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PHEROMONE-MEDIATED AGGREGATION IN NONSOCIAL ARTHROPODS: An Evolutionary Ecological Perspective

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■ **Abstract** Although the use of aggregation pheromones has been reported for hundreds of nonsocial arthropod species, the evolutionary ecological aspects of this behavior have received little attention. Despite the elaborate literature on mechanisms, robust data on costs and benefits of aggregation pheromones are scant. Existing literature indicates that, in contrast to the diversity of mechanisms, the ecological conditions in which aggregation pheromones are used are more alike. This points to a few general categories for costs and benefits of aggregation pheromones, and these are discussed. We subsequently review interspecific interactions that may be affected by the use of aggregation pheromones. We encounter a strikingly frequent association of aggregation pheromones with fungi and microorganisms and address cross-attraction by competitor species and exploitation by natural enemies. We show that aggregative behavior by individuals through the use of pheromones can profoundly affect ecological interactions and advocate further evolutionary and ecological investigations of pheromone-mediated aggregation.

INTRODUCTION

Animal aggregations are a general phenomenon that affects many spatial and temporal processes in ecological systems (94). One important mechanism that leads to the formation of animal aggregations is communication among individuals, whereby they actively seek each other out and form assemblies for certain periods. Several modes of communication exist, e.g., auditory, visual, or chemical, and each has its own advantages and disadvantages, such as reach, directionality, speed, and

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specificity (24). Depending on the environment, and on the ecology and physiology of the organisms, a certain set of signals evolves (9, 24).

In insects, as in most other animals, chemical information conveyance is of profound importance (9, 27, 28, 33, 110). Signals in chemical information conveyance are called info- or semiochemicals, and intraspecific signals that induce group formation are called aggregation pheromones. Infochemicals can mediate both intra- and interspecific interactions and thus should be of major interest to biologists in several research areas, such as behavioral ecology, evolutionary ecology, population dynamics, predator-prey interactions, and community ecology. Yet studies on aggregation pheromones have rarely been integrated into functional (i.e., evolutionary) ecological research and these pheromones are investigated mostly by mechanistic and applied approaches. The specialized organs for production and perception of aggregation pheromones and the chemical composition of pheromones have been studied in detail (reviewed in References 23, 26, 30), as well as the endocrine regulation and biosynthetic pathways of pheromone production (reviewed in 117, 132). In addition, the applications of aggregation pheromones in pest management have been widely explored (3, 58, 133). Major questions regarding evolutionary and ecological aspects of aggregation pheromones, however, remain mostly unaddressed. This is a serious limitation, because aggregation pheromones may be pivotal in the evolutionary and ecological dynamics in natural communities, as well as in agricultural settings.

Chemical signals and aggregative behavior are of tremendous importance to the ecology of insects. Moreover, they should be considered jointly to understand their ecological significance for individuals as well as population-level processes (144). Although a number of reviews have covered the ecology and evolution of either aggregation behavior (94, 100, 101) or chemical cues (27, 34, 110, 139), none have reviewed the combination of the two in an integrated manner. Additionally, the few and mostly older reviews that did incorporate evolutionary ecological aspects of aggregation pheromones were restricted to single taxonomic groups (2, 102, 137) or to groups defined by one specific aspect of their ecology (72, 83).

In this review we discuss the literature on aggregation pheromones in nonsocial arthropods from an evolutionary and ecological perspective and address the multitude of effects at the individual, population, and community levels. Although the literature is dominated by research on mechanistic aspects, this is not the focus of this review and we only briefly summarize the great diversity found in physiological and behavioral studies. Our major aim is to apply a cost-benefit perspective to provide a set of functional explanations for aggregation pheromones. Our analysis shows that the ecological conditions under which aggregation pheromones are used are strikingly similar among taxa. Therefore, the central hypothesis of our paper is that a small set of functional explanations applies to a large number of insect species. This allows us to draw general conclusions on the evolution of aggregation pheromones. Furthermore, we outline the interspecific interactions that may be affected by the use of aggregation pheromones, and discuss patterns that we find across many taxa. Finally, we argue for expansion of research into the evolutionary ecology of pheromone-mediated aggregations of insects.

AGGREGATION PHEROMONES: PHYSIOLOGY AND BEHAVIORAL RESPONSES

Aggregation pheromones attract and/or arrest conspecifics to the locality of release. Several more explicit definitions have been proposed, differing in designation of the sex of emitters and responders (23, 58, 83, 118). In our view, the ecological significance of group-forming by pheromones does not critically depend on the sex of emitter or responder. We therefore use a slight modification of Shorey's (118) definition of aggregation pheromones: released compound(s) causing aggregative behavior in conspecifics of both sexes or in the same sex as the emitter. This definition includes the pheromones that result in intrasexual aggregation but excludes the sex pheromones of one sex solely attracting responders of the opposite sex.

A simple query for "aggregation* and pheromon*" in CAB-abstracts from 1972 to March 2004 resulted in 1365 hits, and we made a selection from these articles for our review. The number of hits is likely an underestimate for articles on aggregation pheromone, because what we included in our definition of aggregation pheromones might be called sex or oviposition pheromones by others. We do not include social insects in our survey because colony members are so interdependent that the principle of group living has a meaning different from that in nonsocial insects. The studies on aggregation pheromones have widely divergent approaches, focusing on different factors influencing production and response, using field or laboratory setups, and applying different criteria and study aims.

