/5%	7	32.60± 7.08 (22.54 − 45.19)	27.21± 28.78 (11.50 − 84.50)	2.00±0.97 (0.53 − 2.95)	—	<108:30
IX	Perimylops	Larva	Lower	9.2.88	15°/5%	8	43.14± 9.31 (21.43 − 50.99)	73.41± 30.57 (11.50 − 120.00)	0.74±0.46 (0.42 − 1.86)	84:00	<130:00
X	Perimylops	Adult	Lower	9.2.88	15°/5%	10	39.79±11.30 (21.76 − 51.58)	55.80± 42.34 (11.50 − 119.50)	1.34±1.03 (0.41 − 3.29)	<107:30	<129:30
XI	Hydromedion	Adult	Upper	15.2.88	15°/5%	9	41.78± 9.58 (23.32 − 53.91)	49.44± 29.49 (13.50 − 96.00)	1.06±0.43 (0.49 − 1.73)	<60:30	<65:49
XII	Perimylops	Adult	Upper	14.2.88	15°/5%	10	32.75± 9.80 (19.70 − 46.79)	36.65± 39.00 (11.50±108.00)	1.75±1.11 (0.39 − 3.60)	<37:00	<119:30
XIII	Hydromedion	Adult	Lower	19.2.88	15°/5%	6	47.31±10.86 (26.68 − 56.53)	65.25± 32.30 (15.00 − 99.50)	0.91±0.47 (0.56 − 1.78)	<76:00	<111:00
XIV	Hydromedion	Adult	Lower	19.2.88	10°/5%	7	32.44± 9.02 (24.26 − 46.41)	20.22± 17.76 (13.50 − 60.50)	2.02±0.74 (0.77 − 3.23)	<25:00	<71:00

Table 4. Summary of desiccation experiments with Perimylops antarcticus. Values are mean±SD. NS $P > 0.05$; *$P < 0.05$; ***$P < 0.001$

	Larva (n = 19)		Adult (n = 36)			
	Lower site (n = 8)	Upper site (n = 11)	Lower site (n = 15)		Upper site (n = 21)	
Max weight loss (% FW)	43.14± 9.31	NS x̄ 42.47± 6.57	41.99± 4.04 ***	35.41±11.55	NS x̄ 33.63± 9.57	32.37± 7.92
Time to max weight loss (h)	73.47±30.57	*** x̄ 112.91±48.47	141.59±37.74 ***	45.34±37.53	NS x̄ 35.47±32.96	28.42±28.01
Rate of weight loss (% FW/h)	0.74± 0.46	* x̄ 0.50± 0.37	0.32± 0.15 ***	1.29± 0.85	NS x̄ 1.55±0.88	1.73± 0.87
Time to 50% mortality (h:min)	84:00		152:30+	<68:30		30:20
Time to 100% mortality (h:min)	<130:00		<195:00	<83:20		<83:40

Table 5. Summary of desiccation experiments with *Hydromedion sparsutum*. Values are mean ± SD. NS $P>0.05$

	Larva (n = 11)			Adult (n = 24)		
	Lower site (n = 11)	Upper site —		Lower site (n = 15)		Upper site (n = 9)
Max weight loss (% FW)	33.11 ± 11.92 33.11 ± 11.92	—	NS	37.22 ± 12.17 $\bar{x}$ 38.94 ± 11.27	NS	41.78 ± 9.58
Time to max weight loss (h)	39.21 ± 20.03 39.21 ± 20.03	—	NS	40.12 ± 34.81 $\bar{x}$ 43.62 ± 32.58	NS	49.44 ± 29.49
Rate of weight loss (% FW/h)	1.01 ± 0.42 1.01 ± 0.42	—	NS	1.61 ± 9.31 $\bar{x}$ 1.40 ± 0.82	NS	1.06 ± 0.43
Time to 50% mortality (h:min)	47:25 +			<43:00		<60:30
Time to 100% mortality (h:min)	<72:00			<80:35		<65:49

Table 6. Summary of desiccation experiments with *Notiomaso australis*. Values are mean ± SD. NS $P>0.05$; ** $P<0.01$; *** $P<0.001$

	Lower site (n = 13)		Upper site (n = 8)
Max weight loss (% FW)	20.30 ± 4.22 $\bar{x}$ 16.24 ± 6.48	***	9.65 ± 3.02
Time to max weight loss (h)	11.46 ± 5.74 $\bar{x}$ 8.81 ± 5.56	**	4.50 ± 0.00
Rate of weight loss (% FW/h)	2.28 ± 1.22 $\bar{x}$ 2.23 ± 1.03	NS	2.14 ± 0.67
Time to 50% mortality (h:min)	14:15 +		—
Time to 100% mortality (h:min)	<30:30		<21:30

loss. For adult beetles, the trend was unclear: at the lower site differences between the two species were not significant, but at the upper site, adult *Perimylops* was able to withstand significantly less water loss and lost water at a faster rate than adult *Hydromedion*. This result is the opposite of that obtained for the larval stages.

