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Antarctic Collembolans Use Chemical Signals to Promote Aggregation and Egg Laying

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Abstract Terrestrial arthropods that reside in Antarctica are exposed to considerable periods of environmental stress, thus factors that promote identification of favorable microhabitats are extremely important. In this study, we report the presence of chemical cues that induce oviposition and aggregation in two species of Antarctic collembolans, *Cryptopygus antarcticus* and *Friesea grisea*. Responses of the Collembola were enhanced by low temperatures but were not altered by humidity. One of the major physiological benefits derived from an aggregation was a substantial reduction in water loss rates. Although *F. grisea* and *C. antarcticus* were commonly found in cross-species aggregations, we found no evidence to suggest cross-species attraction. When individuals were exposed to areas previously occupied by groups of Collembola, more eggs were laid. Thus, chemicals released by the collembolans appear to induce both aggregation and oviposition in these Antarctic species.

Keywords Aggregation · oviposition · pheromone · Collembola · Antarctica

Introduction

During our work on the Antarctic Peninsula, we frequently encountered mixed aggregations, sometimes numbering over tens of thousands, of two Collembola species, *Cryptopygus antarcticus* and *Friesea grisea*. All developmental stages of both species, as well as their eggs (Schulte et al. 2008), were present in these aggregations. Although individuals of these species were also found in mats of algae

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and among moss, the largest numbers were found in large clusters on protected undersurfaces of rocks. Additionally, these distributions are at least partially influenced by moisture levels and locating protective niches for molting and egg laying (Hayward et al. 2004; Worland 2005; Worland et al. 2006; Sinclair et al. 2006). Semiochemicals are well known as aggregation pheromones in several temperate zone species of Collembola (e.g. Joose and Verhoef 1974; Verhoef et al. 1977; Christiansen et al. 1992; Wertheim et al. 2005), but it is unclear whether similar chemical signals operate in the extreme environment of Antarctica.

In this paper we ask several questions about the use of semiochemicals in these Antarctic Collembola. Are chemicals produced by Collembola used as aggregation pheromones? Are the chemicals species-specific or do they act across species? How do the low temperatures and relative humidities of Antarctica influence chemical recognition? How long does the signal persist? Do semiochemicals stimulate egg deposition? Our results indicate that aggregation pheromones as well as egg-laying stimulants contribute to the massive assemblies of Collembola and their eggs observed in Antarctica.

Materials and Methods

Collembola

Two species of Collembola, *C. antarcticus* and *F. grisea*, were collected on Humble Island, near Palmer Station, Anvers Island, Antarctica (64°45′ S, 64°04′ W) in January, 2007, by collecting organic debris in plastic bags. The debris was suspended in water, and large aggregations of collembolans subsequently formed on the water surface (Hawes et al. 2008). The two species were stored in separate 500 cc containers within sealed desiccators held at 100% RH, 4°C. The exact age of the specimens was not known, but all individuals used in experiments were of similar size (approximately 100 μg for *C. antarcticus* and 120 μg *F. grisea*). Collembola were handled with an aspirator throughout the experiments to prevent cuticular damage.

Attractant Preparation

Two different assays were prepared for each species. First, paper discs (Wescor, SS-033) were held with individual Collembola or groups of 10, 25, 50, 100, 200, and 500 individuals for 48 h at 100% RH, 4°C in complete darkness (0 h:24 h; L/D). Second, Collembola were washed three times with either acetone, hexane, methanol, or water to concentrations of 5, 10, 25, 50, 100, 200, and 500/ml. Additionally, groups of Collembola were washed with solvent a fourth time to verify that all surface components had been removed in the initial three-wash extraction procedure.

Attraction Assays

A standard four quadrant assay was used to test the responses of *C. antarcticus* and *F. grisea* (Arlian and Vyszenski-Moher 1995). Chemical (25 μl) applications or

Collembola-exposed discs were alternated with controls on 9 cm i.d. filter paper disks (Fisher, St. Louis, MO). Collembola were released individually and in groups of 25, 50 or 100 and allowed to move freely throughout the arena. The number of individuals within each quadrant was recorded at multiple intervals for 120 h. The procedure was replicated until 200 individuals or five replicates were analyzed for each treatment. Experiments were conducted at 100% RH in complete darkness, with the exception of 2 min exposures to light when location was noted. Experiments were also conducted with varying relative humidities at 4°C and at multiple temperatures at 100% RH.