In our survey, over 300 nonsocial arthropod species belonging to 51 families in 12 different orders were reported to use aggregation pheromones (Table 1). In most species, the chemical composition of the pheromone is known. Our aim for this section is to describe the diversity and similarities in mechanisms that are involved in communication through aggregation pheromones.

Pheromone Emission and Response

Pheromones can originate from specialized secretory glands or from body orifices and organs involved in digestion and reproduction (e.g., mouth, anus, and aedeagus). The emission of pheromones can be controlled by the sender, or they can be ungovernable or continuous. The senders can comprise males, females, both sexes, and/or immature stages (eggs, nymphs/larvae, and pupae). In several dipteran species, the pheromones released by the females are male-derived: Males produce the pheromone and transfer it to females during copulation (12, 19, 112). The perception of pheromones often involves advanced chemosensory organs, located primarily on the antennae, tarsi, or mouth appendages.

Individuals can differ considerably in the amount of pheromone they produce, owing to genetics (54, 84, 114) and to plastic behavior, such as by reducing the

TABLE 1 Nonsocial arthropod taxa that are shown or suggested to possess an aggregation pheromone, as reported in the literature from 1972 to March 2004[a]

Order	Family: Genus
Acari	**Acaridae:** *Caloglyphus, Lardoglyphus, Schwiebea*; **Ixodidae:** *Amblyomma, Dermacentor, Ixodes, Ornithodoros*; **Epidermoptidae:** *Dermatophagoides*; **Varroidae:** *Varroa*
Blattodea	**Blattellidae:** *Blattella, Periplaneta, Supella*
Coleoptera	**Bostrichidae:** *Dinoderus, Prostephanus, Rhyzopertha*; **Chrysomelidae:** *Acalymma, Leptinotarsa, Oulema, Phratora, Phyllotreta*; **Coccinellidae:** *Hippodamia*; **Curculionidae:** *Anthonomus, Conotrachelus, Cosmopolites, Hylobius, Metamasius, Phlyctinus, Pissodes, Rhabdoscelus, Rhynchophorus, Scyphophorus, Sitona, Sitophilus, Smicronyx, Sphenophorus*; **Dermestidae:** *Dermestes*; **Laemophloeidae:** *Cryptolestes*; **Nitidulidae:** *Carpophilus, Colopterus*; **Platypodidae:** *Platypus*; **Scarabaeidae:** *Cotinis, Holotrichia, Macrodactylus, Maladera, Oryctes, Popillia, Scapanes*; **Scolytidae:** *Dendroctonus, Dryocoetes, Gnathotrichus, Ips, Orthotomicus, Pityogenes, Pityokteines, Pityophthorus, Scolytus, Taphrorychus, Tomicus, Trypodendron*; **Silvanidae:** *Ahasverus, Cathartus, Oryzaephilus*; **Tenebrionidae:** *Blaps, Gnatocerus, Tribolium*
Collembola	**Entomobryidae:** *Orchesella*; **Hypogastruridae:** *Hypogastrura*; **Onychiuridae:** *Onychiurus*; **Poduridae:** *Anurida*; **Tomoceridae:** *Tomocerus*
Dermaptera	**Forficulidae:** *Forficula*
Diptera	**Anthomyiidae:** *Delia*; **Calliphoridae:** *Lucilia*; **Culicidae:** *Aedes, Culex*; **Drosophilidae:** *Drosophila*; **Glossinidae:** *Glossina*; **Muscidae:** *Musca*; **Psychodidae:** *Lutzomyia, Phlebotomus*; **Simuliidae:** *Simulium*; **Tephritidae:** *Bacterocera*
Hemiptera	**Alydidae:** *Riptortus*; **Aphididae:** *Aphis, Brevicoryne, Hyadaphis, Lipaphis, Phorodon, Rhopalosiphum, Sitobion, Tuberocephalus*; **Coreidae:** *Leptoglossus, Serinetha*; **Lygaeidae:** *Oncopeltus*; **Miridae:** *Lygus*; **Pentatomidae:** *Bagrada, Biprorulus, Eurydema, Euschistus, Nezara, Piezodorus, Plautia, Podisus, Stiretrus*; **Pyrrhocoridae:** *Dysdercus*; **Reduviidae:** *Panstrongylus, Pristhesancus, Rhodnius, Triatoma*
Hymenoptera	**Aphididae:** *Lysiphlebus*; **Cephidae:** *Cephus*; **Chalcididae:** *Brachymeria*; **Ichneumonidae:** *Megarhyssa, Rhyssa*
Lepidoptera	**Noctuidae:** *Mamestra*; **Tineidae:** *Tineola*; **Tortricidae:** *Cydia*; **Plutellidae:** *Plutella*
Orthoptera	**Acrididae:** *Hieroglyphus, Locusta, Schistocerca*
Thysanoptera	**Thripidae:** *Frankliniella, Thrips*
Thysanura	**Lepismatidae:** *Thermobia*

[a] The table is composed from the 1365 hits in CAB-abstracts for the query "aggregation* AND pheromon*".