The adults of both *Perimylops* and *Hydromedion* from the upper site lost weight more rapidly when tested at 22° than at 15°C (Table 8). In addition, the time prior to death was shorter at the higher temperature. Differences in the amount of water lost or the rate of weight loss between

adult *Hydromedion* from the lower site at 10° versus 15°C were not significant. *Eretmoptera* larvae, collected only from the alpine fellfield, died within 6 h of being exposed to the desiccating conditions (Table 3, Experiment VI), and are thus not included in these comparative tests.

Figure 2 illustrates the relationship between weight loss and body mass for five individual arthropods, all of which were collected at the lower site and maintained at 15°C and 5% RH. These represent the results from the longest-surviving individual in each species, and it can be seen that *Hydromedion* adults, which have the highest body weights, have the lowest rates of weight-loss, whereas
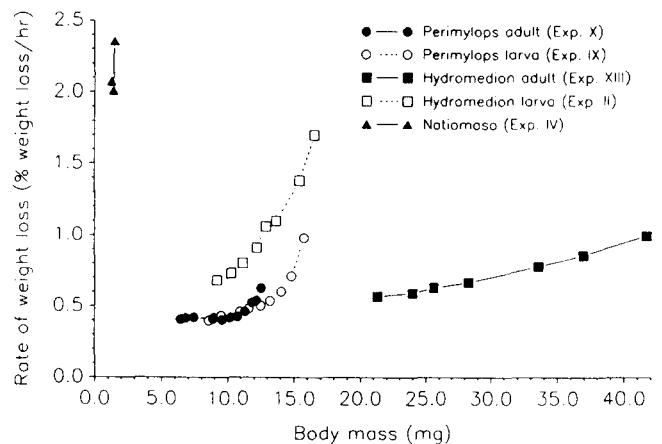
Fig. 2. Relationship between rate of weight loss and body mass for five arthropods from South Georgia (lower site). Rate of water loss is calculated from the start of each experiment, all of which were conducted at 15°C and 5% RH. Only the longest-surviving individual in each species is shown. Roman numerals in parentheses after each species refers to number of experiment in Table 3

Table 7. Comparison of (a) max weight loss (% FW), (b) time to max weight loss (h) and (c) rate of weight loss (% FW/h) for the two beetle species. NS $P > 0.05$; * $P < 0.05$; ** $P < 0.01$. Each entry is mean $\pm$ SD (n)

			Perimylops antarcticus			*Hydromedion sparsutum*
Larva	Lower site	(a)	43.14 ± 9.31	(8)	NS	33.11 ± 11.92 (11)
		(b)	73.47 ± 30.57	(8)	**	39.21 ± 20.03 (11)
		(c)	0.74 ± 0.46	(8)	NS	1.01 ± 0.42 (11)
	Upper site	(a)	41.99 ± 4.04	(11)		—
		(b)	141.59 ± 37.74	(11)		—
		(c)	0.32 ± 0.15	(11)		—
Adult	Lower site	(a)	35.41 ± 11.55	(15)	NS	37.22 ± 12.17 (15)
		(b)	45.34 ± 37.53	(15)	NS	40.12 ± 34.81 (15)
		(c)	1.29 ± 0.85	(15)	NS	1.61 ± 0.31 (15)
	Upper site	(a)	32.37 ± 7.92	(21)	*	41.78 ± 9.58 (9)
		(b)	28.42 ± 28.01	(21)	NS	49.44 ± 29.49 (9)
		(c)	1.72 ± 0.87	(21)	*	1.06 ± 0.43 (9)

Table 8. Comparisons of desiccation resistance of *Perimylops antarcticus* and *Hydromedion sparsutum* over three temperatures at 5% RH. NS $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). Each entry is mean $\pm$ SD (n)

