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Pheromone-based Arrestment Behavior in the Common Silverfish, *Lepisma saccharina*, and Giant Silverfish, *Ctenolepisma longicaudata*

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Abstract Aggregations of the common silverfish, *Lepisma saccharina*, and giant silverfish, *Ctenolepisma longicaudata* (both Thysanura: Lepismatidae), are mediated by species-specific pheromones. In dual-choice, still-air olfactometer experiments, filter paper previously exposed to 12 male, female, or juvenile *L. saccharina* or *C. longicaudata* arrested conspecifics regardless of developmental stage or sex. Arrestment responses required physical contact with the pheromone. Insect-derived frass, scales, antennae, and setae, as well as salivary gland content, are not the source of the contact pheromone in *L. saccharina.* *Lepisma saccharina* did not respond to the pheromone of *C. longicaudata*, nor to that of another thysanuran, the firebrat *Thermobia domestica*. However, *C. longicaudata* responded to pheromones of both *L. saccharina* and *T. domestica*, whereas *T. domestica* responded to the *C. longicaudata* but not *L. saccharina* pheromone. These results support the hypothesis that a closer phylogenetic relationship exists between *C. longicaudata* and *T. domestica* than between *C. longicaudata* and *L. saccharina*, but a definitive conclusion must await molecular genetic analyses of all three species.

Keywords *Lepisma saccharina* · *Ctenolepisma longicaudata* · *Thermobia domestica* · Thysanura · Zygentoma · Lepismatidae · Contact pheromone · Aggregation · Arrestment

Introduction

Most pheromones identified to date are low-molecular weight lepidopteran sex pheromones (Birch 1974; Jurenka and Roelofs 1993) that remain airborne and mediate long-range attraction of mates for limited time (Chapman 1998). Pheromones that lack volatility are perceived when an insect contacts a substrate to which the pheromone adheres. Such contact pheromones occur in collembolans (Manica et al. 2001), cockroaches (Nishida et al. 1979; Nojima et al. 1999), termites (Henderson 1998), locusts (McCaffery et al. 1998), and

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thysanurans (Trembay and Gries 2003). Most of these insects inhabit enclosed microhabitats with little air movement, potentially rendering volatile pheromones less effective than contact pheromones. Moreover, many species that deploy contact pheromones for communication belong to primitive taxonomic insect orders (Grimaldi and Engel 2005). Identification of these chemicals will contribute to our understanding of pheromone evolution (Roelofs et al. 2002; Wertheim et al. 2005).

Here, we studied pheromonal communication in three primitive, synanthropic thysanurans, the common silverfish, *Lepisma saccharina* L., giant silverfish, *Ctenolepisma longicaudata* Escherich, and the firebrat, *Thermobia domestica* (Packard). Male, female, and nymph *T. domestica* produce, and respond to an aggregation pheromone (Trembay and Gries 2003) but require physical contact to perceive it. A similar communication system may exist in *L. saccharina* and *C. longicaudata*, as they also aggregate within human dwellings. Aggregating thysanurans maintain contact via antennae and caudal appendages (Tremblay 2002; NW, personal observation), suggesting that the pheromone may be associated with these or other body parts, although one cannot discount salivary secretions as yet another potential source. All three species can be found in the same shelter (NW, personal observation), and thus may be able to recognize con- and heterospecific pheromones.

Our objectives were to test the following hypotheses: 1) male, female, and nymph *L. saccharina* and *C. longicaudata* produce and respond to aggregation pheromone; 2) pheromone perception requires physical contact; 3) frass, scales, antennae, caudal filaments, or salivary secretions constitute the source of the *L. saccharina* pheromone; and 4) pheromones of *L. saccharina*, *C. longicaudata*, and *T. domestica* elicit a behavioral response by closely related heterospecifics.