emission in the presence of other senders (14, 82), by following diurnal rhythms (92), or by regulation depending on feeding, age, or mating status (11, 82, 86, 97, 112). Many aggregation pheromones consist of a blend of compounds, and the ratio of compounds can vary among individuals (54) and geographically (21, 128). In *Oryzaephilus surinamensis* (Coleoptera: Silvanidae) and *Metamasius hemipterus hemipterus* (Coleoptera: Curculionidae), the sex ratio of the responders can be influenced by the ratio of the different compounds in the pheromone blend that selectively attract males and females (105, 145). Also, the response of individual insects is often largely affected by physiological state (e.g., hunger, mating condition, age, and molting cycle) (4, 11, 38, 63, 66, 77) and extrinsic factors (e.g., time of day, season, density of conspecifics of same or opposite sex, and temperature) (8, 14, 77, 89). Many species show a strongly increased response, or in fact only respond, to aggregation pheromone when it is accompanied by a coattractant, e.g., odors of food or breeding substrates (12, 15, 105). Aggregation pheromones on a breeding substrate, often released by other females (26, 64, 67, 141), or by eggs, larvae, or pupae (19, 73, 83), can induce "aggregated oviposition," i.e., multiple females oviposit either concurrently or sequentially on the same breeding substrate. This is yet another mechanism that leads to a pheromone-mediated aggregation of individuals in a particular location, be it at the level of the ovipositing females or the offspring.

Apart from the aggregative behavior that the pheromones induce, they sometimes also induce morphological and physiological changes, influence growth rate, and affect the development of larvae (26, 80, 103). Some aggregation pheromones are defensive secretions when released in high concentrations and/or additionally act as alarm pheromones, inciting immediate dispersal in conspecifics (2 and references therein; 68, 75). For fruit flies and desert locusts, pheromones may induce aggregation at long range but can inhibit courtship at close range (115, 149).

Similarities Within and Among Taxa

Similarities in the mechanisms of aggregation pheromone use are apparent among species of the same family and even among families of the same order. For example, in Coleoptera these pheromones are mostly produced by only one of the sexes, and the response to pheromone is highly dependent on food as a coattractant (14, 15). In Diptera, pheromones are often used in the context of aggregated oviposition (19, 64, 67). In several species of Hemiptera, aggregation pheromones are accompanied by defensive secretions and/or alarm pheromones (2, 30, 88). The evolutionary explanation for these similarities, if any, is unknown.

The species reported to use aggregation pheromones belong to various trophic groups: herbivores feeding on healthy or damaged plants and fruits, healthy, damaged, and dead trees, and stored products; predators, parasitoids, and hematophagous insects; or fungivores and detrivores feeding on microorganisms and mycelia. Within each trophic group, different taxa show similarities, indicating convergent evolution. Comparatively few insects feeding on healthy plants and leaves use aggregation pheromones, considering the large number of insect species in this niche. Those few species that do, often feed gregariously. The low incidence of leaf-feeding among insects with aggregation pheromones contrasts with the frequent aggregations of caterpillars that arise from clutch-laying butterflies (123). The major difference between pheromone-mediated aggregation and clutch laying is the higher degree of relatedness among the group members in the latter situation. The carnivorous and hematophagous taxa in our survey (e.g., ticks, coccinellids, mosquitos, tsetse flies, predatory bugs, and parasitoids) aggregate mostly during a nonfeeding or inactive phase (seasonally, daily, or during molting) or in a nonpredatory developmental stage (parasitoid adults and mosquito larvae). An exception is the aggregated blood feeding, mediated by a pheromone, in sand flies, *Phlebotomus papatasi* (Diptera: Psychodidae) (113), and in ticks, *Amblyomma* spp. (Acari: Ixodidae) (90).

BENEFITS OF THE USE OF AGGREGATION PHEROMONES

The function of aggregation pheromones is defined as broadly as "forming an aggregation that serves for protection, reproduction, feeding or a combination thereof" (23). This is nonspecific and in practice includes most fundamental aspects of life. In contrast, Landolt (72) states that many aggregation pheromones are male-produced sex attractants, which is a narrow interpretation of the benefits of aggregation. Whatever the mechanism, and whether it is through attraction, arrestment, or both, the result of aggregation pheromones is a grouping of individuals in a particular location. Despite the enormous diversity in mechanisms that lead to grouping in insects, we find striking similarities in the ecological conditions under which aggregation pheromones are being used. This may suggest a limited set of functional explanations for the use of aggregation pheromones. Here we discuss literature on the benefits associated with aggregation pheromones and group living.

Generally, the benefits of the use of aggregation pheromones in insects have not been investigated but merely suggested, sometimes using group selection arguments, such as "aggregation pheromones are beneficial because they help conspecifics to find a food source" (10, 86, 113). Such an argument is not satisfying from an evolutionary perspective (also see Reference 1). Although a responder may indeed benefit by exploiting (involuntary) cues, an emitter is expected to experience costs (e.g., competition) and would therefore be under selection pressure not to emit pheromone. For the trait to evolve, both responder and emitter must benefit, although not necessarily to the same degree.

Even more basic is the question whether the use of pheromone is adaptive. One could presume that the chemicals involved in information conveyance are merely by-products of metabolic or respiratory processes and have no explicit function in intraspecific communication. This might be true in particular cases and it could certainly occur as a first step in the evolution of cues into aggregation pheromones. However, a profusion of specialized glands and behaviors strongly indicates that selection pressures have shaped the chemicals as signals in communication, instead of selecting for the minimum information conveyance. Furthermore, although many pheromones are derived from host plant precursors, the biosynthesis is in most cases at least partially de novo (117, 132). Additionally, an optimality approach also suggests that the use of aggregation pheromones is adaptive: A number of costs are apparent (see below), and yet the pheromone is integrated into the biology of the insects, which means that benefits in theory outweigh these costs. Otherwise, aggregation pheromones would have been lost through natural selection. At issue, therefore, is how aggregation pheromones are beneficial and how they may have evolved. We explicitly focus on benefits to the participating individuals.