Temperature		10°C		15°C		22°C
Perimylops adults upper site	Max weight loss (% FW)	—		32.36 ± 7.92 (21)	NS	28.84 ± 5.51 (6)
	Time to max weight loss (h)	—		28.42 ± 28.01 (21)	NS	7.25 ± 0.00 (6)
	Rate of weight loss (% FW/h)	—		1.73 ± 0.87 (21)	*	3.98 ± 0.76 (6)
Hydromedion adults lower site	Max weight loss (% FW)	32.44 ± 9.02 (7)	NS	37.22 ± 12.17 (15)		—
	Time to max weight loss (h)	20.22 ± 17.76 (7)	NS	40.12 ± 34.81 (15)		—
	Rate of weight loss (% FW/h)	2.02 ± 0.74 (7)	NS	1.61 ± 0.31 (15)		—
Hydromedion adults upper site	Max weight loss (% FW) max	—		41.78 ± 9.58 (9)	*	28.73 ± 0.93 (3)
	Time to max weight loss (h)	—		49.44 ± 29.49 (9)	**	7.25 + 0.00 (3)
	Rate of weight loss (% FW/h)	—		1.06 ± 0.43 (9)	***	3.96 ± 0.13 (3)

Notiomaso, by far the lowest in body weight of these experimental animals, had a very high rate of weight loss under these desiccating experimental conditions. The other three individuals (*Perimylops* adult and larva, *Hydromedion* larva) were very similar in body mass and in rate of weight loss.

Discussion

The two phytophagous perimylopid beetles, *Perimylops antarcticus* and *Hydromedion sparsutum* occupy a diversity of ecological habitats on South Georgia (Watt 1970; Block and Sømme 1983; Vogel 1985). Vogel (1985) considered them as the most important insects in the terrestrial ecosystem, since they consume fresh plant material which is then made available to the chain of decomposers in the

soil. At Husvik, South Georgia, continuous vegetation cover reaches to between 100–200 m a.s.l. At higher elevations the vegetation is sparse and patchily distributed, the main concentrations consisting of mosses growing along creeks and seepage areas of melt water from snowfields and glaciers. Most of the ground is covered by loose gravel, the stones of which are often covered by a layer of microphytes (lichen, algae and cyanobacteria). It is in this type of exposed habitat that *Perimylops* is more abundant than *Hydromedion*. Sømme et al. (1989) have shown that *Perimylops* adults and larvae feed preferentially on the moss, *Andreaea*, which is abundant at high altitudes in fellfields on South Georgia. Furthermore, the larvae tend to feed on the microphyte flora on the rock surfaces, and are thus frequently exposed to harsh conditions. The selective consumption of mosses and microphytes so typical of *Perimylops* suggests an adaptation to

these more extreme environments where other plant sources are scarce. The body water content and desiccation resistance of larval and adult *Perimylops* tend to confirm this type of adaptation, especially in the larval stage. The fractional body water content is basically higher in *Perimylops* than in *Hydromedion*, although it is lower in upper site populations of both species than in those from the lower site. In contrast, *Hydromedion* which has a wider habitat distribution in the lowlands, which lives in more moist environments and which feeds mainly on the more succulent grasses and *Acaena* spp. that grow there (Sømme et al. 1989), has the lowest proportion of water of all five species studied. However, the adult *Hydromedion* is structurally the most robust of the species studied (particularly in relation to its elytra) and has the thickest cuticle. Then come *Perimylops* adults in this respect, the two beetle larvae, *Eretmoptera* larvae, and, finally, the two species of spiders. The cuticle contains little water but has a significant mass, and may contribute a significant proportion of the observed differences in water content within and between species. The water contents of the soft, internal tissues may thus be more similar to each other than the raw data suggest. However, this does not explain the gradual reduction in water content throughout the season, a rate loss of 0.21% FW/day for *Perimylops* adults (upper site) and 0.12% FW/day for *Hydromedion* adults (lower site), these two sets of data being the only ones complete enough to make these calculations. It is likely that this gradual decline in water content is an important component in the overall series of physiological preparations necessary for successful overwintering.

When examined for resistance to desiccation, the larvae of *Perimylops* exhibited a greater ability to survive significant water loss, not only when compared with the adults of their own species, but also with both life stages of the closely related *Hydromedion*. This is consistent with the results of Sømme et al. (1989) as well as our own observations that the larvae of *Perimylops* can often be found in mid-summer on the surface of rocks feeding on mosses and lichens and, therefore, exposed to the desiccating conditions of both sun and wind. Occasionally, adult *Perimylops* were also found moving across the surface of snow banks at higher elevations, whereas *Hydromedion* were never collected in such exposed conditions. The only anomaly in our results was detected among *Hydromedion* adults at the upper site where they are able to withstand a significantly greater water loss and lost water at a slower rate under desiccating conditions than the adults of *Perimylops*. This cannot be explained at present.

