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Chemical Communication in the Gregarious Psocid *Cerastipsocus sivorii* (Psocoptera: Psocidae)

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Abstract The objectives of this study were: (1) to test the existence of an aggregation pheromone in the gregarious psocid *Cerastipsocus sivorii*; (2) to compare the attractiveness of odors from different aggregations; (3) to test whether nymphs are able to chemically recognize damage-released alarm signals. In a choice experiment conducted in the laboratory, we showed that psocids are able to detect chemical cues from groups of conspecifics. Laboratory experiments also showed that nymphs are capable of chemically recognizing the aggregations where they came from. Finally, in a field experiment, most aggregations dispersed when exposed to the body fluids of a crushed conspecific, but no aggregations dispersed upon exposure to a crushed termite. The implications of these results for the evolution of sociality in psocopterans are discussed.

Keywords Aggregation pheromone · alarm signal · damage-released pheromone · defense · kin recognition · social behavior

Introduction

The need for protection from predators may have been one of the major forces selecting for gregariousness in prey animals (Hamilton, 1971; Treisman, 1975). In

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fact, there is a great amount of evidence supporting the role of group living as an anti-predator mechanism in insects (review in Vulinec, 1990). Gregariousness may increase the ability of detecting a predator, induce a confusion effect upon that predator, and enhance the efficiency of prey aggressive defenses (Vulinec, 1990). The spatial aggregation also confers defensive advantages to the individuals through passive mechanisms such as the attack-abatement effect, i.e., the combination of dilution and avoidance effects (Turner and Pitcher, 1986; Wrona and Dixon, 1991). Besides the defensive advantages, insects living in groups benefit from slower water loss, increased foraging efficiency, enhanced thermoregulation, and improvement of mating success (reviews in Shelly and Whittier, 1997; Danks, 2002).

To enjoy the multiple benefits of living in aggregations, individuals often have to face the challenge of locating and remaining with other individuals. In the case of herbivorous insects, individuals on the same host plant may never have to deal with this particular problem if they have hatched from eggs already aggregated in clusters (Cocroft, 2001). However, there are cases of herbivores that hatch from eggs deposited in different locations and have to actively get together (e.g. Fritz, 1982). Furthermore, individuals may temporarily abandon aggregations to forage (Machado et al. 2000), and sometimes the whole group may disperse to escape from a predator (Machado et al. 2002; Requena et al. 2007), both processes leading individuals to stray. To guide their route back to their original group of conspecifics, stray individuals may use cues from different modalities, such as visual, vibrational, and chemical (e.g. Aldrich and Blum, 1978; Cocroft, 2001).

In most cases, the direct benefits of gregariousness are sufficient to make grouping worthwhile, whether or not the individuals are genetically related (Costa and Pierce, 1997). In many species, for instance, groups that encounter each other merge into a single larger group composed of individuals from different family groups (see Cocroft, 2001 and references within). There are also cases in which aggregations are formed by individuals from different species or even genera (Sauphanor and Sureau, 1993; Machado and Vasconcelos, 1998). In those cases, the individuals are part of what Hamilton (1971) called a *selfish herd,* and no kin recognition is expected among them. However, aggregating with related individuals might confer extra fitness advantages through kin selection (Fellowes, 1998), and individuals from some species do prefer to form groups with relatives (e.g. Rivault and Cloarec, 1998). The resulting cluster of related individuals is an *unselfish swarm* (Young et al. 1994), in which kin recognition is expected as the mechanism that allows individuals to preferentially join groups of relatives. Therefore, according to Fellowes (1998), the occurrence or absence of kin recognition mechanisms allows us to distinguish whether a gregarious species forms selfish herds or unselfish swarms.

Besides group formation, prey animals can also diminish the frequency of predator encountering or improve the chances of surviving these encounters by assessing predation risks, which can be done through chemical cues (Bryer et al. 2001). One group of chemicals that serve this function is composed of cues released directly from the predator, termed predator chemicals or predator kairomones (reviewed by Kats and Dill, 1998). On the other hand, chemicals released by conspecifics when they detect or are captured by a predator, termed alarm pheromones or chemical alarm signals, also represent chemical cues through which prey animals can assess predation risk (reviewed by Chivers and Smith, 1998). If

those chemical cues emitted by conspecifics are released only following their capture or after they are injured by a predator, they are called damage-released alarm signals (Chivers et al. 1996). Among arthropods, the responses of alarm signal receivers may include dispersal, increased use of refuge, aggressive response, decreased movements, decreased foraging, and avoidance of the area where the signal was received (Dicke and Grostal, 2001).