Methods and Materials

Collection and Rearing of Experimental Insects

Thermobia domestica, *C. longicaudata*, and *L. saccharina* were collected by placing Petri dish (14×8 cm) traps baited with Quaker® oats on or around autoclaves and boilers at Simon Fraser University. Approximately 1,000 *L. saccharina* were also obtained from a laboratory colony at the University of Sussex. Insects were maintained in glass rearing jars (10×12 cm) provisioned with a moist cotton wick, a Petri dish (3×1 cm) containing Quaker® oats, and a corrugated cone of filter paper (CCOFP; Whatman® No. 1, 125-mm diam) as a shelter. Each jar housed either 100 males, females or juveniles, or a mixed group (100 insects total) of all stages. Jars were kept in a Plexiglas® container (30×22×22 cm) in contact with a heating rock (Zoo Med Labs, Inc., San Luis Obispo, CA, USA) so that the within-jar temperature ranged between 24° and 38°C depending on the proximity to the heat source. A within-jar relative humidity of 70–85% was maintained by leaving an open jar of water in contact with the heating rock. This range of humidity and temperature ensured optimal abiotic conditions for each of these species (Sweetman 1938, 1939; Spencer 1959). Insects were reared and tested under an 8L:16D photoperiod (Sweetman 1938, 1939).

General Bioassay Procedures

Lepisma saccharina, *T. domestica*, and *C. longicaudata* naturally reside within confined spaces with little or no air movement (Spencer 1930; Sweetman 1938). Thus, still-air "olfactometers" were used for all experiments. They consisted of a central Pyrex® glass

Petri dish connected to two lateral Petri dishes (each dish 9×3 cm) via tubing (2×2.5 cm) (Trembay and Gries 2003). Olfactometers were housed within opaque plastic bins (35×31×11 cm) (Columbia Plastics Ltd. ®, Vancouver, BC, CA), allowing diffuse but not directional light to enter. Each lateral chamber of an olfactometer received a filter paper (Whatman® No. 1, 125-mm diam) that was folded twice and formed into a cone, with the tip facing the central chamber. Cones served as shelters, resulting in few nonresponding individuals during bioassays (NW, personal observation). For each replicate, an insect (previously isolated for 16 hr) was released into the central chamber 6 hr after the onset of scotophase, and its position was recorded 16 hr later (2 hr before the start of scotophase). Each replicate was run at 24±2°C and 70–85% relative humidity (RH). Olfactometers were washed with hot water and Sparklene™ detergent, and were oven-dried at 125°C for 3 hr between each assay.

Specific Experiments

In experiments 1–9 and 10–18, we tested the hypothesis that male, female, and nymph *L. saccharina* and *C. longicaudata* produce and respond to species-specific pheromone. The CCOFP (see above) was removed from rearing jars after 3 d of exposure to 100 insects, brushed off to remove insect-derived frass and scales, and then cut into eight equal pieces. A single piece was then inserted into the paper cone located within the treatment chamber of each olfactometer. The paper cone in the corresponding control chamber received a piece of CCOFP that had been removed from rearing jars containing oats and a moist wick, but no insects.

In experiments 19–20 and 21–22, we tested the hypothesis that female *L. saccharina* (experiments 19–20) and *C. longicaudata* (experiments 21–22) require physical contact to perceive and respond to their aggregation pheromone. Considering that pheromone production and perception was neither gender- nor adult-specific in preceding experiments, this hypothesis was tested only with females. A CCOFP exposed for 3 d to a mixed group of male, female, and nymph conspecifics (100 insects total) was placed so as to be accessible (see above) or inaccessible in the treatment chamber of an olfactometer. Inaccessible stimuli were suspended above a nylon mesh, stretched over the rim of the chamber and thus out of reach for test insects. Control stimuli from rearing jars containing only oats and a moist wick were tested in a similar manner. One female *L. saccharina* or *C. longicaudata* was bioassayed in each replicate.

In experiments 23–26, we tested the hypothesis that *L. saccharina*-derived frass (experiment 23), body scales (experiment 24), antennae or caudal filaments (experiment 25), or salivary gland secretions (experiment 26) constitute the source of the aggregation pheromone. The test stimuli were prepared from: (1) dry fecal pellets (0.5 mg) recovered from female rearing jars after 3 d; (2) scales (0.5 mg) brushed off dorsal and ventral surfaces of 10 cold-anaesthetized females; (3) four antennae and six caudal filaments removed from four cold-anaesthetized females, or (4) macerated salivary glands excised from three cold-anaesthetized females. Each stimulus was spread within the paper cone shelter of a randomly assigned treatment chamber of an olfactometer. Paper cone shelters within the control chamber received no test stimulus. One female *L. saccharina* was bioassayed in each replicate.

