Aggregation in non-social insects

an evolutionary analysis

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Summary

Insect aggregations are formed and maintained for a number of reasons, and by a number of mechanisms. Some aggregations are simply the result of an uneven distribution of resources: the animals are no more aggregated than would be expected by random distribution over the available resource patches (Parrish and Edelstein-Keshet, 1999; Stephens and Sutherland, 1999). In other cases, animals may be arrested or attracted by stimuli from conspecifics, but may not be interested in the conspecific per se. The stimuli serve, instead, as a reliable indicator of an ephemeral or cryptic resource. There are also those cases where individual fitness is positively dependent on density of conspecifics (Stephens and Sutherland, 1999). A larger group of conspecifics may be more efficient in overcoming active or passive defenses (see e.g. Coulson, 1979; Alcock, 1982; Byers, 1989; Schlyter and Birgersson, 1999; Raffa, 2001), or may otherwise enhance a resource, by mechanisms such as inoculation of a substrate with microorganisms which may render it more suitable as a food source for their larvae (see e.g. Davies, 1962; Ralph, 1976; Lockwood and Story, 1985; Turchin and Kareiva, 1989; McCall and Cameron, 1995; Wertheim et al., 2002b). The subject of this introductory paper is aggregation in nonsocial insects. Mechanisms in formation and maintenance of aggregations are covered, with particular emphasis on pheromones. Interactions between pheromones and semiochemicals from non-conspecifics (e.g. host plants) are explored. Fitness effects of aggregation are also discussed. Suggested fitness costs and benefits are presented, with examples from nature. Special attention is paid to those cases in which the fitness effects of aggregation have been explicitly tested.

Introduction

Aggregation and signaling

Studies have shown that several mechanisms enable insects to form cohesive groups (reviewed in Parrish and Edelstein-Keshet, 1999; Stephens and Sutherland, 1999; Wertheim et al., 2005). In some cases, an insect benefits from the presence of conspecifics, and so may signal to attract them. If the recipient of the signal benefits from responding, there is a basis for a communication system. If the sender doesn't benefit from attracting conspecifics, it should not emit an active signal, but try to remain cryptic and give as few cues as possible to its' position. Likewise, if a recipient does not benefit from responding to a signal, it should not do so. Thus, for a communication system to exist, both sender and recipient must benefit (Maynard Smith and Harper, 2003).

A signal may be intercepted by parties other than the intended recipient, e.g. parasites and predators. Several species of parasitoid wasps use mating and aggregation pheromones emitted by their prey as a cue to find them. Competitors may also intercept a signal. In some cases, a pheromone emitted to attract a mate is used as a cue to find a suitable food resource by conspecifics of the same sex as the emitter of the signal.

Fitness effects of aggregating

The balance of cost and benefit for aggregating is situation-dependent. A bark beetle female overhearing the volatile chemical mating call of another female may choose to follow the signal to try and find a suitable host (Alcock, 1982; Schlyter and Birgersson, 1999). The result of this decision depends on several factors, some of which may be hard to gauge for the overhearing female at the time of response. The health of the host tree, and in consequence, the strength of its' active defenses, determines how many beetles are needed before infestation is successful. The number of conspecifics attacking will thus determine whether the female is headed to die encapsulated in resin, for a successful attack and fruitful reproduction, or into intense competition. The choice is further complicated in that it is affected not only by the number of bark beetles already present on the host tree, but also by the choices made by other host-searching bark beetles, and by their number – the current population density (Alcock, 1982). The success of an individual thus not only depends on the strategy it employs, but also on the strategies that conspecifics employ. For instance, in a bark beetle species that attack only dead trees, and where females can detect but do not respond to the mating call of other females, the first female to adopt the strategy of using the pheromone as a cue to find a host may be very successful. As this strategy becomes more common in the population, it will incur a higher level of competition, and females that try to find an uncolonized host may reap higher rewards than those using a pheromone signal to find a suitable host. If the female can estimate the number of conspecifics already present on the host, e.g. by the intensity of the pheromone signal, an equilibrium strategy may develop where females will choose a previously infested host (easier to find, but with a higher level of competition) up to a certain level of conspecific density, and over that density they will choose to search for a new host (hard to find, but with less competition). Such an equilibrium strategy, where all variations on the behavior (e.g. always choose to follow a pheromone, always seek new host) are less successful, was termed an evolutionarily stable strategy (ESS) by John Maynard Smith (1982). There may be situations in which no evolutionarily stable strategy is possible (Maynard Smith and Harper, 2003). Instead, the sender and receiver are locked in a constant arms race, where both parts continually update their strategy to try and get ahead of each other.

Mechanisms in formation and maintenance of groups

Chemical signals

Olfaction and taste, the senses that detect airborne and contact chemicals, are used by insects for vital behaviour such as food search, oviposition site location, and mate finding (see e.g. Visser, 1986; Aldrich, 1988; Renwick, 1989; Metcalf and Metcalf, 1992; Hartlieb and Anderson, 1999). They are also commonly used in the initiation and maintenance of insect aggregations. The volatile compounds released by a plant under attack by insect herbivores often change in composition both quantitatively and qualitatively compared to the volatiles released by an undamaged plant. Adult larger pine shoot beetles, *Tomicus piniperda*, breed mainly in dead or severely stressed trees, and there is evidence for the use of ethanol as a signal of host stress due to previous infestation, which could be indicative of a more suitable host (Schlyter and Birgersson, 1999).

Several insect species have been reported to use pheromones to mediate aggregation, e.g. the Japanese beetle *Popillia japonica* (Klein et al., 1973), the confused flour beetle *Tribolium confusum* (O'Ceallachain and Ryan, 1977), the fruit fly *Drosophila melanogaster* (Bartelt et al., 1985), the southern green stink bug *Nezara viridula* (Lockwood and Story, 1985), the square-necked grain beetle *Cathartus quadricollis* (Pierce et al., 1988), the saw-toothed grain beetle *Oryzaephilus surinamensis* (White and Chambers, 1989), the flea beetle *Phyllotreta cruciferae* (Peng and Weiss, 1992), the Australian sap beetle *Carpophiluys davidsoni* (Bartelt and James, 1994), the assassin bug *Pristhesancus plagipennis* (James et al., 1994), the haematophagus bug *Triatoma infestans* (Lorenzo Figueiras et al., 1994), the West Indian sugarcane borer *Metamasius hemipterus* (Ramirez-Lucas et al., 1996), and the larger grain borer *Prostephanus truncatus* (Hodges et al., 2002). An aggregation pheromone might arrest passing conspecifics, or it might induce conspecifics to move towards the emitter of the pheromone, i.e. attract conspecifics.