Nymphs from several species of *Cerastipsocus* bark lice form dense aggregations, resting and feeding in groups on tree trunks (Mockford, 1993), and it has already been suggested that the gregarious behavior in these animals is a strategy to reduce the effect of bark gleaning predators (New and Collins, 1987). However, the communication among members of a given aggregation and the possible existence of an alarm or an aggregation pheromone in the group has never been investigated so far. *Cerastipsocus sivorii* is a Neotropical psocid that lives in dense herds composed of nymphs of various instars, which remain together after adulthood is reached, but disperse soon after adults lose tenerality (Requena et al. 2007). In a previous work, we have found that when aggregations are attacked by predators, such as ants, jumping spiders, and assassin bugs, the nymphs rapidly disperse and each individual presents excited bursts of non-directional running, suggesting the existence of an alarm pheromone (Requena et al. 2007). After dispersion, nymphs get back together in new aggregations after up to 30 min, and individuals of *C. sivorii* seem to be able to detect conspecifics from distances as far as 50 cm. Moreover, different aggregations normally merge in nature, and strays may join the first group of conspecific they find on the bark, even when it is an unfamiliar group. These observations lead us to suggest that, if nymphs of *C. sivorii* use some kind of chemical cue for detecting and joining conspecifics, this putative aggregation pheromone is probably not relative-specific (Requena et al. 2007).

The main objective of the present study was to test if there is chemical communication among individuals of the gregarious psocid *C. sivorii.* Our first aim was to experimentally test the existence of an aggregation pheromone that maintains cohesion between members of a given aggregation and, after a disturbance, serves as a chemical cue used by stray individuals to re-group. Secondly, we experimentally compared the relative attractiveness of odors from different aggregations to stray individuals, in an attempt to elucidate if they have the ability to discriminate between different conspecific odors, and chemically recognize individuals from their original aggregation. Finally, we also tested whether nymphs are able to recognize when a conspecific is captured at the vicinity, through some sort of damage-released alarm signal.

Material and Methods

Study Area

The study was carried out on the campus of the Universidade Estadual de Campinas (22º49′S; 47º04′W), São Paulo state, southeastern Brazil. Annual rainfall is about 1,360 mm and mean temperature 20.6ºC (data from the Instituto Agronômico de Campinas). The regional climate is markedly seasonal, with a warm-wet season from

September to April and a cold-dry season from May to August. The vegetation on the campus consists of large lawns with sparse trees and scattered small flowering shrubs (Vanini et al. 2000). Aggregations of *Cerastipsocus sivorii* are found on tree trunks (including native and exotic species) in the study site (see details in Requena et al. 2007).

Aggregation Pheromone

In July 2003, we collected 14 aggregations of *C. sivorii* and took them to the laboratory to carry out choice experiments in a small opaque plastic arena (Fig. 1). The mobility of *C. sivorii* nymphs is so high that they can move easily from one end of the arena to the other within a few seconds. To test the existence of an aggregation pheromone, we presented experimental individuals with a choice between two circular filter papers (diameter=2.8 cm), each one of them covering half of the arena (Fig. 1). One of these papers was clean (control) and the other one conditioned with conspecific odors (treatment). We randomly designated the side of the control and treatment papers in the arena by the flip of a coin before each trial. We obtained conditioned papers by placing them in a vial with 30 nymphs from the same aggregation that provided the experimental individual for 24 h. During this period, the papers were conditioned by contamination with general body contact of nymphs and feces (cf. Rivault and Cloarec, 1998). For this experiment, we selected only small aggregations (up to 50 individuals) containing nymphs of the same instar in order to increase the probability that each aggregation was composed of relatives that had hatched from the same clutch. Although each aggregation used contained nymphs at the same instar, nymph-instar among different experimental aggregations differed.

We conducted experimental trials with the conditioned filter papers immediately after the completion of the 24 h conditioning period. Until the experimental individuals were required for testing, we kept them in separate vials, resting and feeding on a piece of bark (from the tree where they were found) on the bottom. On each trial (n=14), we caged the individual inside a plastic tube placed in the center of the arena (black circle in Fig. 1), where the two filter papers met, for a period of 1 min. After this acclimatizing period, we released the individual and continuously recorded its position on the arena for a period of 5 min, obtaining the total amount of time spent by the experimental individual on each side of the arena. There were two