In general, an Allee effect (125) can explain the evolution of aggregative behavior: At low population densities, positive density dependence may arise because of difficulties in mate-finding or because a critical number must be exceeded before resources can be successfully exploited (18, 124). Benefits for living in groups are further described in a classic paper by Pulliam (101). In some cases, additional benefits seem directly related to the chemical compound itself, for example, when it acts as a courtship inhibitor (149), defensive secretion, or antimicrobial agent (20). We summarize the benefits of pheromone-induced aggregations in four general categories: (*a*) increasing the efficiency of resource use, (*b*) finding mates, (*c*) protection from natural enemies, and (*d*) protection from environmental conditions.

Efficient Resource Use and Overcoming Host Resistance

Facilitating food-finding by conspecifics has frequently been suggested as a function of the use of aggregation pheromones. Formulated as such, this implies altruistic behavior and group selection and should therefore be avoided (see above). Besides, the deduction is not consistent with the observation that responses are often found only when the pheromone is accompanied by food odors: If the individuals respond only when they can perceive the food odors, why would they need pheromones, and how can it explain the preference for food odors with pheromones above food odors alone? Nonetheless, the use of aggregation pheromones indeed results in communal feeding in many insect species. Frequently, a food source is required for the production of pheromone and food odors are required for responses. Therefore, under certain circumstances aggregative behavior may enhance individual efficiency in resource exploitation.

A benefit of communal feeding can comprise the reduced per capita cost of initiating attack on a new food source. Nymphs of *Oncopeltus fasciatus* (Hemiptera: Lygaeidae) are attracted to odors of conspecific nymphs and young adults (4). Nymphal survival for these bugs is increased in larger groups when their food source, seeds, is offered as unopened pods but not when they are fed seeds. The nutrients of the seeds in the closed pods become available for ingestion only by the joint secretion of lytic enzymes (104). Similarly, adult *Aphis fabae* (Hemiptera: Aphididae) tend to cluster on leaves of their host plants and are arrested by odors of conspecifics (69). The onset of sustained phloem ingestion may take hours, during which the aphids probe the leaves for sieve element sites and start secreting saliva into the phloem, presumably to alter its characteristics for more efficient uptake. The saliva injection per aphid is reduced on previously infested leaves and phloem ingestion is significantly increased (99). Qualitatively similar effects were found for aphids feeding in colonies versus solitary aphids, although these differences were not statistically significant (99). This is in agreement with the observation that individual aphids feeding in groups initially become larger and their colonies grow faster, although later on crowding reduces reproduction (140). Finally, both male and female *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae) are attracted to conspecific beetles feeding on oilseed rape (95). Individuals all tend to feed on the same cotyledon (96). The amount of feeding per beetle on oilseed rape was positively density dependent for low densities, indicating that they need to aggregate to optimally utilize their host plant (96). The authors suggest that gregarious feeding enhances the successful opening of the wax layer that covers the leaves (95). Studies on other Chrysomelidae indicate that the principal benefit of gregariousness occurs during the establishment phase, not during further resource exploitation (45).

The benefits of aggregation pheromones in bark beetles (Scolytidae) are the best documented and are commonly known as overcoming host resistance (reviewed in References 22, 25, 102). "Primary" bark beetles attack healthy living trees and can surmount host tree defense mechanisms (resin flow, toxins) through the joint tunneling and inoculation of the tree with fungi, which the pheromone-producing sex carries in specialized mycangia (93, 148). Single beetles have no chance of successful colonization and reproduction, but a rapid communal attack kills the tree and renders it suitable for feeding by both the adults and the larvae (22, 25). Many related species attack recently killed or stressed trees ("secondary" bark beetles) or dead trees (saprophytic bark beetles), and several of these species also use aggregation pheromones (72, 93, 148). It is thought that aggregation pheromones must have occurred in an ancestral nonkilling species, because the rapid mass attack that is needed to kill a tree could not have evolved without a preexisting efficient communication system (114). This ancestral trait may simply reflect a mate-finding system (148). Alternatively, it may be related to carrying fungi in the mycangia. The frequent relationship between fungi and wood-feeding insects is thought to be mutualistic: Fungi convert the often indigestible material into more readily available nutrients and the insects act as vectors for dispersal of the microorganisms (71, 79, 93). Whether and why aggregation pheromones are involved in this latter relationship is as yet unresolved (also see Aggregation Pheromones and Microbial Organisms, below).