Eavesdropping

Aggregations may also form when individuals intercept a pheromone intended to e.g. attract a mate, and use it for other purposes. In some cases, the pheromone alone will incite sexual attraction in the opposite sex, but will cause aggregation by both sexes when combined with host odors (Wertheim et al., 2005). Virgin Japanese beetle females, *Popillia japonica* (Coleoptera, Scarabaeidae), attract high numbers of of males, but few females (Klein et al., 1973). A combination of virgin females and a mix of synthetic plant odor compounds caught a larger amount of females and a similar amount of males as compared to traps baited with only virgin females (ibid.). Similar results were found when the synthesized female pheromone was combined with a mix of synthetic plant odor compounds (ibid.).

Interaction between pheromones and host odors

Aggregation pheromones may also interact with odors from hosts. In some cases, attraction to the pheromone is enhanced by combination with host volatiles: the male-released aggregation pheromone of the beetle *Carpophilus dimidiatus* (Coleoptera, Nitidulidae) is attractive to both sexes, and attractiveness is further increased when a source of food odor (whole-wheat bread dough) was added to traps as a co-attractant. The dough was physically inaccessible to beetles entering the trap, and separated from the pheromone bait (Bartelt et al., 1995). This synergism has also been observed for other *Carpophilus* species (Bartelt and James, 1994). Attraction to a male-released aggregation pheromone is also enhanced by combination with host odors in the beetle *Rhyzopertha dominica* (Coleoptera, Bostrichidae) (Bashir et al., 2001), and the West Indian sugarcane borer, *Metamasius hemipterus* (Coleoptera, Curculionidae) (Ramirez-Lucas et al., 1996).

Adult *Drosophila melanogaster* (Diptera, Drosophilidae) aggregate on suitable substrates (such as fermenting fruit) to mate, feed and (for females) to oviposit. The response of both male and female *D. melanogaster* to the aggregation pheromone of this species is dependent on combination with odors from a suitable food source – the pheromone alone is not attractive (Bartelt et al., 1985). The active substance has been identified as cis-vaccenyl acetate, cVA (ibid.). Males deposit cVA onto the substrate when feeding, and females receive cVA from males during copulation, and subsequently deposit it when ovipositing (Butterworth, 1969). As cVA is attractive to both male and female *D. melanogaster* when combined with food odours, these behaviors all contribute to aggregation. Other insect species have been observed to release aggregation pheromones only when feeding on a suitable host., e.g. males of the square-necked grain beetle, *Cathartus quadricollis*, (Pierce et al., 1988). Although no pheromone has been identified, this is also likely to be the case in the flea beetle, *Phyllotreta cruciferae*, where both males and females are attracted to conspecifics feeding on oilseed rape, but not to beetles that are not feeding, or to plants damaged by other insects (Peng and Weiss, 1992).

Dose dependency of pheromones

Dose-dependent response to aggregation pheromones has also been observed, where low to intermediate doses are highly attractive, but high doses cause aversion. This might be an attempt by the responding individual to avoid overcrowding, like in the previously mentioned bark beetle example. Another example of this might be seen in the housefly, *Musca domestica*. Sexually mature female houseflies emit a pheromone that induces aggregated ovipositing in conspecific females when added to a fermented wheat bran substrate (Jiang et al., 2002). Oviposition bioassays with identified pheromone components show a dose-response relationship, where oviposition rates increase with dose up to a point, and thereafter decrease (Jiang et al., 2002). First instar larvae of *N. viridula* show dose-dependent attraction to whole-body extracts (fig. 1), where intermediate doses are more attractive than high doses (Lockwood and Story, 1985). Several bark beetle species also show dose-dependent response to aggregation pheromones released by conspecifics (reviewed in Raffa, 2001).

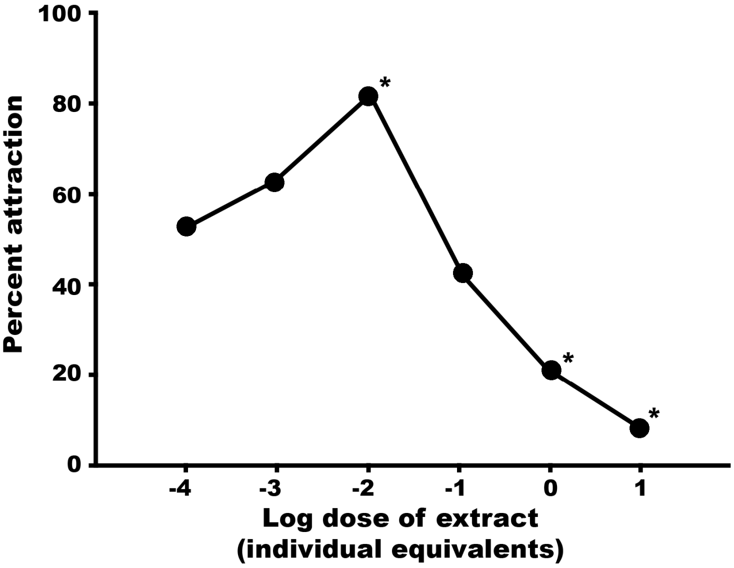

Fig. 1. Percent attracted individuals as a function of log dose of whole-body extract. * denotes a response significantly different from random choice (ANOVA followed by Least Significant Difference post-hoc test, P < 0.001). After Lockwood and Story, 1985.

Calling individuals may also reduce pheromone emission as conspecific density increases, possibly to decrease attraction and avoid overcrowding. An example of decreased pheromone emission with increasing density can be seen in *C. dimidiatus* males, where the uptake of pheromones by odor collection filters decreased with increasing numbers of males in the collection chamber (Bartelt et al., 1995).