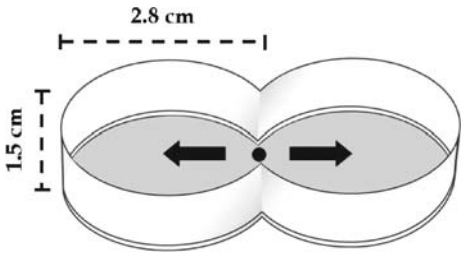

Fig. 1 Opaque plastic arena (height=1.5 cm; diameter of each side=2.8 cm) used in the aggregation pheromone and kin recognition experiments with gregarious nymphs of the psocid *Cerastipsocus sivorii*. The black circle indicates where we released experimental nymphs.

possible positions for the nymphs: on the control or on the treatment paper. If the individual remained motionless during the whole test, we discarded that test. We never used the same filter paper more than once and, after each trial, we washed the arena and the acclimatizing plastic tube with 70% ethanol and water.

Kin Recognition

Using 28 aggregations also collected in July 2003, we carried out another choice experiment, this time to test if stray nymphs of *C. sivorii* could distinguish between two different aggregations′ odor and thus chemically recognize the aggregation from which they came. We performed this experiment in the same arena used in the aggregation pheromone experiment, and the protocol was almost the same. However, this time we presented individuals (n=14) with a choice between two conditioned filter papers. We conditioned one of these papers with odor from 30 nymphs of the same aggregation that provided the experimental individual (familiar = treatment), and another filter paper conditioned with 30 nymphs from a different aggregation (unfamiliar = control). We collected each experimental aggregation from a different tree (spaced out by at least 5 m) and, once more, used only small aggregations containing nymphs at the same instar in order to increase the probability that each of them was composed of relatives that had hatched from the same clutch. Although each aggregation used contained only nymphs at the same instar, nymph-instar among different experimental aggregations differed.

Alarm Communication

In July 2004, we conducted a field experiment on alarm communication using 33 aggregations found in the study site. We designated these aggregations randomly to one out of three experimental groups. In the first experimental group, we crushed one individual collected from a non-experimental aggregation (to avoid the disturbance of the experimental aggregations) with a cotton swab (7.5 cm long) soaked with distilled water. Then, we held the tip of the cotton swab soaked with body fluids from the crushed individual at the distance of 1–2 cm from the periphery of an aggregation resting on the bark surface (n=11 aggregations). We repeated the same procedure using a crushed termite worker of *Cornitermes snyderi* (Termitidae) instead of a psocid, and a cotton swab soaked only with distilled water as controls (n=11 aggregations in each group). The termite control group was designed to test if the putative chemical cues detected by alarmed psocids are generalized insect substances or specific pheromones found only in conspecifics. Termite workers are suitable organisms for this test because they lack exocrine systems that produce alarm and defense substances (Prestwitch, 1984). Therefore, alarm responses by psocids to a crushed termite worker would be evidence that their alarm behavior is not specific and may be elicited by body fluids of non-closely related insects.

We counted the number of individuals in all tested aggregations before each trial, and aggregation size did not differ significantly between the three experimental groups (X ± SD=79.6±34.9 individuals for the crushed psocid group, 56.9±25.5 individuals for the crushed termite group, and 80.5±30.2 for the distilled water group; ANOVA: $p>0.05$). We always used new cotton swabs in each trial for all

experimental groups, and we did not test the same psocid aggregation more than once. Since repeated use of the same crushed individual could reduce the concentration of the possible damage-released pheromone, we crushed a new psocid and termite for each trial.

As a response for the manipulations, we recorded the behavior of the individuals during a 60 s period after the presentation of the swab. Since it is not easy to distinguish or define alarm in a bioassay (Billen and Morgan, 1998), we adopted the concept of 'panic alarm' proposed by Wilson and Regnier (1971), in which respondent animals present excited bursts of non-directional running. Thus, we categorized aggregations into two behavioral groups in accordance with the response of individuals: (1) individuals in a 'respondent' group presented a panic alarm response and abandoned the resting location, resulting in the complete dispersal of the aggregation; (2) individuals in a 'non-respondent' group remained in the resting location during and after the trial.

Statistical Analysis

For the aggregation pheromone and kin recognition experiments, we used two paired t-tests to compare the time spent by the experimental individuals on each side of the arena. Next, we grouped the data from the alarm communication experiment in a 3×2 contingency table and compared the number of respondent and non-respondent aggregations in each experimental group using a G test.