The rates of water loss reported here for these perimylopid beetles are considerably higher than those reported from closely-related tenebrionid beetles from xeric habitats in East Africa (Zachariassen et al. 1987) and from high altitude beetles from Tenerife (Ottesen and Sømme 1987). In those studies, values of water loss rate ranged from 0.017% to 0.102% FW/h for East African beetles and 0.017% to 0.030% FW/h for beetles from Tenerife. South Georgian perimylopid beetles, which range in water loss rate from 0.32% to 1.73% FW/h depending on life stage and collection site, are more like carabid beetles from other severe habitats. In xeric, mesic and hygric habitats in

East Africa the range in carabids is from 0.058% to 1.500% FW/h (Zachariassen et al. 1987), and in the high altitude carabid from Tenerife the value is 1.63% FW/h (Ottesen and Sømme 1987). These two forementioned studies, however, were carried out at 21°C, whereas the present studies were conducted mainly at 15°C. From the trial carried out to determine the effect of temperature on the rate of water loss in *Perimylops* and *Hydromedion* (see Table 8) it is obvious that rates increase significantly between 15° and 22°C, from 1.73% to 3.98% FW/h in *Perimylops* beetles and from 1.06% to 3.96% FW/h in *Hydromedion* beetles, increases by factors of × 2.3 and × 3.7 respectively. Unlike the majority of beetles from xeric habitats where the rate of water loss is believed to be reduced by fusion of the elytra (Zachariassen et al. 1987), the South Georgian perimylopids, although flightless, do not have fused elytra. This may partially account for the higher water loss rates, although the differences in habitat type are probably of greater adaptive significance in this respect.

The overall perspective for these two species, then, is that *Perimylops* larvae which exploit the most exposed conditions, have high body water content and the greatest resistance to desiccation. These larvae sustain significantly larger amounts of weight loss prior to death, lose water at a slower rate and have greater survival under desiccating conditions than either the adults of their own species or the adults and larvae of *Hydromedion*. The larva may be the principal overwintering stage in *Perimylops* (Watt 1970), but adults also tend to have reduced body water content in the late summer, indicating that they too may overwinter (Block et al., unpublished). It is not known precisely how *Hydromedion* overwinters, but adults and larvae of several instars were collected with equal frequency during the final sampling period of our study (4–6 March, 1988). Watt (1970) recorded collecting adults in all months of the year except June and August, and larvae in all months except August, suggesting also that overwintering in this species occurs in both adult and larval life stages. This situation parallels that of an arctic beetle, *Pytho americanus*, which overwinters in both life stages (Ring and Tesar 1980).

Among the spiders, sufficient information could be obtained only from *Notiomaso* at both sites. *Perimaso* is much more rare than *Notiomaso* and restricted to habitats at lower altitudes around sea level. *Notiomaso* data support the conclusion that arthropods from lowland areas on South Georgia have more water in their tissues than those from higher sites. There is a paucity of information on the biology of antarctic spiders in general (Forster 1970), but from our results it appears that spiders have a more limited distribution than their insect prey. It is interesting to note, however, that the spiders collected from lower sites were able to withstand greater water loss for longer periods of time than those collected from the more exposed upper sites. This indicates that *Notiomaso* is better adapted to lower habitats where the diversity and abundance of invertebrate prey is greater. The desiccation tolerance of *Notiomaso* is much lower than that of *Perimylops* and *Hydromedion*, and under controlled, dehydrating conditions they lose water relatively quickly and reach 100% mortality faster than the coleopterans. Again, this

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tends to support the conclusion that this species of spider is better adapted to the moister, and slightly warmer conditions of the coastal zone of South Georgia. It should be remembered, however, that it may be due to its relatively large surface area to volume ratio that *Notiomaso* loses water at a faster rate than the other, larger species. Small animals may be better able to penetrate into protected microhabitats, and despite their higher water loss rates may live perfectly well side by side with larger animals that have a lower water loss rate. The *Notiomaso* results are also consistent with those obtained from several species of spiders from the temperate zone (Baehr and Eisenbeis 1985), and the body water contents are almost identical, being 71.5%–77.6% FW for spiders from South Georgia and 71.1%–77.8% FW for spiders from a forest near Tübingen, Federal Republic of Germany. In the temperate study it was noted that those species which occupy a more exposed habitat (upper soil and litter) show a higher degree of resistance to desiccation than the hygrophilous species which live in open wet meadows, in wet litter or in moss.