In *Drosophila melanogaster* (Diptera: Drosophilidae) and *Delia antiqua* (Diptera: Anthomyiidae), aggregation pheromones deposited by adult females on a larval resource induce aggregated oviposition (67, 141). For both species, larval food quality is improved by the presence of other larvae (51, 111) and adult females change the breeding substrate to the advantage of their offspring by transmitting microorganisms onto the breeding substrate (43, 56). Drosophilid larvae cultivate their resource: They reduce fungal contamination by tunneling through the substrate and are more efficient in doing so in a group (5, 142). Intermediate larval densities resulted in the lowest mortality and shortest developmental period (109, 111). Furthermore, an increase in the number of females on a breeding substrate significantly enhanced the survival and development of their offspring, which was also related to reduced fungal contamination of the substrate (142). Sharing an oviposition substrate thus yields a benefit for individual female fruit flies, through the interaction among adults, larvae, and microorganisms (109, 142). Correspondingly, the females showed a significant decrease in the strength of their response to aggregation pheromone when the breeding substrate was of high quality, which is to be expected if aggregated oviposition primarily benefits larvae exploiting poor-quality resources (141). Also, for sand flies, *Lutzomyia longipalpis* (Diptera: Psychodidae), high larval densities reduce fungal contamination (37), and mosquito larvae in groups prevent the formation of scum on their eutrophic food sources (83). In both taxa, females display pheromone-induced aggregated oviposition (19, 37, 83). Aggregation can also prevent food deterioration for herbivores. When aphids are clustered on the same leaves within a food plant, the plant survives throughout colony development, whereas dispersal of the same number of aphids across leaves causes earlier plant wilting and mortality, which impels (risky) migration and lower individual and cumulative body weights (140). The more stable interaction with the host plant can probably be attributed to sustained photosynthesis in the undamaged plant parts (140).

Mate-Finding

In a small number of species, the onset of pheromone production coincides with sexual maturity (11), or the presence of females and/or mating reduces pheromone production (16, 97), or mating reduces responses to pheromones (63). In some species in which only one sex produces the pheromone, it is mainly the opposite sex that responds (145). All this hints that the pheromone mediates sexual interactions, especially mate-finding. If mate-finding were the main purpose of the pheromones, the attraction of males to male-produced pheromones could be seen as a by-product or cost of attracting females. Although attraction of other males is not benefiting the emitter, it may evolve if the costs of "not calling" are larger than the costs of "having to share" the responding females with eavesdropping males.

Being in a group can facilitate mate-finding, resulting in energy saving, even though the function of the aggregation itself may not be related primarily to sexual interactions. For example, *Orchesella villosa, O. cincta* (Collembola: Entomobryidae) and *Tomocerus minor* (Collembola: Tomoceridae) form pheromone-mediated aggregations during molting that are associated with resistance to desiccation (see below) (136, 137). They reproduce directly after molting, whereby males deposit and leave their spermatophores for females to find and pick up. The chance of donating or finding a spermatophore is greatly increased if the two sexes are near one another instead of randomly distributed (66, 136).

Some authors speculated that intrasexual responses to sex pheromone can result in benefits, because communal calling increases the efficiency of mate-finding by increasing the active space of the pheromone (9). Different models for the evolution of lekking behavior also predict a positive relationship between lek size and the number of females that visit the lek, but this is not always found (65). The benefits that males obtain from lekking may be decisively determined by their individual quality, whereby high-quality males in large leks gain access to more females, but per capita mating rates fall (65).

In other species, it is unlikely that aggregation pheromones play any role in sexual interactions, because no sexual interactions have been observed after group formation [e.g., many dipteran families in which females respond to female pheromones, asexual stages of Aphididae, but also mixed sex aggregations of, for example, *Plautia stali* (Heteroptera: Pentatomidae) (89)], mated individuals show as strong a response as virgins (92, 97), and nymphal aggregations break up before reaching maturity (4). In several species of Dermaptera, Blattodea, Hemiptera, and Orthoptera, aggregations comprise different developmental stages, making a purely sexual function unlikely (31, 49). The presence of separate volatile sex pheromones, as reported for approximately 10% of the species in our survey, could make a prominent sexual role for aggregation pheromones redundant in these species.

The opposite of mate-finding may also select for group formation: Females in groups may be less harassed by courting males and could achieve higher oviposition rates, as was found for the African damselfly, *Platycypha caligata* (Odonata: Chlorocyphidae) (81). This situation can arise, for example, when females position themselves in packs that are relatively inaccessible to males. Aggregated oviposition by *D. melanogaster* did not result in increased rates of oviposition (141).

Protection from Natural Enemies

Being in a group may be advantageous in several ways with respect to risk of predation or parasitism. First, when individuals engage in active defense, the chances of successfully counter-attacking enemies might increase with group size. Furthermore, warning or aposematic coloration to fend off an attack may be a more effective strategy when exploited in a group, either because a group allows for faster/easier learning by the predator (larger stimulus input) or because the chance of being encountered by an experienced predator is larger (41, 108). Active defense and unpalatability in insects is executed mainly by means of chemicals that are pungent, irritating, or burning. For example, in *Nezara viridula* (Hemiptera: Pentatomidae) active defense by aggregated nymphs significantly lowered the per capita risk of predation by some but not all predators (76).

Alternatively, sufficiently large groups that are not capable of active defense are sometimes less efficiently exploited by predators or parasitoids ("dilution of risk").

owing to handling time effects, satiation, and, in parasitoids, re-encounters with already-parasitized hosts (50). Additionally, the chance of being captured is lower for individuals at the center of a group than for those at the margins, i.e., the "selfish herd" principle (48). This last principle applies to the eggs in communal egg masses of *Simulium damnosum* (Diptera: Simuliidae) that are attacked from the outside by predators, yielding the advantage to eggs in the center (83). For most species in which dilution of risk has been loosely suggested as a benefit of aggregation, no actual evidence is provided for a reduced per capita risk in mortality owing to natural enemies (83). This is the case, for example, for aggregated oviposition, in which diluted risk has been suggested both for the females during oviposition and for the swarm of offspring during mass emergence (26, 83). However, a field study on an aggregating aphid species, *Aphis varians* (Hemiptera: Aphididae), did show a significant and considerable increase in population growth rates with increasing colony size, and by careful experimentation this could be attributed to dilution of risk, even though the main predators' numbers and feeding rates increased at higher prey densities (135). A similar study on another aphid species, *Aphis fabae*, did not show a dilution effect, but colony sizes and predator densities were lower (55).

