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Foster Forbes Purrington
Ohio State University

Patricia A. Kendall

John E. Bater
Ohio State University

Benjamin R. Stinner
Ohio Agricultural Research and Development Center

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ALARM PHEROMONE IN A GREGARIOUS PODUROMORPH COLLEMBOLAN (COLLEMBOLA: HYPOGASTRURIDAE)¹Foster Forbes Purrington², Patricia A. Kendall³, John E. Bater²,
and Benjamin R. Stinner⁴

ABSTRACT

We report an alarm pheromone in the gregarious poduromorph collembolan, *Hypogastrura pannosa*. Cuticular rupture results in emission of a rapidly vaporizing hexane-soluble material with an active space diameter of ca. 1 cm. Conspecifics encountering the vapor front respond with stereotypic aversion and dispersal behaviors. This is the first report on the presence of an alarm pheromone in the order Collembola.

Alarm pheromones are well known in eusocial insects (Isoptera, Hymenoptera) where responses involve complex defensive, recruitment and dispersal behaviors (reviewed by Blum 1985, Hölldobler and Wilson 1990). In his studies of the quasi-social treehopper, *Umbonia crassicornis* Amyut & Serville (Homoptera: Membracidae), Wood (1976) showed that abdominal wounding of nymphs prompted chemically mediated alarm and active defense of offspring by brooding female parents.

Socially less organized taxa such as several species of gregarious bugs in three families of the Hemiptera (reviewed by Blum 1985) also use alarm pheromones, and they are widespread if not universal among the aphids (Homoptera: Aphidae) (e.g. Nault and Bowers 1974). An alarm pheromone is present in the mold mite, *Tyrophagus putrescentiae* (Schränk) (Acarina: Acaridae) and in several related species (Kuwahara et al. 1980).

We now report an alarm pheromone for the first time in a fifth insect order, the Collembola.

MATERIALS AND METHODS

We obtained eggs and adults of *Hypogastrura pannosa* Macnamara (Collembola: Hypogastruridae) from rotting fruit of native persimmon (*Diospyros virginiana* L.) on 10 Oct. 1989 at Wooster, Ohio. *Isotomurus bimus* Christiansen & Bellinger (Isotomidae) and *Lepidocyrtus pallidus* Reuter (Entomobryidae) were collected from a greenhouse mist-bed on 15 Mar. 1990 at Wooster. *Neanura muscorum* (Templeton) (Neanuridae), *Megalothorax minimus* (Willem) (Neelidae), and *Smin-*

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²Department of Entomology, The Ohio State University, Columbus, OH 43210.

³Apple Creek, OH.

⁴Department of Entomology, Ohio Agricultural Research and Development Center, Wooster, OH 44691.

thurinus elegans (Fitch) (Sminthuridae) were also taken at Wooster, from extractions of leaf litter in a dense landscape planting of mature American holly (*Ilex opaca*). *Folsomia candida* Willem (Isotomidae) was obtained from laboratory cultures at the O.A.R.D.C., Wooster. We collected *Onychiurus encarpatus* Denis (Onychiuridae) from an agricultural field soil (winter wheat) at the USDA North Appalachian Experimental Watershed site, Coshocton, Ohio on 19 Apr. 1990. To obtain collembolans from soil and litter we used a modified Tullgren funnel extractor at the Soil Ecology Laboratory, O.A.R.D.C., Wooster, Ohio.

Collembola were maintained on active dry yeast in containers with moist plaster of Paris floors at 28°C.

To determine solubility characteristics and alarm inducing properties of the active material, we placed ca. 5000 *H. pannosa* adults into 1 ml acetone, and an equal number into 1 ml hexane (2 μ l = ca. 10 adult-equivalents). We challenged a variety of collembolan species with these extracts dried onto filter paper points held with forceps or mounted on insect pins.

RESULTS AND DISCUSSION

Crushed *Hypogastrura pannosa* with broken cuticles evoked immediate alarm responses when held a few mm above conspecifics in a culture jar. The behavioral response sequence of a freely traversing individual to perception of the released volatiles typically included a stop with antennal waving, grading immediately into a general recoil. Extracts of *H. pannosa* eluted in hexane and completely evaporated onto filter paper points, at concentrations ranging from two to 10 adult-equivalents, gave results approximately similar to those using single crushed individuals, with no clear elevation of response intensity at higher concentrations. Neither extracts in acetone, pure acetone, nor pure hexane evaporated onto filter paper points evoked responses.