The specialized chironomid, *Eretmoptera murphyi*, is restricted to continuously moist conditions on South Georgia and the few specimens collected were subjected to a restricted number of experimental tests because of their rarity. The larvae were found only at the upper site and their body water content was the highest of all experimental animals, almost 78% of fresh weight. This compares with the larvae of *Perimylops* from the same site and with both species of spiders from the lower site. The fact that they cannot survive desiccating conditions for even 6 h indicates that they, like most chironomid larvae, are physiologically restricted to moist environments. That they are found only in fellfield mosses at the upper site may be due to competition with the only other South Georgian chironomid, *Parochlus steineni*, (Brundin 1970; Edwards and Usher 1985). Peckham (1971) reports that the larvae of another antarctic midge, *Belgica antarctica*, are similarly unable to withstand desiccation and have a body water content in the region of 79% fresh weight compared with 78% for *Eretmoptera*.

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References

Baehr B, Eisenbeis G (1985) Comparative investigations on the resistance to desiccation in Lycosidae, Hahniidae, Linyphiidae and Micryphantidae (Arachnida, Araneae). Zool JB (Syst) 112:225–234

Block W (1984) Terrestrial microbiology, invertebrates and ecosystems. In: Laws RM (ed) Antarctic ecology, vol 1. Academic Press, London, pp 163–236
Block W (1988) South Georgian entomology. Antenna 12:97–102
Block W, Sømme L (1983) Low temperature adaptations in beetles from the sub-Antarctic island of South Georgia. Polar Biol 2:109–114
Block W, Sømme L, Ring RA, Ottesen P, Worland MR (1988) Adaptations of arthropods to the sub-Antarctic environment. Br Antarct Surv Bull 81:65–67
Brundin L (1970) Diptera: Chironomidae of South Georgia. Pac Insects Monogr 23:276
Cannon RJC, Block W (1988) Cold tolerance of microarthropods. Biol Rev 63:23–27
Edney EB (1977) Water balance in land arthropods. Zoophysiol Ecol 9:282 pp Springer, Berlin
Edwards M, Usher MB (1985) The winged antarctic midge *Parochlus steineni* (Gerke) (Diptera: Chironomidae) in the South Shetland Islands. Biol J Linn Soc 26:83–93
Forster RR (1970) Araneae: Spiders of South Georgia. Pac Insects Monogr 23:31–42
Gressitt JL (1970) Subantarctic entomology, particularly of South Georgia and Heard Island. Pac Insects Monogr 23:1–374
Headland R (1984) The Island of South Georgia. Cambridge University Press, Cambridge, UK, 293 pp
Leinaas HP, Sømme L (1984) Adaptations in *Xenylla maritima* and *Anurophorus laricis* (Collembola) to lichen habitats on alpine rocks. Oikos 43:197–206
Ottesen P, Sømme L (1987) Adaptations to high altitudes in beetles from Tenerife. Vieraea 17:127–226
Peckham V (1971) Notes on the chironomid midge *Belgica antarctica* Jacobs at Anvers Island in the maritime antarctic. Pac Insects Monogr 25:145–166
Ring RA (1980) Insects and their cells. In: Low temperature preservation in medicine and biology. Ashwood-Smith, MJ, Farrant J (eds) Pitman Medical Publ Co, Tunbridge Wells (UK), pp 187–217
Ring RA, Tesar D (1980) Cold-hardiness of the arctic beetle, *Pytho americanus* Kirby (Coleoptera, Pythidae (Salpingidae)). J Insect Physiol 26:763–774
Salt RW (1961) Principles of insect cold hardiness. Annu Rev Entomol 6:55–74
Smith RI Lewis, Walton DWH (1975) South Georgia, subantarctic. Ecol Bull 20:399–423
Sømme L, Ring RA, Block W, Worland MR (1989) Feeding in two phytophagous beetles *Hydromedion sparsutum* and *Perimylops antarcticus* from South Georgia. Polar Biol 10: 141–143
Storey KB, Storey JM (1988) Freeze tolerance in animals. Physiol Rev 68:28–84
Vogel M (1985) The distribution and ecology of epigeic invertebrates on the subantarctic island of South Georgia. Spixiana 8:153–163
Watt JC (1970) Coleoptera: Perimylopidae of South Georgia. Pac Insects Monogr 23:243–253
Worland MR, Block W, Sømme L, Ring RA (in press) Microclimates in fellfield and grassland habitats at South Georgia. Antarct Sci
Zachariassen KE, Andersen J, Moloiy GMO, Kamau JMZ (1987) Transpiratory water loss and metabolism of beetles from arid areas in East Africa. Comp Biochem Physiol 86A:403–408
Zar JH (1984) Biostatistical analysis, 2nd edn. Prentice-Hall Inc Publ, Englewood Cliffs NH, 718 pp