Data was presented as the percentage attracted to the samples and, additionally, as the relative efficacy of attraction (REA; Yunker et al. 1992). The REA was calculated as follows:

$$\text{REA} = 100 \times [(\%\,\text{unattracted to control}) - (\%\,\text{unattracted to test})]/(\%\,\text{unattracted to control}).$$

The number of Collembola in the control quadrants from an average of all of the experiments served as the value for the "unattracted to control" used in the REA calculation. Chi-square (χ^2) was used to compare observed and expected (50%) values (Sokal and Rohlf 1981) at a significance of 0.05. Positive REA values indicated that an attractant was present, and a negative value was indicative of a repellant.

C. antarcticus was used to determine if aggregation pheromones or other factors had an effect on egg production. Individuals or groups of 10, 25, 50, 100, 200 or 500 Collembola were released onto 9 cm i.d. filter paper disks (Fisher) for pre-treatment. After 24 h at 100% RH in complete darkness, the Collembola were removed with an aspirator, and frass, eggs, exuviae, and spermatophores were removed from the paper discs with compressed air. Immediately after all debris had been removed, groups of 150 female Collembola were added and the eggs were counted after 120 h. The oviposition experiment was replicated ten times.

Determination of Water Loss Rates

When *C. antarcticus* are held at 0% RH, water loss is a function of exponential decay with no interference from water in the atmosphere (Wharton 1985; Benoit et al. 2005). This allows water loss to be determined according to,

$$m_t = m_0 e^{-kt}$$

or $\ln (m_t/m_0) = -kt$, where m_0 is the initial mass, m_t is the water mass at any time, t, and k is the percentage water lost between m_0 and m_t (Wharton 1985). The water mass is expressed as a difference between the initial and dry mass. The weighing interval for determining the water loss rate was 1 h, and the Collembola were held at 4°C. Dry mass was determined according to Hadley (1994): specimens were killed by freezing, then placed at 0.00a_v and 65°C until the mass was constant over a 2 day period. The electrobalance used in these experiments was a CAHN 25 (Ventron Co.; Cerritos, CA; precision of 0.2 μg SD and accuracy of ±6 μg at 1 mg). For experiments with groups of Collembola, a single individual, marked with a small spot of paint (Pactra, Van Nuys, CA) was used to determine the water requirements

and then subsequently returned to the cluster. Rates were derived from measurements of 30 individuals. Water loss rates of *F. grisea* were not determined due to the low numbers of this species that were available. Analysis of variance was used to compare the water loss rates.

Results

Formation of Aggregations

Mixed aggregations of *C. antarcticus* and *F. grisea* were commonly encountered in the field, sometimes with thousands of individuals present within a limited area. In our laboratory experiments, both species of Collembola moved freely throughout the bioassay arena. For the first 30 min, the Collembola moved quickly over the filter paper and moved deliberately toward treated areas with treated disks when they were in close proximity (1 cm) to the extracts or treated filter discs. Also, individuals stopped and changed directions more frequently in areas with paper disks previously exposed to other Collembola. Although individuals remained in the treated areas longer than in untreated areas, many were never fully arrested but continued to crawl between the treated and untreated areas. When treated-filter paper disks were placed 6 mm above the filter paper disk, attraction was still noted (data not shown), indicating that direct contact with the attractant was not needed. After 30 min, there were significantly more individuals present in treated areas than in the untreated quadrants (ANOVA, $P<0.05$; Fig. 1). Attraction was noted only for the first 12 h when *C. antarcticus* and *F. grisea* were tested in groups of ten or individually (Fig. 2a,b). The same result was noted when group size was increased to 25, 50 and 100 individuals (data not shown).