Pheromone blend effects

A pheromone can consist of a single chemical, but is often composed of several compounds. The ratio between the compounds can distinguish the pheromone of one species from that of another species that (partially or completely) uses the same compounds in its' pheromone blend. The adaptive value of this has not been established, but different ratios between compounds in aggregation pheromones sometimes attract male and female conspecifics to different degrees. This has been observed for the male-released pheromone of the saw-toothed grain beetle, *Oryzaephilus surinamensis* (Coleoptera, Silvanidae), where the ratio between the components affects the attraction of male and female adult beetles (White and Chambers, 1989). A similar pattern is seen for attraction to the male-released pheromone of the West Indian sugarcane borer, *Metamasius hemipterus* (Coleoptera, Curculionidae), where some components of the pheromone blend mainly attract females, and others attract both sexes (Ramirez-Lucas et al., 1996). In the bark beetle *Ips typographus*, a lower proportion of attracted males than attracted females landed on sticky traps baited with pheromone components, indicating sex differences in close-range orientation (Schlyter and Birgersson, 1999). A similar pattern has been observed for the bark beetle *Ips paraconfusus* (Byers, 1989).

Pre-exposure

Previous exposure can also mediate response to a pheromone. In the stored product pest the confused flour beetle *Tribolium confusum* (Coleoptera, Tenebrionidae), males emit an aggregation pheromone attractive to both sexes, while the female emits a sex pheromone attractive to males (O'Ceallachain and Ryan, 1977). The response of male and female beetles to both pheromones depends on their previous exposure, albeit the adaptive value of this is unclear. If they have already experienced the male pheromone, both sexes show a lower degree of attraction to it, but male attraction to the female pheromone is increased (ibid.). Exposure to female pheromone lowered male attraction to that pheromone, and male response was not fully restored until 48 hours after exposure. Simultaneous exposure to both male and female pheromone had an identical effect to that of exposure to male pheromone only. The ecological reasons behind these shifts in attraction remain unclear (ibid.).

Non-chemical signals

Apart from pheromones, some species use visual cues and signals to regulate aggregation. Nymphs of the southern green stink bug, *Nezara viridula* (Hemiptera, Pentatomidae), hatch in groups, and aggregation is maintained initially by visual and tactile stimuli that arrest movement in conspecifics (Lockwood and Story, 1985). As the nymphs grow older, they start to produce a density-regulating pheromone that is attractive at low to intermediate concentrations, but repellent at high concentrations (ibid.).

Benefits and costs of living in a group

Living in close proximity to a number of conspecifics may entail a number of fitness costs and benefits for an individual. For behavior resulting in aggregations of conspecifics to persist, the net effect on fitness must on average be positive or neutral compared to alternative behavior. Studies that give empirical data on the costs and benefits of group living for the individual are rare, and proposed fitness effects are often speculative. An exception is the wealth of data available for bark beetles (reviewed in Raffa, 2001), discussed below in section 3.1.2.

For an aggregation of close relatives, individuals may engage in behavior that is beneficial to others in the group, but detrimental to their own health or safety, while still increasing their fitness. As long as the net benefit to the individual and to its' relatives (factoring in the degree of relatedness) outweigh the cost, the behavior is beneficial.

Benefits

Protection from natural enemies

A commonly suggested benefit of living in a group is protection from natural enemies, especially predators. A number of mechanisms have been proposed, one being dilution of risk, where the prey becomes less exposed to predation when in an aggregation. This could be due to a predator or parasite being less efficient in utilizing its' prey when the prey is in an aggregation. Fireweed aphids, *Aphis varians* (Homoptera, Aphididae), are preyed upon by ladybird beetles (mainly *Hippodamia convergens*). The rate of population increase for colonies exposed to predators increases with colony size; for colonies protected from predators, population increase rates were overall higher, but declined with colony size (Turchin and Kareiva, 1989). Although the exact mechanism is unclear, colonies exposed to predators experience a dilution effect, where predator feeding efficiency (expressed as mean number of predators per colony multiplied by mean number of prey killed per predator) cannot keep up when colony size of their prey increases. Hence, the per capita risk for an aphid to fall prey to a coccinelid beetle decreases, as the colony of which it is part increases in size (ibid.).

Some insects have active defenses, e.g. emitting a repellent or bitter substance. Being in an aggregation might increase the efficiency of such a defense. First- to third-instar nymphs of the southern green stink bug, *N. viridula*, form dense aggregations (Lockwood and Story, 1985). Natural enemies were more efficiently repelled by the active defense of an aggregation of nymphs than by single individuals.

Individuals that are part of an aggregation may also benefit from an increased level of vigilance. Densely aggregated grey pine aphids, *Schizolachnus pineti*, are alerted to attack by syrphid larvae by the struggling aphid victim, whose swinging abdomen and kicking hind legs appear to send a touch-mediated message to neighbors (Kidd, 1982). The neighbors, in turn, pass this message on, and members of the colony may either choose to walk away or drop off the pine needle to avoid predation (ibid.). The syrphid larvae respond to this behavior by trying to lift their prey away from the other aphids before it has a chance to alert its' neighbors (ibid). In experiments where a syrphid larvae was introduced to aphid colonies of varying sizes, the percent of aphids escaping predation increased with increasing colony size (fig. 2, ibid).

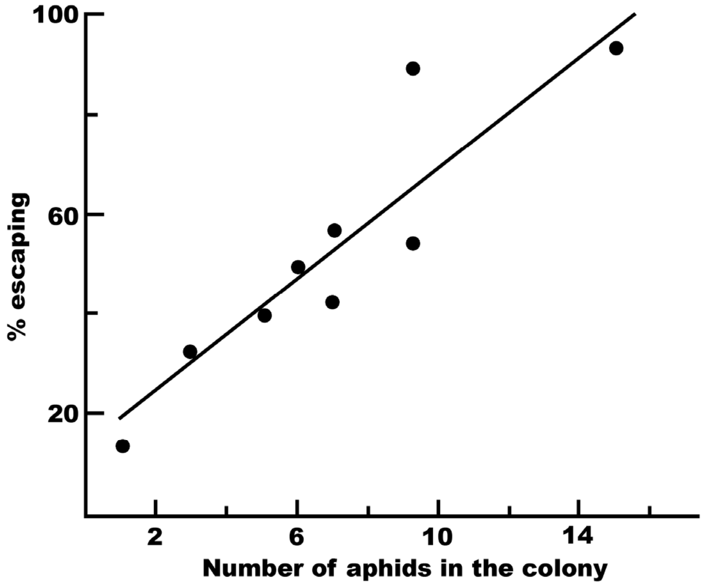

Fig. 2. Percentage of aphids escaping predation (from a single introduced syrphid larvae predator) as an effect of colony size ($Y = 5.58 X + 13.75$, $n = 12$; comparing slope to $b = 0$: $t = 5.7$, d.f. = 10, $p < 0.001$). After Kidd, 1982.