Results

Aggregation Pheromone and Kin Recognition

In the aggregation pheromone experiment, tested individuals spent significantly more time in the treatment side of the arena than in the control side (paired t test=8.78; d.f.=13; $p<0.001$; Table 1). In the kin recognition experiment, individuals spent significantly more time in the side of the arena containing a filter paper conditioned with familiar

Table 1 Total Time Spent by Experimental Individuals on each side of the Experimental Arena (Fig. 1) Designed to test the Existence of an Aggregation Pheromone and Kin Recognition in the Psocid *Cerastipsocus sivorii*

Experiment	Time spent in each side of the arena (in seconds)	
	Control (n=14)	Treatment (n=14)
Aggregation pheromone	49±43 (2–142)	251±43 (158–298)
Kin recognition	108.21±57.05 (2–206)	191.79±57.05 (94–298)

Each side of the experimental arena contained a filter paper that was clean (control; aggregation pheromone experiment), conditioned with odors from the same aggregation that provided the experimental individual (treatment; both experiments), or conditioned with odors from different conspecific aggregations (control; kin recognition experiment). Data are presented as mean±standard deviation, with the range in parenthesis.

odors (treatment) than in the side containing a filter paper conditioned with unfamiliar odors (control; paired t test=2.74; d.f.=13; p=0.008; Table 1).

Alarm Communication

We found a significant difference in the frequency of respondent aggregations between experimental groups (G=14.19; d.f.=2; p<0.001). More aggregations responded in the crushed psocid group than on both control and crushed termite groups (Fig. 2). Upon chemical stimulation, respondent individuals quickly dispersed from their resting location (X ± SD=19.14±14.59 s, range 2–40 s, n=7). Nymphs fled away running, while adults frequently dropped from the tree trunk and sometimes flew away.

Discussion

Aggregation Pheromone and Kin Recognition

Acoustic and vibrational organs have already been recorded in the order Psocoptera, but their role in the communication among gregarious psocids remains entirely unexplored (Costa, 2006). Although we still do not know the relative importance of different types of communication in psocids, chemical cues probably play a crucial role in the formation and maintenance of the aggregations in *C. sivorii*, since individuals are able to detect odors from groups of conspecifics. Our study is the first demonstration that psocids exhibit chemical communication, and the cues deposited on the filter papers by psocid aggregations in our experiment fits Brossut's (1975) definition of an aggregation pheromone, which can be either produced by a specialized exocrine glandular system or may be constituted of metabolic exudates. This aggregation pheromone could be used by stray nymphs of *C. sivorii* to find and

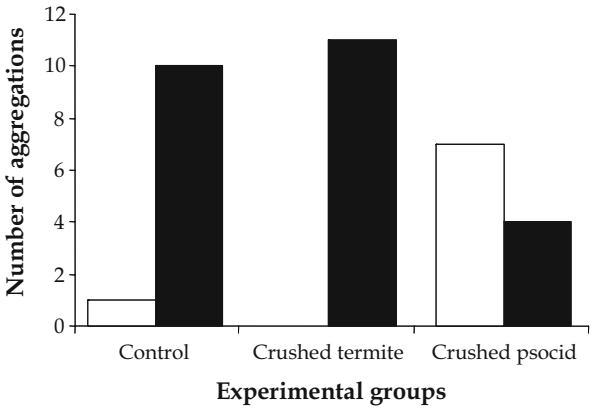

Fig. 2 Number of respondent (white bars) and non-respondent (black bars) aggregations of the psocid *Cerastipsocus sivorii* in each experimental group of the field experiment about damage-released pheromone. Significantly more aggregations responded in the crushed psocid group than in either control or crushed termite groups.

re-join any group of conspecifics after a dispersion event promoted by a predator attack, and also to maintain the cohesion among individuals during foraging and walking in group.

Given that group living in *C. sivorii* probably decreases each individual's chances of being singled out by a predator (Requena et al. 2007), these psocids should benefit from joining any group of conspecifics, as in a typical *selfish herd* (Hamilton, 1971). Therefore, we expected that *C. sivorii* nymphs would lack a preference for grouping with relatives, and hence would not discriminate between familiar and unfamiliar odors in our choice experiments. Nevertheless, our data clearly showed that nymphs of *C. sivorii* are capable of chemically recognizing the aggregations where they came from and prefer grouping with relatives. Similar results were obtained for the cockroach *Blattella germanica*, whose individuals also recognize and prefer resting sites impregnated with odors from familiar individuals (Rivault and Cloarec, 1998). Kin recognition and a preference to join groups of relatives are behavioral features associated with unselfish swarms, rather than selfish herds (Young et al. 1994). Unselfish swarms are expected to present cooperative prey defense mechanisms, which would cause predators to be less efficient when facing larger aggregations. As a consequence, an individual in a group of relatives will maximize its inclusive fitness because the extra animals surviving as a result of increasing group size are related. We suggest that *C. sivorii* does form unselfish swarms and the alarm behavior exhibited by aggregated individuals (see below) may represent the above mentioned cooperative defense mechanism. If that is true, grouping with relatives would be favored by kin selection in psocid aggregations.