When different types of cuticular extracts were tested, methanol washes displayed the most attraction, followed by water and acetone, and hexane extracts showed no attraction. Thus, the remaining studies were conducted using methanol as the pheromone carrier. When concentration of the applied extract was low (one and ten individuals/ml), there was no significant increase in the number of Collembola in the treated quadrants (Table 1). Higher concentrations (extracts from 100, 500 or 1,000 individuals/ml) generated responses similar to those from conditioned areas (Table 1). As observed for the conditioned areas, the responses to extract-treated areas persisted for only 12 h. The presence of high, positive REAs for the conditioned areas and for high concentration extracts from the same species verified that both species of Collembola were attracted to individuals of their own species.

Effects of Humidity and Temperature on Aggregations

For both species, attraction occurred at temperatures as low as 0°C under a 100% RH regime (Figs. 3 and 4). The number of Collembola in the treated quadrants remained relatively constant from 0°C to approximately 10°C (Fig. 3a,b), then declined until 20°C, above which no preferences were observed. It is important to note that at high temperatures, mobility, measured as the number of Collembola moving between quadrants, greatly increased.

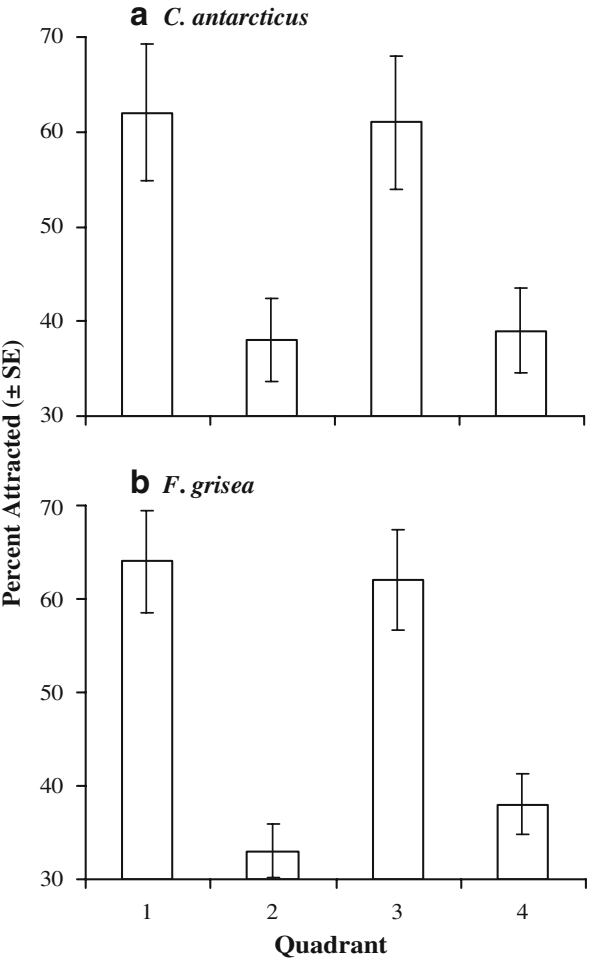

Fig. 1 Preference of *C. antarcticus* (**a**) and *F. grisea* (**b**) to areas with disks that were pre-conditioned with 100 Collembola for 24 h. Quadrants 1 and 3 were the conditioned areas, and the location of Collembola was measured after 30 min. Preference was noted for the conditioned area (χ^2, $P<0.05$). Naive Collembola were used for each experiment, and the values represent 20 replicates of ten individual each.

When aggregation was tested in response to humidity at 4°C, no differences were noted (Fig. 4a,b; ANOVA, $P>0.05$), with the exception that a higher level of attraction was noted for *C. antarcticus* at 100% RH (ANOVA; $P<0.05$). Thus, relative humidity appeared to have little, if any, influence on the ability of *C. antarcticus* and *F. grisea* to detect the aggregation pheromone, while low temperature promoted the aggregation response.