Aggregation may also result in benefits for insects that use aposematic coloration. Insects with aposematic coloration have high-contrast colors to warn potential predators that they are unpalatable or have efficient active defenses, such as stings. In a "novel world" experiment with the great tit (*Parus major*) as a predator, several advantages were shown for aggregations of types of simulated prey that had aposematic coloration (Riipi et al., 2001). Detectability increased only asymptotically with group size, and was only marginally increased due to conspicuous (aposematic) signals (ibid.). Furthermore, a dilution effect was present, where naïve birds left the group after discovering that the prey was unpalatable, and avoidance learning of the signal was faster when the prey was grouped (ibid.).

Increased efficiency in resource utilization

An aggregation of conspecifics can sometimes utilize a resource more efficiently than single individuals. Some insects inoculate a substrate with microorganisms that enhance the substrate as a food resource for their larvae. Larvae would then have an increased benefit of resource enhancement when females oviposit in aggregation (Wertheim et al., 2002a). Female *D. melanogaster* emit an aggregation pheromone onto the substrate when ovipositing (Bartelt et al., 1985). Increased adult density on the substrate during egg-laying resulted in decreased larval mortality, decreased fungal cover, and larger emerging flies (Wertheim et al., 2002b). Direct application of the pheromone compound had no direct effect on these indicators of larval fitness (ibid.). Fungal growth on the substrate, which was negatively related to larval survival, also decreased with increasing number of larvae (ibid.). Adult drosophilids act as vectors for dispersal of yeasts, on which both larvae and adults feed (Gilbert, 1980). Adults inoculation of the substrate with yeast may thus make it more palatable for larvae (Wertheim et al., 2002b).

Aggregated attack on a host capable of active defense can succeed where single individuals would perish. Some species of bark beetle (Coleoptera, Scolytidae) are capable of overcoming the active defenses of living, healthy host trees by means of pheromone-mediated synchronous attack of numerous individuals (reviewed in Alcock, 1982; Wood, 1982; Byers, 1989; Paine et al., 1997; Raffa, 2001). Primary bark beetles (e.g. *Dendroctonus frontalis* (Wood, 1982), *D. vitei*, *D. mexicanus*, *D. adjunctus*, *D. brevicomis* (Wood, 1982), *D. ponderosae* (Alcock, 1982; Wood, 1982; Raffa, 2001), *D. jeffreyi*, and *Ips typographus*) attack healthy trees when they are at normal population densities, but can also attack stressed trees at low population levels. Secondary bark beetles (e.g. *I. pini* (Kleipzig et al., 1991), *Scolytus ventralis*, *D. rufipennis*, *D. pseudotsugae*, *D. simplex*, and *Tomicus piniperda*) mainly attack stressed or injured trees, but can attack healthy trees when they are at high population densities. The secondary bark beetles *S. ventralis* and *T. piniperda* do not seem to utilize pheromones in aggregation, but instead rely on host cues (Schlyter and Birgersson, 1999).

The amount of substrate available for the development of bark beetle larvae on any given tree is limited, and bark beetles thus face con- and intraspecific competition (Raffa, 2001). When attacking a healthy host, bark beetles face lowered fitness or outright mortality unless enough attacking individuals are present (ibid.). For bark beetles attacking live hosts, the optimum number of bark beetles colonizing a square meter thus depends on a trade-off between the necessity to overcome host defenses, and competition for larval substrate (ibid.). Bark beetle species that attack dead hosts attain maximum fitness at lower densities, in several cases just a single beetle pair (fig. 3, ibid.). Primary bark beetles attacking dead trees maximize their fitness at lower attack densities compared to when they attack live trees (ibid.). Data for optimal attack densities on live hosts for the secondary bark beetle species *D. pseudotsugae*, *Ips avulses*, *I. gadicollis*, *I. cembrae*, and *I. pini* are not available for inclusion in fig 3.

Aggregation as a mechanism for overcoming the active defenses of live host trees may have evolved from overhearing of pheromone signals sent by secondary bark beetles (that attack dead hosts) to attract mates (Schlyter and Birgersson, 1999). Avoiding that competitors overhear a sex pheromone or stopping them from accessing the resource is difficult, meaning that the calling beetles have little alternative but accept competition from eavesdropping conspecifics (ibid.).