Finally, by being surrounded by others, the vigilance of the group as a whole can increase, enhancing the chance of spotting and fleeing from a natural enemy before it initiates an attack. A co-occurrence of aggregation and alarm pheromones may suggest that the individuals benefit from group living by increased vigilance. To our knowledge, this has never been formally tested for any of the species. That it could work is illustrated by the gray pine aphid *Schizolachnus pineti* (Hemiptera: Aphididae), in which apterae and nymphs actively form aggregations by responding to the presence of other aphids (70). Individuals in large aggregations experienced a higher probability of predator escape because of increased vigilance, whereby predator presence was signaled to colony members by vigorous movements (70). A comparative study on aphids also revealed significant correlations between morphological traits (length of the alarm pheromone disseminating cornicles) and ecological traits, which were in agreement with a benefit of scent warning by alarm pheromones in aggregated colonies (88).

As sound as these ecological strategies seem, their evolution might be hampered by limited benefits and considerable costs at low to intermediate group sizes, reaching net benefits only at high densities (120). The relation between the number of prey present and the number of prey attacked (i.e., the "functional response") is often linear at low densities (50), which means that at these initial (low) densities, benefits are essentially absent. Additionally, being in a group can increase conspicuousness to natural enemies, most notably with aposematic coloration, and this might create an unbridgeable hurdle in the evolution of aggregation. The phenotypic plasticity found in the color morphs of locusts, cryptic at low densities and aposematic at high densities, might have facilitated the evolution of grouping and aposematism, balancing the costs of increased conspicuousness and the benefits of predator avoidance for different densities (129). Notably, some of the proposed functional explanations seem founded on group selection theory and may not be evolutionarily stable and vulnerable to cheaters (e.g., vigilance, risk in the center versus margins, risky active defenses). Relatedness between the individuals, as often found in aphid colonies, for example, might be required before such a strategy could evolve (kin selection). Even though the evidence of an eventually reduced attack by natural enemies can seem convincing, the evolution of aggregative behavior to avoid predation is not always explicable and might originate from alternative benefits. Afterward, selection resulting from natural enemies could further enlarge optimal group sizes (120).

Protection from Environmental Conditions

Insects can alter their physical microenvironment to a certain degree. By forming large groups, several stored-product species can locally increase the temperature by as much as 20°C (57). The conditions in these so-called hot spots are more benign and permissive for breeding, and they induce faster metabolism and larval development (57, 122). The higher moisture contents in hot spots also modify the accessibility of food for insects that penetrate the seed coat, because moist seeds have a lower resistance to seed coat puncture (121).

Group forming in *N. viridula* yielded significant benefits under harsh environmental conditions. Larvae exhibited higher desiccation tolerance when aggregated than when solitary, and they developed faster at low temperature, whereas grouping did not affect developmental time under warmer conditions (76). Male dust mites *Dermatophagoides farinae* (Acari: Epidermoptidae) also actively form clusters, and individual members had a significantly slower water loss rate than solitary individuals did (44). For soil-dwelling collembolans, water saturation levels of the soil affect survival, respiration, and reproduction. In a comparative study, a striking congruence was found between the degree of desiccation susceptibility and the degree of aggregation (66). In addition, aggregation was strongest within species during molting, when they are especially prone to desiccation (66, 136).

The eggs of *S. damnosum* are susceptible to desiccation and cannot withstand prolonged exposure to air (60). Eggs that are deposited in communal egg masses, usually in or just above a water source, can benefit from a gelatinous outer layer and a smaller surface-to-volume ratio, which may reduce the risk of desiccation (83). In addition, on floating debris or plants trailing in streams, the weight of the mass slightly lowers the egg mass into the water while the stem and egg masses remain afloat, which would ensure warming by the sun (32). Finally, the eggs in the center of the mass will be protected from desiccation by outer layers of eggs when water levels fall (83).

COSTS OF THE USE OF AGGREGATION PHEROMONES

Each trait in nature is shaped by a balance between benefits and costs. Costs can be ecological or physiological and can arise as a direct consequence of the trait or of a trade-off. The phenomena of reduced pheromone production per individual under crowded conditions (14, 82), repellent effects of high concentrations of pheromones (98), and anti-aggregation infochemicals (25, 148) indicate that, after reaching a certain group size, the net gain of aggregation may diminish or vanish. Below, we discuss different costs associated with the use of aggregation pheromones.

Competition for Food, Space, and Mates

Individuals within aggregations frequently experience more severe competition for food, space, and mates than they would if they were solitary. The larvae of Scolytidae and Drosophilidae frequently experience severe intraspecific competition for food, exhausting their food source before larval development is complete (25, 46, 102). Population dynamics of aphids (Hemiptera) are thought to be regulated mainly by intraspecific food competition, which affects adult size and fecundity (35). *S. damnosum* females form huge aggregations while egg laying, during which they compete for space and can get entangled in the egg masses and die (32). *N. viridula* individuals fall off plants more easily during strong winds when aggregated in multilayer clusters (76), also indicating competition for space. In mating aggregations and leks, often a limited number of males get most of the matings (131), and the per capita number of matings for males may decline with increasing aggregation size, as was shown for *L. longipalpis* (65).