Cross Attraction between *C. antarcticus* and *F. grisea*

When the collembolans were tested against extracts with individuals of the other species, attraction was extremely low and was significant only for the attraction of *C. antarcticus* to *F. grisea* at high concentrations (500 Collembola/ml). The possibility existed that the attraction was an artifact of storing the Collembola during initial collection. To determine if this was the case, separate cohorts of *F. grisea* and *C.*

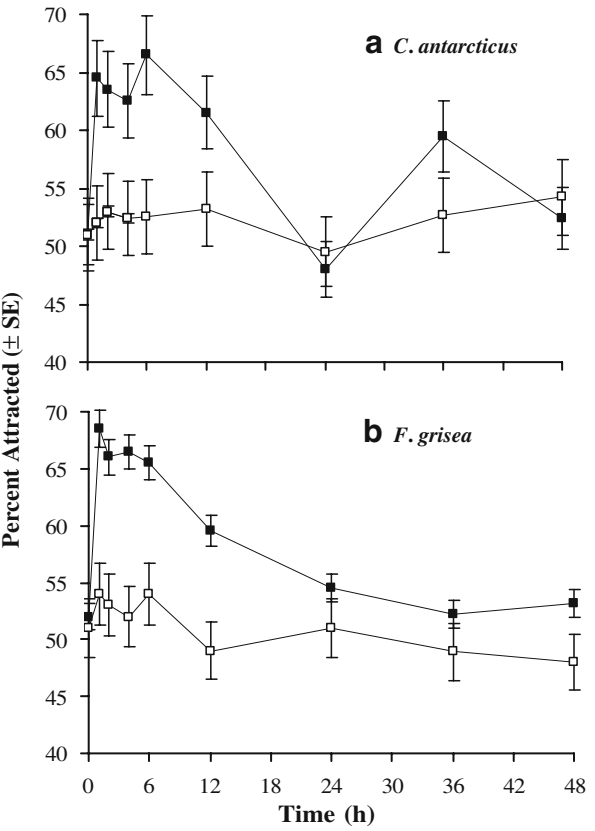

Fig. 2 Attraction as a function of duration of exposure of *C. antarcticus* (**a**) and *F. grisea* (**b**) to areas with disks that were pre-conditioned with 100 Collembola for 24 h. Values represent the percent (± SE) attracted when Collembola were held at 100% RH and measured at multiple intervals for 48 h. *Closed squares* represent the percent of Collembola attracted to quadrants previously exposed to Collembola, and *open squares* are the percent attracted to areas that had no previous Collembola exposure. Each value represents 20 replicates of ten individuals.

antarcticus were washed thoroughly with water and held separately for 10 days. Extracts and areas previously exposed to *C. antarcticus* and *F. grisea* showed no attraction to the opposite species (ANOVA, $P>0.05$). Although the two species are commonly found together in the field, the chemical attractants appear to be species-specific.

Table 1 Responses of Antarctic Collembola to Their Own Body Surface Extracts

Extract sample	*Cryptopygus antarcticus*			*Friesea grisea*		
	N/200	%	REA	*N*/200	%	REA
Methanol-control	102	51.0	0	106	53.0	0
1 individual	108	54.0	1.9	107	53.5	0.9
10 individuals	116	58.0	8.6	114	57.0	7.0
100 individual	129	64.5*	17.8	128	64.0*	17.2
500 individuals	139	69.5*	23.7	141	70.5*	24.8
1,000 individuals	138	69.0*	23.2	142	71.0*	25.4

REAs were calculated using combined controls, and 50% attraction served as the expected value in the χ^2 calculations; ($P<0.05$). *N*/200=number of individuals out of 200 that were present in the quadrants containing the extract.
REA relative efficacy of attraction
*$P<0.05$ (χ^2)