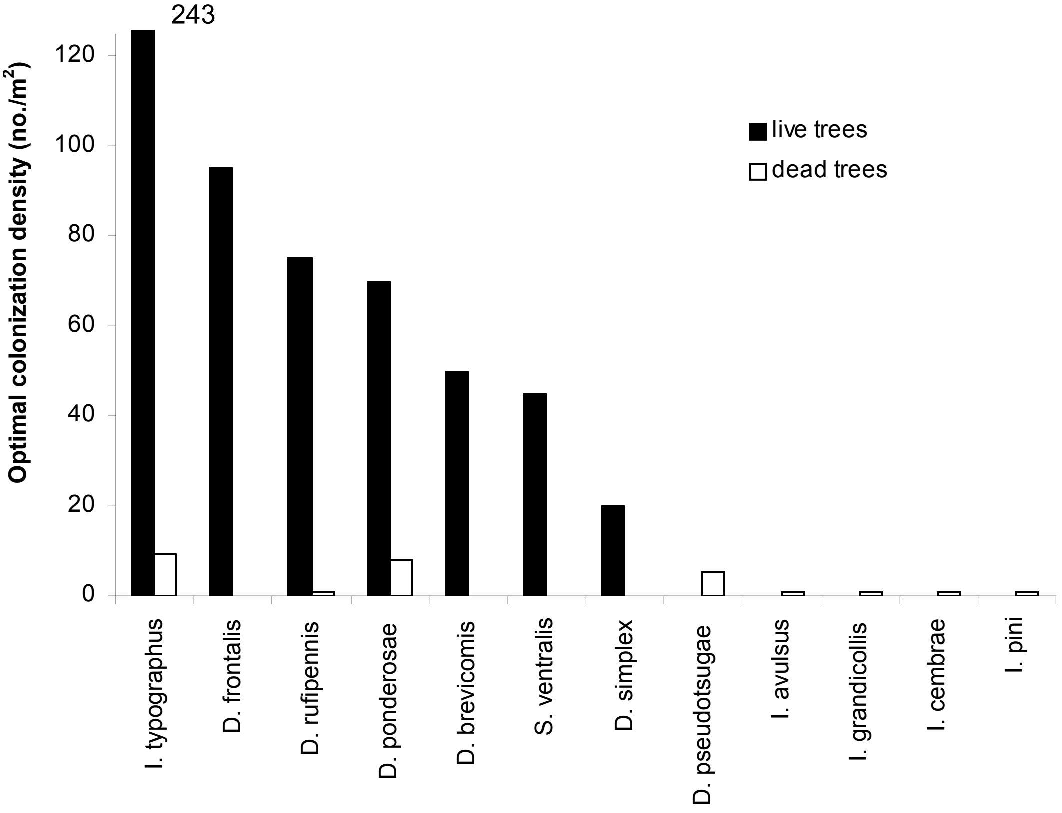

Fig. 3. Colonization density leading to the highest level of realized fitness, as estimated from analysis of original data. Population density given for the sex that selects the host: males in *Ips*, females in *Scolytus* and *Dendroctonus*. Data not available for all combinations of species and host status (dead or alive). After Raffa 2001.

Even on hosts where defense is passive rather than active, communal feeding can be beneficial, for instance if it results in a higher efficiency in breaking down physical barriers, such as waxy layers on leaves, the pod surrounding the seeds, etc. Nymphs of the large milkweed bug, *Oncopeltus fasciatus* (Hemiptera, Lygaeidae) benefit from aggregation in penetrating the pod wall surrounding milkweed seeds, suffering lower mortality in groups of twenty than in groups of five (Ralph, 1976). *Aphis fabae* (Homoptera, Aphididae) have been shown to need less time to successfully penetrate to the phloem, need to inject less saliva, and ingest more phloem on previously infested leaves compared to uninfested leaves (Prado and Tjallingii, 1997).

Beneficial change of local microclimate

An aggregation of insects might also alter the local microclimate, where e.g. temperature and humidity could be changed to more advantageous levels. Higher temperature could facilitate growth for nymphs and larvae, and a higher relative humidity might decrease water loss for aggregated individuals (Wertheim et al., 2005). In environments with low relative humidity, aggregated nymphs of the southern green stink bug, *N. viridula*, develop faster and have a lower mortality rate (Lockwood and Story, 1985), suggesting that the aggregation may serve a role in preserving moisture. Aggregated nymphs also showed faster development than solitary nymphs when the surrounding habitat was at a low temperature (ibid.). The dense clusters of nymphs are also better able to adhere to their substrate, which might help them withstand severe weather that could otherwise cause mortality.

For egg-masses susceptible to desiccation, the ratio of surface area to volume will decrease with number, assuming that the egg masses are of similar shape. The blackfly *Simulium damnosum* (Diptera, Culicomorpha) lays eggs in communal egg masses (Davies, 1962), and females prefer oviposition sites that contain conspecific eggs, or volatile chemicals emanating from eggs, suggesting the presence of a pheromone (McCall and Cameron, 1995). Eggs of *S. damnosum* cannot withstand prolonged exposure to air, and the egg masses may be more resistant to drought than single eggs would be (ibid.).

Costs

Increased detectability by natural enemies

An increased visibility to predators and parasites is often suggested as a major detriment of aggregated behavior. Active signals are sometimes overheard by parties other than the intended recipient. In *D. melanogaster*, the use of aggregation pheromones makes the larvae more conspicuous to the parasitoid *Leptopilina heterotoma* (Wertheim et al., 2003). In field experiments, a larger fraction of larvae on substrates treated with pheromone were parasitized compared to larvae on a pheromone-free substrate (ibid.). *L. heterotoma* also showed a higher attraction towards pheromone-enriched substrates than pheromone-free substrates in wind tunnel experiments (ibid.). The predatory beetle *Thanasimus undatulus* (Coleoptera, Cleridae) is attracted to traps baited with pheromone from the spruce beetle, *D. rufipennis* (Poland and Borden, 1997). The use of a pheromone for mating and aggregation thus incurs an increased risk of predation in the spruce beetle (ibid.).

Increased competition due to overheard aggregation signals

A con- or interspecific competitor may intercept an aggregation signal, e.g. a pheromone. Adult males of the larger grain borer, *Prostephanus truncatus* (Coleoptera, Bostrichidae) emit pheromones that are attractive to both males and females (Hodges et al., 2002). Once females have arrived, males stop emitting pheromones, indicating that the main role of the pheromone is the attraction of females, and that other males opportunistically aggregate to the pheromone (Hodges et al., 2002). While bark beetles attacking live hosts can benefit from the presence of conspecifics (in overcoming host defenses) up to a certain optimal density (fig. 3), arrival of further individuals may cause decreased fitness in those already present, due to competition for the limited amount of substrate available for larval development (Raffa, 2001). Bark beetles attacking dead hosts generally maximize their fitness at low densities, often just a single beetle pair (fig. 3, ibid.). Overhearing of aggregation signals is thus niche- and situation-dependent in bark beetles.

Increased risk of infection by pathogens

Being in a group might increase the probability of infection by pathogens. *Triatoma infestans* (Hemiptera, Reduviidae) deposit their faeces outside their communal shelter, and it has been suggested that this reduces the risk of acquiring the flagellate parasite *Blastocrithidia triatomae* (Lorenzo and Lazzari, 1996). It is unkown whether this behavior is undertaken by single individuals, or if there is any density-dependent aspects to it.