In experiments 27–35, we tested the hypothesis that *L. saccharina*, *C. longicaudata*, and *T. domestica* respond to pheromones from con- and heterospecifics. Test stimuli consisted of a piece of CCOFP (see experiments 1–18) previously exposed to a mixed group of male, female, and juvenile insects. This was inserted into paper cones within the treatment

chamber of each olfactometer. Control chambers contained a piece of CCOFP from rearing jars containing only oats and a moist wick. One female *L. saccharina*, *C. longicaudata*, or *T. domestica* was bioassayed in each replicate.

Numbers of insects responding to test stimuli in each experiment were analyzed by χ^2 test, with JMP™ software (SAS®, Cary NC, USA). The significance level was set at $P \leq 0.05$. Insects found within the central chamber or connecting tunnels of olfactometers at termination of experiments were considered nonresponders and were not included in statistical analyses.

Results and Discussion

Male, female, and juvenile *L. saccharina* all exhibited significant arrestment responses to a piece of CCOFP previously exposed to either male, female, or juvenile conspecifics (Fig. 1). Similar results were obtained with *C. longicaudata* (Fig. 2). Female *L. saccharina* and *C. longicaudata* required physical contact with the pheromone to respond to it (Fig. 3). Neither dried insect-derived frass, body scales, antennae, caudal filaments, nor macerated salivary glands removed from females elicited significant arrestment responses by female *L. saccharina* (Fig. 4). Females of all species responded to conspecific pheromones, but varied in their response to those of heterospecifics. Female *C. longicaudata* were arrested by both heterospecific pheromones, female *L. saccharina* by neither, and female *T. domestica* responded only to that from *C. longicaudata* (Fig. 5).

The arrestant type pheromone of *T. domestica* (Trembay and Gries 2003), *L. saccharina* and *C. longicaudata* (this study) may be particularly suitable for marking potential shelters that provide appropriate microclimatic conditions (temperature, humidity), protection from predators, as well as access to food, water, and potential mates. We argue that increases in population density and consequently pheromone deposition may facilitate detection of suitable shelters, and may thus be correlated with the fitness of individual thysanurans. This correlation, an Allee effect (Stephens et al. 1999), is believed to be the driving force behind the evolution of aggregation pheromones (Wertheim et al. 2005) and may also help explain the increased survival of *T. domestica* nymphs when they were reared in groups rather than in isolation (Sweetman 1938).

Nonvolatile insect pheromones identified thus far are discrete or complexed fatty acids (Naumann et al. 1991; Finidori-Logli et al. 1996; Kugimiya et al. 2002), saccharides

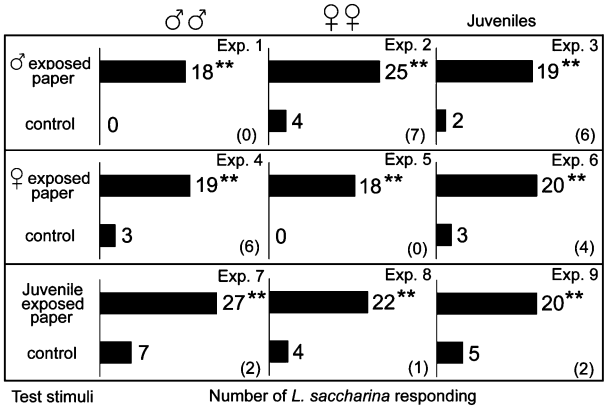

Fig. 1 Number of male, female, or juvenile *L. saccharina* responding to a piece of filter paper previously exposed to male, female, or juvenile *L. saccharina*. Numbers near bars indicate the number of insects responding to the test stimulus. An asterisk (*) indicates a significant preference for a particular test stimulus (χ^2 test; $^*P<0.05$, $^{**}P<0.01$). Numbers in brackets indicate numbers of nonresponding insects

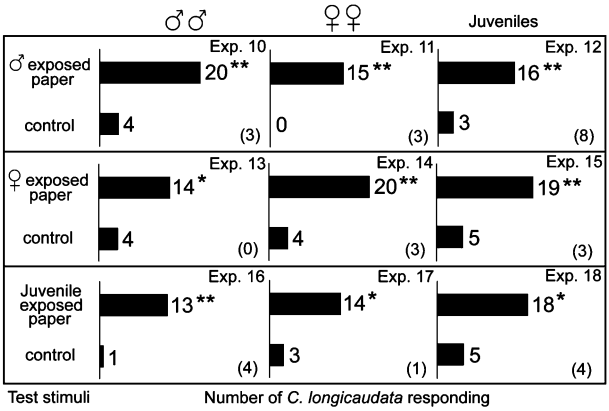

Fig. 2 Number of male, female, or juvenile *C. longicaudata* responding to a piece of filter paper previously exposed to male, female, or juvenile *C. longicaudata*. Numbers near bars indicate the number of insects responding to the test stimulus. An asterisk (*) indicates a significant preference for a particular test stimulus (χ^2 test; $^*P<0.05$, $^{**}P<0.01$). Numbers in brackets indicate numbers of nonresponding insects