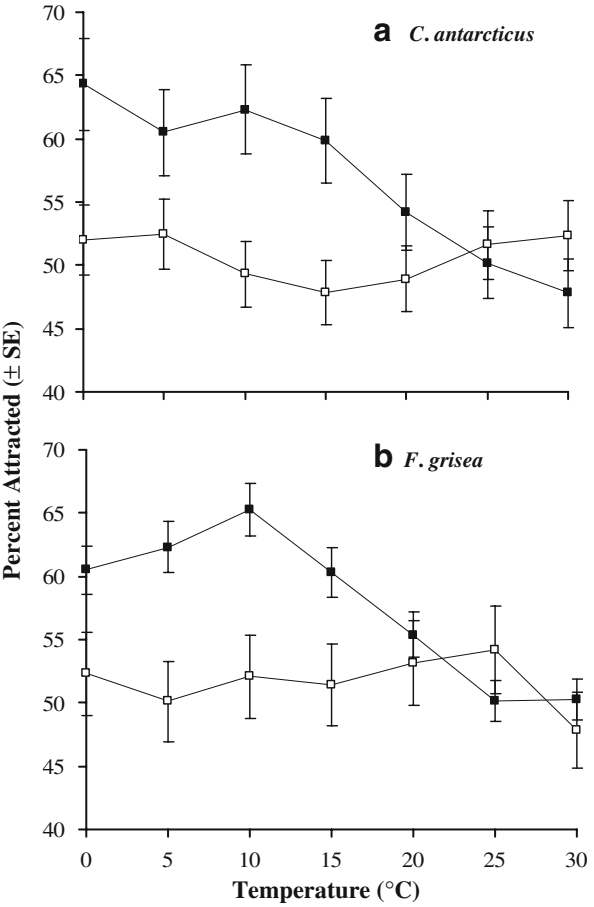

Fig. 3 Temperature-induced differences in the attraction of *C. antarcticus* (**a**) and *F. grisea* (**b**) to Collembola-conditioned areas (disk conditioned with 100 individuals for 24 h). Values represent the percent attracted when Collembola were held at 100% RH and measured after 2 h. *Closed squares* represent the percentages of Collembola in treated areas, and the *open squares* are the percentage in quadrants not exposed to Collembola. Each value represents 20 replicates of ten individuals.

Water Loss Rates

For experiments that determined water loss rates, the collembolans used were similar in size, shape and body water pool, implying that surface area to volume effects on water loss rates were negligible. Additionally, water mass correlated positively with dry mass ($R>0.97$) in all cases. Groups of *C. antarcticus* lost water more slowly (6.9%/h for groups of 100) than single individuals (11.2%/h). Interestingly, water loss rates did not decline linearly, but reached a point when increases in group size only minimally decreased the water loss rates (Fig. 5). This indicates that clustering caused the water loss rate to decay exponentially as group size increased, according to the equation $y=11.8x^{-0.11}$ (Fig. 5). We conclude that individuals in a group retain water better than single individuals.

Factors Influencing Oviposition

Large clusters of Collembola eggs are commonly found together with the postembryonic stages under rocks and organic debris. To evaluate the possibility