Increased competition

A high density of conspecifics can lead to competition for resources, such as food, space, or mates. Males of the sandfly, *Lutzomyia longipalpis*, form leks: aggregations at sites that females visit to mate, where males defend individual territories (Jones and Quinnell, 2002). With increasing size of the lek, higher-quality males obtain significantly more mates, while per capita mating rates fall (Jones and Quinnell, 2002). Accordingly, females show a strong preference for selecting larger leks over smaller (Jones and Quinnell, 2002). In dense aggregations on high-quality substrates, *D. melanogaster* larvae faced severe intraspecific competition, increasing mortality, and decreasing adult size (Wertheim et al., 2002b). This contrasts with the beneficial effects at low to intermediate densities previously mentioned. Competition has been found to have similar effects for several fungus-feeding drosophilids (Grimaldi and Jaenike, 1984).

Deterioration of local microclimate

Aggregations might also cause local conditions to deteriorate, where active chemical defenses in plants increase with density of attackers (Rhoades, 1985; Geervliet et al., 1998), or levels of heat or humidity in a substrate lead to an increased probability for infection by pathogens, such as fungi (Sinha and Wallace, 1966). For communal egg masses, eggs at the center of the mass may experience oxygen deprivation once the size of the egg mass increases beyond a certain point (Imhof and Smith, 1979). Indirect plant defenses may also increase when herbivores aggregate. Ovipositing females of the parasitoids *Cotesia glomerata* and *C. rubecula* (Hymenoptera, Braconidae) can distinguish brussel sprout plants with a high density of *Pieris rapae* caterpillars from uninfested plants, while low density infestations were not detected (Geervliet et al., 1998).

Discussion

An aggregation may have different fitness effects on individuals from which signals causing aggregations originate (senders) and individuals reacting to the signals (receivers). In the case of a positive effect of conspecific density on individual fitness, the sender benefits from attracting the receiver to the resource. If the sender does not benefit, selective pressures should act to silence the signal that leads the receiver to the resource (Maynard Smith and Harper, 2003). This selection process may be hampered for a number of reasons. The receiver may, for instance, be overhearing a pheromone signal that serves the vital purpose of attracting mates to the sender (see e.g. Klein et al., 1973). Any change to make the signal more cryptic to the eavesdropping receiver, could also render it less efficient in attracting a mate, leading to fitness loss.

As was previously discussed, the line between eavesdropping and mutual benefit may be thin, however: for the bark beetle *D. ponderosae*, it depends on the quality of the host. Females of *D. ponderosae* emit a pheromone that attracts males for mating (Schlyter and Birgersson, 1999). If the host is a dead tree, other females responding to the pheromone will increase food competition for the calling female, effectively lowering her fitness. The receiving females would then effectively be overhearing the signal. However, in those cases where females colonize living trees, additional females arriving will, up to a point, help overcome the active defenses of the tree, such as resin flow, leading to mutual benefit. Females that are colonizing a healthy tree have also been shown to emit more pheromones than those colonizing a dead tree (Alcock, 1982).

Even on a dead tree, however, the interests of the caller and the eavesdropper are not entirely opposed: both want to avoid unnecessary resource competition. Females of *D. pseudotsugae* emit a pheromone that attracts males for mating. After mating, large quantities of this pheromone are released. The response of overhearing females is dependent on dose: while low doses are attractive, higher doses induce a large portion of responders to seek other parts of the same tree, or another host entirely (Raffa, 2001).

The effects of the signal are thus situation dependent. Host quality and current density of conspecifics affect fitness effects for callers and receivers (in fact, determining whether the receivers will be eavesdroppers or cooperators). Choices made by future responders will also affect the fitness of the current callers and responders. Population levels may also affect the number of possible responders, in turn affecting the outcome of different calling or responding strategies (Raffa, 2001).

The division of aggregation signals into those for which aggregation is the sole observed result, and those that serve other purposes as well, may thus be problematic. While some cases of pure cooperation or pure eavesdropping exist, in others it may be difficult to distinguish. A clear example of a signal used in cooperation is the aggregation pheromone of *D. melanogaster* that attract conspecifics for aggregated mating and oviposition, which has positive effects on larval fitness (Wertheim et al., 2002b). The sex pheromone of the Japanese beetle is an example of eavesdropping - it acts as an aggregation signal when combined with host odors (Klein et al., 1981). The benefit of aggregation to the sender is unclear, and the signal may thus be defined as an overheard sex pheromone rather than a true aggregation signal. In other cases, especially in bark beetles, the balance of fitness costs and benefits to both sender and receiver is dependent both on host health as well as the choices of other senders and receivers. In such a situation, it can be difficult to distinguish a dedicated aggregation signal from an appropriated sex attraction signal (Alcock, 1982).

Wertheim (2005) points to the frequent association between insect aggregations and symbiotic microorganisms. Positive density-dependent effects have been observed when such symbionts are present, helping to offset negative aggregation effects due to e.g. competition, but whether symbionts are a necessary or sufficient condition for the formation or evolutionary origin of aggregations is less clear. Schlyter and Birgersson (1999) suggest that aggregation behavior occurs when a species utilizes a limited or patchy resource base that cannot be defended. If the species has a pheromone calling system for mate attraction, this may be co-opted by conspecifics as a cue for finding the resource. Such a system is likely to be the evolutionary ancestor of the current bark beetle aggregation pheromone systems that empower several species to overcome the active defenses of healthy trees by synchronous attack of multiple beetles (Schlyter and Birgersson, 1999).

While experimental documentation of fitness effects of aggregation is somewhat scarce, convincing cases do exist. Positive effects of conspecific density include the dilution effect on ladybird predation on Fireweed aphids, *A. varians* (Turchin and Kareiva, 1989), and the positive effects of increasing adult density on larval substrate in *D. melanogaster* (Wertheim et al., 2002b). Convincing negative effects of increasing conspecific density on fitness include increased risk of parasitism (Wertheim et al., 2003) and increased competition for *D. melanogaster* larvae (Wertheim et al., 2002b). For several bark beetle species, field experiments show clear evidence of both cooperative and competitive effects of aggregation, as mentioned in previous sections (reviewed in Raffa, 2001). For most of the suggested costs and benefits, however, experimental evidence yet remains to be collected. In cases where data on fitness effects is available, it needs to be extended to include a wider selection of species and situations.