After flinching and general bodily contraction, behavior in the presence of the alarm releasing material included either 'freezing' or turn-and-run, although 'freezing' was not frequent. In this species the ultimate collembolan option of springing was seldom seen used as an escape strategy in the context of alarm behavior; by far the most frequently observed alarm sequence was stop-flinch-turn-run.

Emission of alarm releasing volatiles from a single freshly crushed *H. pannosa* generated an active space of ca. 1 cm. diam. This zone, which was virtually cleared of conspecifics within 60 s, typically remained cleared for more than one h. All instars were alarmed similarly by the vaporizing materials; hatchling *H. pannosa* are well endowed with alarm releasing compounds and when crushed they too triggered strong aversion in conspecifics. Crushed eggs, however, did not cause noticeable alarm.

Recently, from studies he made of *H. socialis* (Uzel), Leinaas (1988) speculates on the function of eversible anal glands, suggesting their possible role in the release of alarm inducing volatiles, analogous to the terminal eversible sex pheromone gland of the female moth abdomen. He asserts that in *H. socialis* jumps are invariably accompanied by eversion of anal sacs. It is difficult for us to accept his implication that the putative release of alarm inducer chemicals is a concomitant of saltation in *H. socialis* or any gregarious collembolan, that such "crying wolf" has any adaptive value for sociality.

In our studies, short of rupturing the integument, no amount of jostling, probing, or other mechanical harassment of adult *H. pannosa* by us resulted in stereotypic aversion behavior by nearby conspecifics. For that reason we do not, on the basis of our preliminary findings, support a view that these insects propagate alarm pheromone by everting anal sacs or with any controlled glandular emission.

In Table 1 we show results of test responses of eight species in seven collembolan

Table 1. Cross-taxa alarm/aversion responses between and within 8 species in 7 collembolan families to freshly crushed individuals of these species. 1/, 2/.

		Response code: POTENT: ++, SLIGHT: + .							
		CHALLENGER SPECIES (crushed)							
		A	B	C	D	E	F	G	H
RESPONDER	A								
	B	+	++						
SPECIES	C								
	D	+	+						
	E								
	F								
	G								+
	H								

1/ Each score ≥ 5 replications.

2/ Species codes:

A. <i>Onychiurus encarpatus</i>	Onychiuridae
B. <i>Hypogastrura pannosa</i>	Hypogastruridae
C. <i>Neanura muscorum</i>	Neanuridae
D. <i>Folsomia candida</i>	Isotomidae
E. <i>Isotomurus bimus</i>	Isotomidae
F. <i>Lepidocyrtus pallidus</i>	Entomobryidae
G. <i>Megalothorax minimus</i>	Neelidae
H. <i>Sminthurinus elegans</i>	Sminthuridae

families to freshly crushed individuals of the eight species. *Megalothorax minimus* and *Folsomia candida* both responded slightly to *H. pannosa* volatiles. Crushed *Onychiurus encarpatus* elicited mild aversion in both *F. candida* and *H. pannosa*. Except for *H. pannosa*, however, none of the eight tested species was alarmed by crushed conspecifics, although slight aversion was evident in *M. minimus*.

We interpret these observations and test results as fitting Blum's (1985) correlation of alarm pheromones in arthropod taxa with a gregarious *modus vivendi*. Of the collembolans we observed, *H. pannosa* was by far the most gregarious. Even in sparse cultures they typically formed compact aggregations with frequent and prolonged physical contact between individuals. Their eggs are almost invariably deposited in dumps that can contain into the thousands. Butcher et al. (1971) noted that *H. nivicola* (Fitch) also lays eggs in batches or clumps. Pheromones mediating aggregation behavior have been noted in *H. viatica* Tullberg (Mertens and Bourgoignie 1975, 1977). Synchronized moulting in colonies of *H. lapponica* (Axelson) and *H. socialis* has been demonstrated to result from chemical communication among members, rather than control by external factors (Leinaas 1983). We anticipate that further studies of gregarious hypogastrurid species will reveal additional details of chemically mediated interactions between aggregation members. Particularly, in regard to alarm behavior, it would be valuable to study the responses to known collembolan predators such as mesostigmatid mites and carabid beetles, and to elucidate the chemistry of the alarm pheromones involved.

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