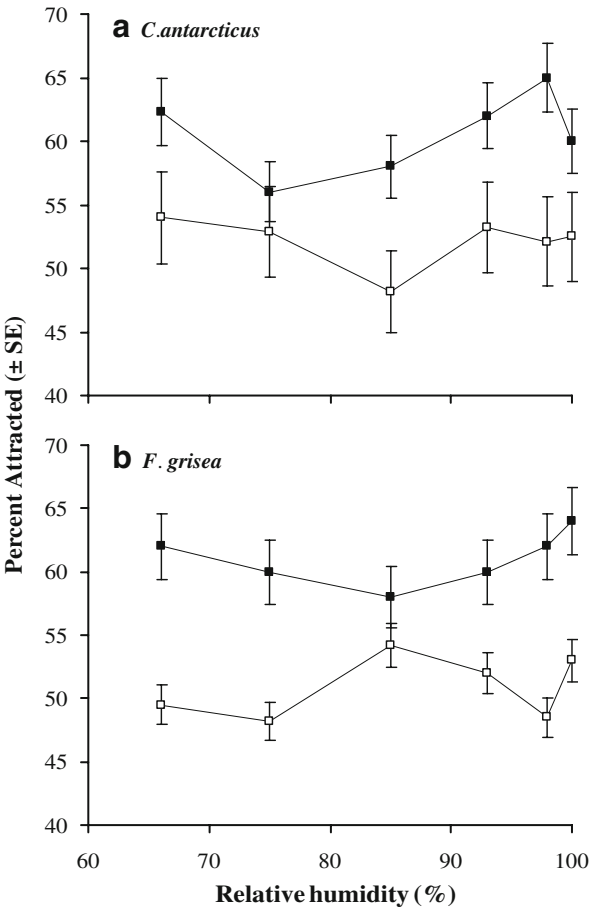

Fig. 4 The effects of humidity on aggregation of *C. antarcticus* (**a**) and *F. grisea* (**b**). Attraction was recorded after 2 h at 4°C to areas with disks that were pre-conditioned with 100 Collembola for 24 h. *Closed squares* represent the percentages of Collembola in treated areas, and the *open squares* are the percentages in quadrants not exposed to Collembola. Each value represents 20 replicates of ten individuals.

that a semiochemical may increase the overall number of eggs laid, groups of 150 collembolans were exposed to areas previously conditioned with Collembola of the same species. Control areas contained an average of 25–30 eggs, while treated areas contained significantly more eggs (Fig. 6; ANOVA; $P<0.05$). Increasing the number of individuals used to condition an area resulted in more oviposition (Fig. 6), with the greatest number of eggs being deposited in areas that were exposed to 500 Collembola. When all of the control samples were pooled, the average number of eggs laid in 120 h was 26, and for areas previously exposed to Collembola the total number of eggs increased to 46. Collembola extracts increased oviposition only at concentrations of 200 Collembola/ml. Thus, chemical factors released by collembolans are capable of eliciting oviposition.

Discussion

For arthropods that reside in Antarctica, survival is dependent on resisting long periods of subfreezing temperature and subsequently maximizing development and

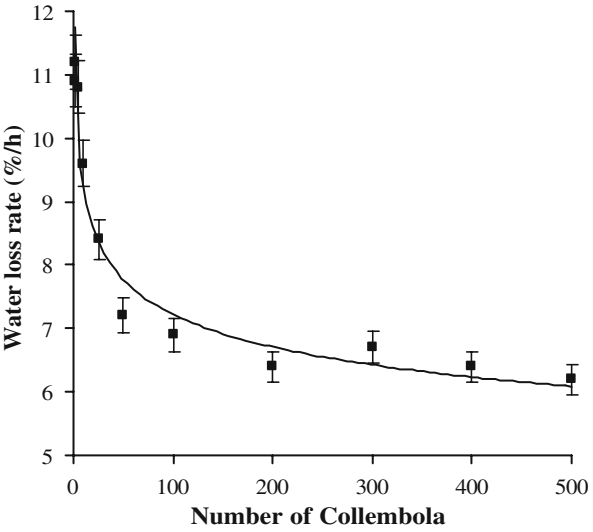

Fig. 5 Water loss rates for *C. antarcticus* as a function of group size. Each point represents the mean (± SE) water loss rate of 20 individual collembolans within a group at 0% RH, 4°C.

reproduction during the short austral summer. For *C. antarcticus*, development occurs at temperatures above 1.5°C, with the optimum being 10°C (Burn 1981, 1984). This species will vacate areas when temperatures are unfavorable for development and at low relative humidities (Hayward et al. 2001, 2003). Thus, desiccation and cold are common environmental stresses that these animals avoid. Long distance movement of these Collembola likely occurs by random distribution by rafting or wind dispersal (Hawes et al. 2007, 2008). Less is known about the physiology of *F. grisea*, but the two species have considerable overlap in habitat, thus it is likely that this species prefers nearly the same conditions as *C. antarcticus*.

The presence of pheromone-induced aggregations in *F. grisea* and *C. antarcticus* is consistent with previous reports for several species of Collembola from the temperate zone (Verhoef and Nagelkerke 1977; Verhoef et al. 1977; Hopkin 1997; Manica et al. 2001; Wertheim et al. 2005). Overall, cues triggering gregarious behavior are fairly common among insects and related arthropods (Wertheim et al. 2005). The pheromones in these two Antarctic species appear to be aggregation pheromones or assembly pheromones. Although the pheromones we describe have some properties commonly associated with both assembly and aggregation pheromones, such as being rather non-volatile in nature and having a long (12 h) residual life, these pheromones have more in common with aggregation pheromones previously described in Collembola (Verhoef et al. 1977; Verhoef 1984).