A true measure of fitness must reflect the end result: to what degree the individual manages to spread its' genes. A phenotype or genotype that entails lowered survival or growth at one stage, may yet ultimately increase the lifetime fitness of the individual. In eusocial insects, the majority of individuals produce no offspring of their own, while still having indirect fitness through the offspring of closely related individuals. Calculating lifetime fitness may necessitate the tracking of particular individuals over time. Tagging individuals and subsequently recapturing or re-measuring relevant variables may present a partial solution. For small or highly mobile species in field situations tracking individuals may not be feasible. The lack of experimental data on fitness effects of aggregation, especially over the whole life cycle, is therefore understandable. The problem may need to be approached for discrete parts of the life cycle, and for life cycle stages or species with little mobility, enabling lab or field testing where individuals can be kept enclosed without undue interference with their natural behavior. Future research with innovative approaches toward testing the fitness effects of aggregation would greatly help our understanding of this fascinating phenomenon.

References

ALCOCK, J. 1982. Natural selection and communication among bark beetles. *Fla. Entomol.* 65: 17-32.

ALDRICH, J. 1988. Chemical Ecology of the Heteroptera. *Annu. Rev. Entomol.* 33: 211-238.

BARTELT, R. J., and JAMES, D. G. 1994. Aggregation pheromone of Australian Sap beetle, *Carpophilus davidsoni* (Coleoptera: Nitidulidae). *J. Chem. Ecol.* 20: 3207-3219.

BARTELT, R. J., SCHANER, A. M., and JACKSON, L. L. 1985. cis-Vaccenyl acetate as an aggregation pheromone in Drosophila melanogaster. *J. Chem. Ecol.* 11: 1747-1756.

BARTELT, R. J., WEAVER, D. K., and ARBOGAST, R. T. 1995. Aggregation pheromone of Carpophilus dimidiatus (F.) (Coleoptera: Nitidulidae) and responses to Carpophilus pheromones in South Carolina. *J. Chem. Ecol.* 21: 1763-1779.

BASHIR, T., BIRKINSHAW, L. A., HALL, D. R., and HODGES, R. J. 2001. Host odours enhance the responses of adult Rhyzopertha dominica to male-produced aggregation pheromone. *Entomol. Exp. Appl.* 101: 273-280.

BUTTERWORTH, F. M. 1969. Lipids of Drosophila: A Newly Detected Lipid in the Male. *Science* 163: 1356-1357.

BYERS, J. A. 1989. Chemical ecology of bark beetles. *Cellular and Molecular Life Sciences (CMLS)* 45: 271-283.

COULSON, R. N. 1979. Population Dynamics of Bark Beetles. *Annu. Rev. Entomol.* 24: 417-447.

DAVIES, J. B. 1962. Egg-Laying Habits of Simulium Damnosum Theobald and Simulium Medusaeforme Form Hargrevesi Gibbins in Northern Nigeria. 196: 149-150.

GEERVLIET, J. B. F., ARIENS, S., DICKE, M., and VET, L. E. M. 1998. Long-Distance Assessment of Patch Profitability through Volatile Infochemicals by the Parasitoids Cotesia glomerata and C. rubecula (Hymenoptera: Braconidae). *Biological Control* 11: 113-121.

GILBERT, D. G. 1980. Dispersal of yeasts and bacteria by Drosophila in a temperate forest. *Oecologia* V46: 135-137.

GRIMALDI, D., and JAENIKE, J. 1984. Competition in Natural Populations of Mycophagous Drosophila. *Ecology* 65: 1113-1120.

HARTLIEB, E., and ANDERSON, P. 1999. Olfactory-released behaviours. pp. 315-349, *in* B. S. Hansson (ed.) Insect olfaction. Springer Verlag, Berlin Heidelberg,

HODGES, R. J., BIRKINSHAW, L. A., FARMAN, D. I., and HALL, D. R. 2002. Intermale variation in aggregation pheromone release in Prostephanus truncatus. *J. Chem. Ecol.* 28: 1665-1674.

IMHOF, J. E., and SMITH, S. M. 1979. Oviposition Behavior, Egg Masses and Hatching Response of the Eggs of five Nearctic Species of *Simulium* (Diptera: Simuliidae). *Bull. Entomol. Res.* 69: 405-426.

JAMES, D. G., MOORE, C. J., and ALDRICH, J. R. 1994. Identification, synthesis, and bioactivity of a male-produced aggregation pheromone in assassin bug, Pristhesancus plagipennis (Hemiptera - Reduviidae). *J. Chem. Ecol.* 20: 3281-3295.

JIANG, Y., LEI, C.-L., and NIU, C.-Y. 2002. Semiochemicals from ovaries of gravid females attract ovipositing female houseflies, Musca domestica. *J. Insect Physiol.* 48: 945-951.

JONES, T. M., and QUINNELL, R. J. 2002. Testing predictions for the evolution of lekking in the sandfly, Lutzomyia longipalpis. *Animal Behaviour* 63: 605-612.

KIDD, N. A. C. 1982. Predator Avoidance as a Result of Aggregation in the Grey Pine Aphid, Schizolachnus pineti. *The Journal of Animal Ecology* 51: 397-412.

KLEIN, M., LADD, T., and LAWRENCE, K. 1973. Simultaneous exposure of phenethyl propionate-eugenol (7:3) and virgin female japanese beetle as a lure. *J. Econ. Entomol.* 66: 373-374.

KLEIN, M. G., TUMLINSON, J. H., LADD, T. L., and DOOLITTLE, R. E. 1981. Japanese beetle (Coleoptera: Scarabaeidae): Response to Synthetic Sex Attractant Plus Phenethyl Propionate: Eugenol. *J. Chem. Ecol.* 7: 1-7.

KLEIPZIG, K. D., RAFFA, K. F., and SMALLEY, E. B. 1991. Association of an Insect-Fungal Complex with Red Pine Decline in Wisconsin. *For. Sci.* 37: 1119-1139.

LOCKWOOD, J. A., and STORY, R. N. 1985. Bifunctional pheromone in the first instar of the southern green stink bug, *Nezara viridula* (L.) (Hemiptera: Pentatomidae): its characterization and interaction with other stimuli. *Ann. Entomol. Soc. Am.* 78: 474-479.

LORENZO FIGUEIRAS, A. N., KENIGSTEN, A., and LAZZARI, C. R. 1994. Aggregation in the haematophagous bug Triatoma infestans: Chemical signals and temporal pattern. *J. Insect Physiol.* 40: 311-316.