One important question arises when we contrast the results from our experiments with previous behavioral observations conducted in the field (Requena et al. 2007). If *C. sivorii* nymphs benefit from and have the ability to preferentially group with relatives, why do aggregations often merge in nature? The answer for this question relies on the fact that the increase in an aggregation's size would also increase the benefits arisen from the attack-abatement effect (Turner and Pitcher, 1986; Wrona and Dixon, 1991) and intensify any cooperative defense mechanism (Young et al. 1994). Therefore, whenever two aggregations meet, they probably benefit from merging and forming a single larger aggregation in which not all individuals are genetically related.

Regarding the precise mechanism through which *C. sivorii* nymphs detect and prefer their own aggregation odors, we cannot exclude the possibility that what seems to be chemical kin-recognition is actually a mechanism solely based on familiarity, rather than relatedness. In social insects, for instance, individuals from the same colony often bear a common odor, which can be the sole result of sharing an environmental odor, for example, due to similar ingested food (see Richard et al. 2004 and references within). Yet, we believe that small aggregations formed by nymphs of the same instar (as those used in our experiments) are composed of relatives that have hatched from the same clutch and will remain together until adulthood is reached (Requena et al. 2007). In these cases, familiar odors in fact carry the information that the aggregation contains individuals with which relatedness is more likely. However, additional experiments manipulating the proportion of relatives in the aggregations, coupled with further choice experiments with these aggregations' odors, are still needed to investigate whether the aggregation's odor preference in psocids refers to familiarity, relatedness or both.

Alarm Communication

Whenever attacked by a predator, aggregations of *C. sivorii* were seen to quickly disperse from the resting site (Requena et al. 2007). Our experiment demonstrated that this dispersion of individuals is spread in the aggregation, at least in part, through chemical cues released by conspecific body fluids. Most experimental aggregations responded when exposed to the body fluids of a crushed conspecific. Hence, the detection of this kind of chemical cue fits the definition of damage-released alarm signal (Chivers et al. 1996), as it indicates a successful event of predation on conspecifics in the vicinity. Since none of the experimental aggregations responded upon the crushed termite stimulus, the chemical cues utilized by psocids are not generalized insect substances, and a certain specificity on the detection of these cues is suggested. By detecting a specific alarm cue, the individual receives the honest information that a predator is around, and that it has recently attacked a receiver's conspecific (Mathis and Smith, 1992).

Given that alarmed psocids bump into each other (Requena et al. 2007), the information about the predator's presence may also be mechanically spread through the aggregation. This mechanical transmission of information is called "Trafalgar effect" (Treherne and Foster, 1981), and has already been reported to tight aggregations of thysanurans, aphids, water-striders, and harvestmen (see references in Machado et al. 2002). Additionally, it is also possible that there is acoustic communication among group members, since it is known that some psocid species tap their abdomens to produce vibrational substrate-borne signals (Dumortier, 1963) whereas others bear a stridulatory organ (Pearman, 1928). Thus, the alarm response of gregarious *C. sivorii* probably starts with one or a few individuals at the aggregation's periphery that chemically perceive the damage-released alarm signal. The following mechanical and putative acoustical signals produced by the first alarmed individuals may cause the erratic scattering of the whole group. Future studies that investigate acoustic communication among psocids by recording behavioral disturbance of the individuals in aggregations with special microphones may shed some light on this subject.

Concluding Remarks

Although psocids are quite common in many types of habitats throughout the world, their biology is still poorly known. The order, however, offers good models to study the evolution of social behavior in insects since it comprises species with different degrees of sociality (Costa, 2006). Our study is the first one to provide information on chemical communication in psocids, and our results have important implications to understand how aggregations remain together and how individuals transmit alarm signals. Moreover, we detected a preference for familiar aggregations by *C. sivorii* nymphs, which indicates that these psocids may possess some kind of kin recognition mechanism, typical of unselfish swarms (Young et al. 1994). We suggest that gregariousness and kin recognition exhibited by *C. sivorii* can be regarded as features of an elementary type of social organization that, in the past, may have constituted the basis for the evolution of colonialism in other families, such as the web-spinning barklice of the family Archipsocidae. Finally, we

recommend that further information should be gathered about the stability of the individuals that compose an aggregation over time and about the average degree of relatedness among those individuals on an attempt to achieve a better understanding of the benefits of gregariousness in psocids.

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