The aggregation pheromones are possibly of fecal origin. Surface extracts from Collembola that were starved for 1 week showed considerably less attractiveness than extracts from Collembola that had been allowed to continually feed. The fact that filter paper extractions from Collembola that had fed previously also were able to induce attraction at lower concentrations than observed with unfed individuals further supports the likelihood of the digestive tract as a source of the pheromone. Additionally, it is important to note that the chemicals inducing aggregation may be a food-derived product, which will cause aggregation, and possibly oviposition, by indicating the presence of areas where collembolans are feeding. A similar

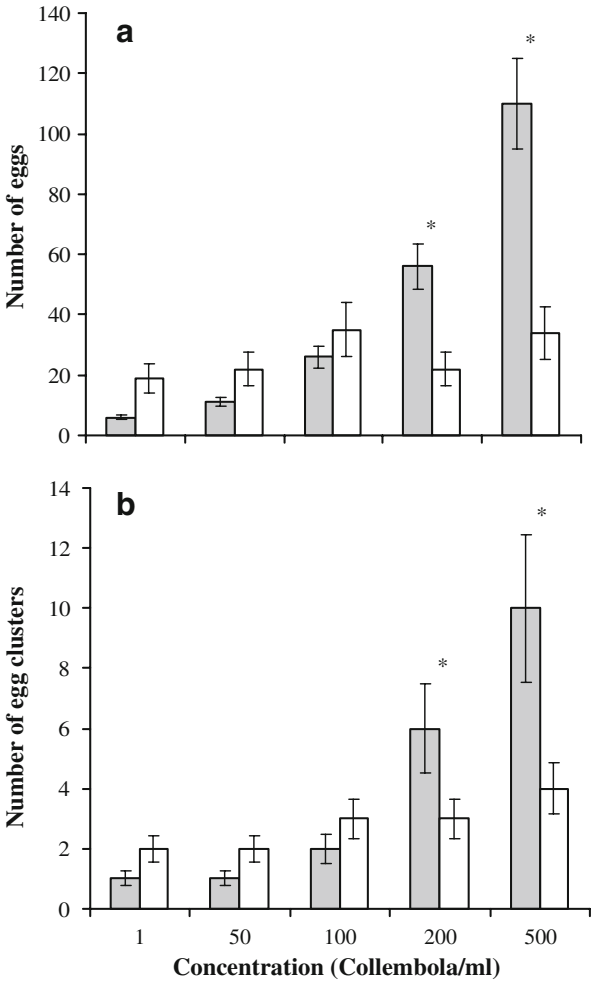

Fig. 6 Effects of adult methanol-extracts on oviposition by *C. antarcticus* based on **a** total number of eggs and **b** the number of egg clusters. Each experiment was replicated ten times with 100 individuals held at 100% RH, 4°C in complete darkness. *Gray bars* are responses to extracts and *white bars* are the responses to acetone controls. *Asterisk* denotes significant difference to acetone control (ANOVA, $P<0.05$).

mechanism was described previously in two other species of Collembola, *Orchesella cincta* and *Tomocerus minor* (Verhoef et al. 1977). For *O. cincta* and *T. minor*, long-term food deprivation reduces, but does not cease, the production of their aggregation pheromones. Additionally, among the Collembola tested by Verhoef et al. (1977), exuviae were not attractive, which suggests that either the cuticle is not a source of the attraction or that pheromone production is interrupted during the pre-molting periods (Brossut et al. 1974; Verhoef et al. 1977). Thus, it is likely *C. antarcticus* and *F. grisea* use mechanisms similar to those previously demonstrated in other Collembola for pheromone production.