(Nojima et al. 1999, 2002), or steroids (Sakuma and Fukami 1993; Kugimiya et al. 2003). All of these pheromones are easily extracted with solvents of polarity similar to that of the pheromones themselves. Our preliminary attempts to extract thysanuran pheromones with diverse polar and nonpolar solvents failed, suggesting that thysanuran pheromones may possess both polar and nonpolar segments. Such amphipathicity would allow micellar formation or polymerization, and adherence of the pheromone to solid substrates. Two amphipathic steroidal glucoside pheromones (Blattellastanoside-A and Blattellastanoside-B) have been isolated from the German cockroach, *Blattella germanica* (Sakuma and Fukami 1993). Similar to thysanuran pheromones, they are produced by males, females, and nymphs, are perceived upon contact, and elicit arrestment (Ishii and Kuwahara 1967, 1968).

The nonvolatile and nonlabile nature of thysanuran pheromones make them suitable as aggregation and shelter markers. Such pheromones resist evaporation even at temperatures of 27–38°C, the range required by *C. longicaudata* and *T. domestica* (Adams 1959; Spencer 1959). Thus, the pheromone would not saturate the confined space typically inhabited by thysanurans, nor cause adaptation and habituation of their olfactory system. Moreover, a nonpolar or amphipathic pheromone does not readily dissolve in the humid microclimate (55–97% RH) that thysanurans require to prevent desiccation (Sweetman 1938, 1939; Adams 1959).

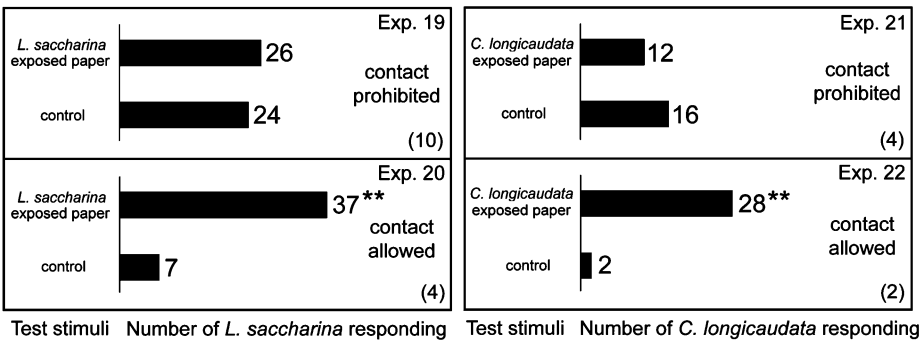

Fig. 3 Number of female *L. saccharina* (left) or *C. longicaudata* (right) responding to a piece of filter paper previously exposed to male, female, or juvenile conspecifics when stimulus contact was prohibited or allowed. Numbers near bars indicate the number of insects responding to the test stimulus. An asterisk (*) indicates a significant preference for a particular test stimulus (χ^2 test; $^*P<0.05$, $^{**}P<0.01$). Numbers in brackets indicate numbers of nonresponding insects

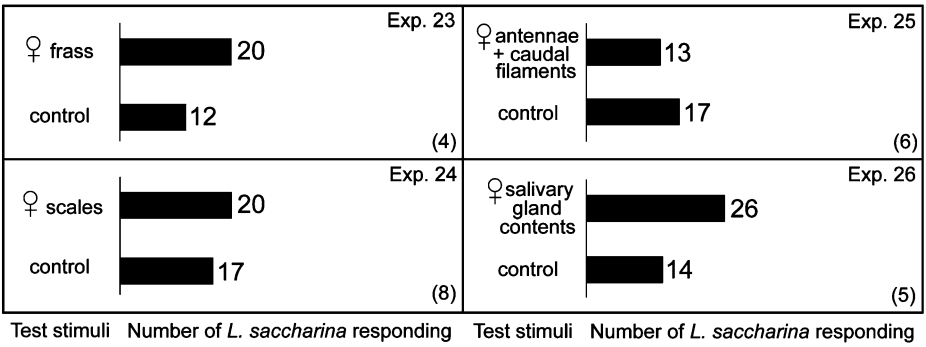

Fig. 4 Number of female *L. saccharina* responding to conspecific frass, scales, antennae and caudal filaments, or salivary gland contents. Numbers near bars indicate the number of insects responding to the test stimulus. In each experiment, there was no significant preference for a test stimulus (χ^2 test; $P<0.05$, $^{**}P<0.01$). Numbers in brackets indicate numbers of nonresponding insects