Transmission of Diseases or Parasites

In epidemiology, transmission of pathogens is expected to proceed faster in groups that are in close contact than via solitary individuals. Fungal disease spreads rapidly through winter aggregations of coccinellids and is considered the main biotic factor causing winter mortality (53). *Triatoma infestans* (Hemiptera: Reduviidae) form aggregations in shelters, and the feces of males, females, and nymphs induce the aggregative behavior. They often deposit the feces just outside the shelter, which was suggested to reduce the risk of disease spread, in particular against the flagellate *Blastocrithidia triatomae* (78).

Deteriorating Environmental Conditions

Especially within egg masses, a deterioration of the physical environment has been reported. Eggs in the center frequently experience oxygen deprivation, which causes development delay and increased mortality (60). For herbivores, communal attack might result in a stronger response of the chemical defense machinery of the plant (42, 107). The increased humidity and metabolism in hot spots increased fungal growth on resources, and late stages of succession in the fungal community corresponded with a reduction in the number of stored-product beetles (122).

Increased Conspicuousness to Natural Enemies

By forming an aggregation, the group as a whole is more conspicuous to natural enemies than a solitary individual would be. Moreover, the natural enemy could exploit the aggregation pheromone to locate their victims (52, 126, 139), which might result in a density-dependent aggregative or "numerical response" of natural enemies. Eavesdropping by natural enemies on the aggregation pheromones of their hosts has been reported for several species (2, 7, 49, 89, 144, 147, 148). The interception of females by noncalling "satellite" males has been suggested as a strategy to avoid parasitism (2). Conversely, the exploitation of pheromones by predators constitutes a selection pressure on male *Ips pini* (Coleoptera: Scolytidae) to refrain from cheating in host exploitation. Males that respond to the pheromone but do not engage in the (initially) risky attack on host trees experienced a significantly higher mortality rate from some predators because they remained more exposed (7).

Physiological Costs

The production of aggregation pheromones involves physiological investments. The amount of pheromone that is produced is sometimes huge and is often replenished during life. Sometimes, specialized glands and organs are involved, which also must be built and maintained (30, 132). The insects that produce pheromones only after feeding, often via feces, might avoid some of these costs (95). The reduced production of pheromones in several coleopteran species in crowded situations indicates that they regulate pheromone production (14, 82). It is unknown how physiologically costly it is to these beetles to produce the aggregation pheromone, and as such, whether the reduction is to use their pheromone sparsely, to avoid overcrowded situations, or both remains speculative.

AGGREGATION PHEROMONES IN INTERSPECIFIC INTERACTIONS

Chemical signals not only affect conspecific behavior and individual fitness, they also mediate intra- and interspecific interactions, affecting population dynamics, evolutionary dynamics, and community structure (138). The pheromone reveals the location and species identity of the senders, their abundance, and, to some degree, their physiological or developmental stage. Other members of the food web can use this information to their own advantage, exploit the characteristic aggregation response that it induces, or both. We discuss three types of interspecific interactions that are frequently influenced by aggregation pheromones.

Aggregation Pheromones and Microbial Organisms

A strikingly large number of species possessing aggregation pheromone are associated with microbial or fungal growth. In about one quarter of the investigated families and over half of the investigated species, feeding occurs directly on microbes or fungi in plants, trees, or fruit, or microbial/fungal infection is associated with feeding by the insect. For *D. antiqua*, for example, microbial decomposition of plant tissues enhances larval survival and developmental rates. The females inoculate substrates, coat their eggs with microorganisms, and preferentially oviposit on already-infested host plants or in groups of females (51, 67). The microbes are thought to predispose healthy onions to more successful attacks by larvae, because healthy onions cannot be penetrated by larvae (39), or make available certain nutrients that enhance larval survival. This is similar to the situation for drosophilid fruit flies, in which adults inoculate the breeding substrate with yeasts, which improves it for larval resource exploitation (17, 43). Aggregated oviposition could enhance yeast infestation beyond the level achieved by a single female, and it significantly enhances larval survival and growth (142).

The hot spots with increased humidity and temperature, induced by stored-product species, have been linked mostly with an increase in metabolic processes and development (see above). However, hot spots also improve conditions for fungal development and microorganisms (122) on which some coleopteran species aggregate and feed (127). The occurrence of aggregation pheromones in stored-product species coincides to a large degree with the occurrence of adult feeding; when adults do not feed, they possess sex pheromones rather than aggregation pheromones (74). Bark beetles also inoculate attacked trees with fungi, upon which both adults and larvae feed thereafter; these fungi can be essential to liberate nutrients from the trees and can be involved in killing living trees (71, 93, 148). Nitidulid beetles feed preferentially on fermenting substrates (e.g., overripe fruit and damaged corn), and several microbial volatiles are attractive to adult beetles (91). They too are reported to inoculate fruit-degrading yeasts onto the substrates (85). After colonization of a fruit, the beetles reproduce (14). Maybe the aggregative behavior enhances inoculation success and renders the fruit more suitable for larval development, as was shown for *D. melanogaster*. The same could apply to *Oryctes rhinoceros* (Coleoptera: Scarabaeidae), the adults of which conduct aggregated attacks on coconut and oil palms, eventually killing the tree. They breed in decaying and fermenting matter, such as rotting palms (47).