The species-specific nature of the aggregation pheromone was somewhat surprising because *C. antarcticus* and *F. grisea* were found together in nearly all of the aggregations we observed on the islands near Palmer Station. Nonspecific aggregation pheromones have been identified in some other taxa including beetles (Levinson and Bar Ilan 1970), cockroaches (Ishii 1970; Bell et al. 1972) and

Collembola (Verhoef et al. 1977), but in most cases aggregation pheromones are species-specific (Borden 1985; Wertheim et al. 2005). When Verhoef et al. (1977) looked for interactions between *O. villosa* and *T. minor* they found that only the response of *O. villosa* was species-specific. Thus, among Collembola both species-specific and non-specific attractants have been observed. For the two Antarctic species tested in this study, it appears that both utilize species-specific aggregation pheromones.

Recently, Hayward et al. (2001, 2003) determined that temperature and humidity influence movement and distribution of *C. antarcticus*. They showed that *C. antarcticus* prefers high relative humidities, particularly when the temperature is high. In relation to temperature, *C. antarcticus* preferred 5–9°C, which correlates to the optimal developmental temperature for this species (Burn 1981, 1984). No research of this type has thus far been done on *F. grisea*, but based on previous collembolan research, temperature and humidity likely influence their distributions (Christiansen 1970; Usher and Hider 1975). Along with effects on overall distribution, temperature exerts significant effects on the response of both *C. antarcticus* an F. *grisea* to aggregation factors: low temperatures promote aggregation. The fact that high temperatures reduce attraction is not surprising since both species are unlikely to survive long periods when exposed to temperatures above the lethal permeability temperature (15°C; Worland and Block 2003). Thus, it appears that under favorable conditions Collembola will respond to aggregation pheromones, but when exposed to potentially adverse conditions, locating a more suitable habitat outweighs the influence of chemical cues.

In the field, clusters of Collembola eggs are fairly common and can number into the thousands (Schulte et al. 2008). Initially, we assumed this was simply a by-product of adult clustering, but our experiments show that the aggregation pheromone or another possible chemical increases oviposition. Females frequently lay ten to 30 eggs at a time (Hopkins 1997; Moss 1998), thus a coordinated egg laying effort could easily account for the huge egg clusters observed. Currently, it is not known if the factors that promote oviposition are active over long distances, but it seems more likely these chemicals will act only locally. Aggregated oviposition is known in many other insects in response to factors released by the females, eggs, larvae or even pupae (Verhoef 1984; Bentley and Day 1989; Jiang et al. 2002; Judd and Borden 1992). An increase in reproduction efficiency has been demonstrated for several other species of Collembola where increased pheromone concentrations decreased the interval from mating to egg laying (Verhoef 1984). The adult collembolans will already be in large clusters resulting from the presence of aggregation pheromones, and these compounds stimulate oviposition which can lead to synchronized oviposition.

One of the major physiological benefits of an aggregation is the reduction in water loss rate, and this is particularly important for Antarctic Collembola due to their high water requirements (Block et al. 1990; Worland and Block 2003). Reduced water loss due to aggregation has been noted in many arthropods, including mites (Glass et al. 2001), beetles (Yoder et al. 1992; Benoit et al. 2005), and other Antarctic individuals (Benoit et al. 2007). How clustering functions to suppress water loss rates is poorly known. One possibility is that the group acts as a superorganism, which decreases the surface area to volume ratio, or alternatively,

respiratory water loss is decreased as a consequence of the lower metabolic rate observed in groups (Yoder et al. 1992). Either way, relative humidity around the organism is elevated by clustering and this, in turn, decreases water loss. Thus, a decrease in water loss rate is a major benefit of aggregating, and *C. antarcticus* and *F. grisea* are likely to benefit from this advantage in the Antarctic environment.

In conclusion, this is the first aggregation pheromone reported for an Antarctic arthropod. The presence of this semiochemical likely benefits *C. antarcticus* and *F. grisea* by multiple methods. First, it reduces their rate of water loss. Secondly, it increases mate access, and thirdly, it reinforces the presence of Collembola in areas with adequate food and moisture resources. The presence of a semiochemical that induces egg laying stimulates females to oviposit in areas where large clusters of Collembola are already present and thus allows the nymphs to develop in microhabitats favorable for growth and survival. Collectively, aggregation pheromones and egg-laying stimulants foster formation of the large clusters of *C. antarcticus* and *F. grisea* that are prevalent on the Antarctic Peninsula.

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