LORENZO, M. G., and LAZZARI, C. R. 1996. The Spatial Pattern of Defaecation in Triatoma infestans and the Role of Faeces as a Chemical Mark of the Refuge. *J. Insect Physiol.* 42: 903-907.

MAYNARD SMITH, J. 1982. Evolution and the Theory of Games. - Cambridge University Press, Cambridge, United Kingdom.

MAYNARD SMITH, J., and HARPER, D. 2003. Animal Signals. - Oxford University Press, New York, USA.

MCCALL, P. J., and CAMERON, M. M. 1995. Oviposition pheromones in insect vectors. *Parasitology Today* 11: 352-355.

METCALF, R. L., and METCALF, E. R. 1992. Plant kairomones in insect ecology and control. *Chapman and Hall, New York.*

O'CEALLACHAIN, D. P., and RYAN, M. F. 1977. Production and perception of pheromones by the beetle Tribolium confusum. *J. Insect Physiol.* 23: 1303-1309.

PAINE, T. D., RAFFA, K. F., and HARRINGTON, T. C. 1997. Interactions among scolytid bark beetles, their associated fungi, and live host conifers. *Annu. Rev. Entomol.* 42: 179-206.

PARRISH, J. K., and EDELSTEIN-KESHET, L. 1999. Complexity, Pattern, and Evolutionary Trade-Offs in Animal Aggregation. *Science* 284: 99-101.

PENG, C., and WEISS, M. J. 1992. Evidence of an aggregation pheromone in the flea beetle, Phyllotreta Cruciferae (Goeze) (Coleoptera: Chrysomelidae). *J. Chem. Ecol.* 18: 875-884.

PIERCE, H. D., PIERCE, A. M., JOHNSTON, B. D., OEHLSCHLAGER, A. C., and BORDEN, J. H. 1988. Aggregation pheromone of square-necked grain beetle,Cathartus quadricollis (GuÃ©r.). *J. Chem. Ecol.* V14: 2169-2184.

POLAND, T. M., and BORDEN, J. H. 1997. Attraction of a bark beetle predator, *Thanasimus undatulus* (Coleoptera: Cleridae), to pheromones of the spruce beetles and two secondary bark beetles (Coleoptera: Scolytidae). *J. Entomol. Soc. Brit. Columbia* 94: 35-41.

PRADO, E., and TJALLINGII, W. F. 1997. Effects of previous plant infestation on sieve element acceptance by two aphids. *Entomol. Exp. Appl.* 82: 189-200.

RAFFA, K. F. 2001. Mixed messages across multiple trophic levels: the ecology of bark beetle chemical communication systems. *Chemoecology* 11: 49-65.

RALPH, C. P. 1976. Natural food requirements of the large milkweed bug, Oncopeltus fasciatus (Hemiptera: Lygaeidae), and their relation to gregariousness and host plant morphology. *Oecologia* 26: 157-175.

RAMIREZ-LUCAS, P., ROCHAT, D., and ZAGATTI, P. 1996. Field trapping of Metamasius hemipterus with synthetic aggregation pheromone. *Entomol. Exp. Appl.* 80: 453-460.

RENWICK, J. A. A. 1989. Chemical Ecology of Oviposition in Phytophagous Insects. *Experientia* 45: 223-228.

RHOADES, D. F. 1985. Offensive-Defensive Interactions between Herbivores and Plants: Their Relevance in Herbivore Population Dynamics and Ecological Theory. *The American Naturalist* 125: 205-238.

RIIPI, M., ALATALO, R. V., LINDSTROM, L., and MAPPES, J. 2001. Multiple benefits of gregariousness cover detectability costs in aposematic aggregations. 413: 512-514.

SCHLYTER, F., and BIRGERSSON, G. 1999. Forest Beetles. *in* J. Hardie and A. K. Minks (eds.), Pheromones in Non-Lepidopteran Insects Associated with Agricultural Plans. CAB International, Oxford, United Kingdom.

SINHA, R. N., and WALLACE, H. A. H. 1966. Ecology of insect-induced hot spots in stored grain in western Canada. *Res. Popul. Ecol.* 8: 107-32.

STEPHENS, P. A., and SUTHERLAND, W. J. 1999. Consequences of the Allee effect for behaviour, ecology and conservation. *Trends Ecol. Evol.* 14: 401-405.

TURCHIN, P., and KAREIVA, P. 1989. Aggregation in Aphis Varians: An Effective Strategy for Reducing Predation Risk. *Ecology* 70: 1008-1016.

WERTHEIM, B., DICKE, M., and VET, L. E. M. 2002a. Behavioural plasticity in support of a benefit for aggregation pheromone use in Drosophila melanogaster. *Entomol. Exp. Appl.* 103: 61-71.

WERTHEIM, B., MARCHAIS, J., VET, L. E. M., and DICKE, M. 2002b. Allee effect in larval resource exploitation in Drosophila: an interaction among density of adults, larvae, and micro-organisms. *Ecol. Entomol.* 27: 608-617.

WERTHEIM, B., VAN BAALEN, E.-J. A., DICKE, M., and VET, L. E. M. 2005. Pheromone-mediated aggregation in nonsocial arthropods: an evolutionary ecological perspective. *Annu. Rev. Entomol.* 50: 321-346.

WERTHEIM, B., VET, L. E. M., and DICKE, M. 2003. Increased risk of parasitism as ecological costs of using aggregation pheromones: Laboratory and field study of Drosophila-Leptopilina interaction. *Oikos* 100: 269-282.

WHITE, P. R., and CHAMBERS, J. 1989. Saw-toothed grain beetle *Oryzaephilus surinamensis* (L.) (Coleoptera - Silvanidae) antennal and behavioral responses to individual components and blends of aggregation pheromone. *J. Chem. Ecol.* 15: 1015-1031.

VISSER, J. H. 1986. Host Odor Perception in Phytophagous Insects. *Annu. Rev. Entomol.* 31: 121-144.

WOOD, D. L. 1982. The Role of Pheromones, Kairomones, and Allomones in the Host Selection and Colonization Behavior of Bark Beetles. *Annu. Rev. Entomol.* 27: 411-446.