The aggregation pheromones of *L. saccharina*, *C. longicaudata* (Figs. 1 and 2), and *T. domestica* (Trembay and Gries 2003) are produced by females, males, and nymphs, suggesting they are derived from a source common to nymphs and adults. However, none of the potential pheromone sources tested previously (Trembay and Gries 2003) or in this study (Fig. 4) elicited significant arrestment in any of these species. Frass and macerated salivary glands appear to have caused some arrestment responses (Fig. 5) and ought to be investigated further, particularly in light of reports that the aggregation pheromone of European earwigs, *Forficula auricularia*, is present in frass and shed cuticle (Walker et al. 1993) or tibial glands (Sauphanor 1992). We also investigated the possibility that the arrestment behavior was caused merely by insect-induced physical and chemical changes of the shelter, or food sources therein. However, we dismissed this possibility, as glass surfaces exposed to insects for several days in the absence of food elicited strong arrestment by conspecifics (data not shown), clearly indicating that the insects deposit signals.

Relatedness between *C. longicaudata*, *T. domestica*, and *L. saccharina* can be investigated based on diverse criteria. Morphologically, *C. longicaudata* and *T. domestica* are more similar to each other than they are to *L. saccharina*. Arrestment response by *C. longicaudata*, but not *L. saccharina*, to the *T. domestica* pheromone (Trembay and Gries 2003), and lack of arrestment response to heterospecific pheromone between *T. domestica*

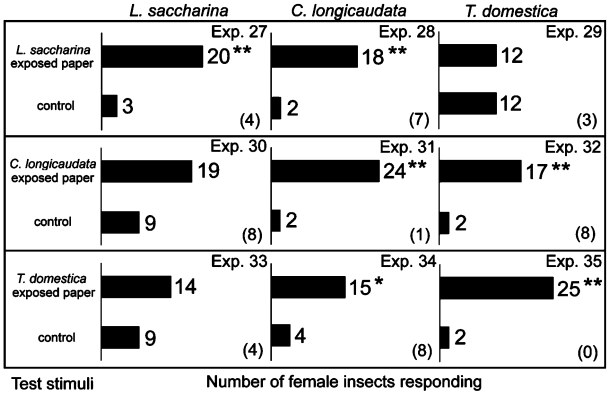

Fig. 5 Number of female *L. saccharina*, *C. longicaudata*, or *T. domestica* responding to a piece of filter paper previously exposed to conspecific or heterospecific male, female, and juveniles. Numbers near bars indicate the number of insects responding to the test stimulus. An asterisk (*) indicates a significant preference for a particular test stimulus (χ^2 test; $^{*}P<0.05$, $^{**}P<0.01$). Numbers in brackets indicate numbers of nonresponding insects

and *L. saccharina* (Fig. 5), all support the idea that *C. longicaudata* and *T. domestica* are more closely related to each other than they are to *L. saccharina* (Mendes 1991). A definitive conclusion, however, must await analyses of all three species by molecular genetics. The fact that *C. longicaudata* females respond to both *L. saccharina* and *T. domestica* pheromone (Fig. 5) is somewhat surprising, but may be explained by the probability of co-inhabiting a shelter with one of these heterospecifics. *Lepisma saccharina* and *T. domestica* prefer shelter temperatures between 21–27°C and 27–43°C, respectively (Spencer 1930, 1959; Sweetman 1938, 1939), and by selecting such discrete temperature regimes they are effectively isolated. In contrast, *C. longicaudata* is readily found in shelters at temperatures between 17°C and 30°C (Lindsay 1940), overlapping those of both *L. saccharina* and *T. domestica*. Thus, *C. longicaudata* may frequently encounter suitable shelters of either *L. saccharina* or *T. domestica* and may have evolved the ability to recognize their respective pheromones.

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