Irrespective of trophic group, about one third of the aggregative families comprise vectors for pathogens and parasites of the host on which they feed. It is generally unknown whether the aggregative behavior of a vector is affected by the presence of the parasite or pathogen. If parasites and pathogens are transmitted disproportionally more frequently by aggregative insects, then the pathogens could benefit from aggregative behavior of their insect vector. In some bacterial and fungal rots, a threshold for establishment has been reported, consistent with a benefit for pathogens of aggregative vectors (6, 40). Perhaps the association with microorganisms evolves more readily in insects that possess aggregation pheromone, or alternatively, the evolution of aggregation pheromones is promoted by an association with microorganisms.

Aggregation Pheromones and Natural Enemies

Aggregation can be beneficial and detrimental in terms of the per capita risk of mortality owing to attack by natural enemies. There are numerous papers on the effects of aggregation and density dependence in predator-prey interactions (reviewed in Reference 50). Aggregated attack on high host densities could stabilize predator-prey population dynamics, because the risk of parasitism becomes more heterogeneous (29).

Aggregative responses of natural enemies to the density of prey were shown in a field study on aphids. Individual predators remained in larger aphid colonies for significantly longer periods; more importantly, large aphid colonies were exploited by larger numbers of predators, and predators remained in habitats with higher numbers of aphids for longer periods (62). Parasitoids of *D. melanogaster* respond to the aggregation pheromones of their hosts during host substrate location in a dose-dependent manner, and they search on substrates with higher densities of hosts for longer periods (144). Additionally, fruit fly larvae in substrates with aggregation pheromone were at a significantly higher risk of parasitism than were larvae in control substrates in a field study (144). Density-dependent aggregative responses of predators, which could be mediated by the prey's aggregation pheromone, can nullify the benefits of a dilution of risk from natural enemies (50; B. Wertheim & R.S. Etienne, manuscript in preparation).

Aggregation Pheromones and Community Ecology

Cross-attraction between species was found in at least nine families in five orders, although most species preferred conspecifics when given the choice (8, 14). Cross-attraction may reflect a constraint: The frequent overlap in pheromone components between related taxa hampers the responders to distinguish between them. More plausible, however, is the hypothesis that cross-attraction is adaptive, i.e., the individual also gains some advantage from aggregating with heterospecifics. Most categories of functional explanations do not hinge on species specificity. Asymmetric cross-attraction (one species is attracted by another but not vice versa) was sometimes reported (8, 13, 14, 137) and such patterns could originate from asymmetric reciprocal competitive impact. Cross-attraction leads to increased interspecific interactions.

Different strains of a species sometimes differ in the composition of their aggregation pheromones, mainly in the ratio of the components (21, 146) or in their responses to combinations of components (13). Low specificity for production of (36) or response to a particular blend (145) has been reported, which would hamper species isolation as a result of pheromonal differentiation. Moreover, the composition of pheromone blends of closely related bark beetle species that overlap (geographically or in host use) is not more different from that of nonoverlapping species (130). When the aggregation pheromones were important for species isolation during speciation, selection was expected for the divergence of blends, and consequently, the relationship between phylogenetic distance and pheromone differences for overlapping and nonoverlapping species would be different (130).

Intraspecific aggregation can enhance species coexistence relative to a random distribution of individuals: When individuals of different species compete for the same resources but cluster independently in parts of the environment, interspecific interactions are reduced relative to the intraspecific interactions. The parts of the environment that are not used by one species can serve as a refuge for others, facilitating coexistence and promoting biodiversity. This has been formalized as the "aggregation model of coexistence" (119) and was shown for a number of insect communities (61, 116, 134, 143). However, cross-attraction can give rise to strong associations between competitor species, which could seriously hamper the facilitation of species coexistence by aggregation. This is a clear example in which aggregative behavior and the communication signals leading to this behavior should be considered jointly to appraise their impact on the ecology of insects.

CONCLUSION

Living organisms use chemicals in their interactions and communication with other organisms. Yet, we often fail to recognize how ubiquitous and important chemical communication is in the ecology of plants and animals. By neglecting the adaptive aspects of this mode of communication, it becomes difficult to assess the ecological significance of the behaviors they induce and the interactions they mediate. Both aggregation and pheromonal communication have a profound impact on many aspects of ecology, and they should be considered jointly to better our understanding of the evolutionary and ecological dynamics in intra- and interspecific interactions. Advances in our understanding of these aspects are needed to link individual behavior to population- and community-level processes. For example, the prediction that closely related bark beetle species differ more in pheromone composition when they co-occur in a habitat applies only when the pheromone is under strong selection by the sexual interaction, but not if significant benefits are gained by host sharing and by clustering with heterospecifics (130). Understanding how and why aggregation pheromones evolve will advance our insight into the ecological significance of these pheromones for insects.

We have reviewed the mechanisms and functions of the use of aggregation pheromones across a large number of taxa. The occurrence of aggregation pheromones has evolved in at least 12 different arthropod orders and has resulted in a diversity of mechanisms. Quite prominently, however, striking similarities were found across and within taxa. For example, the linkage between the possession of aggregation pheromones and the association with fungi and microorganisms was apparent across a large number of taxa. In general, the connection with food exploitation was frequent. Over half the species that were studied for aggregation pheromones involved pest species. This is partly because most research on insects is biased toward species that are important from an anthropocentric point of view. Yet, it is also because of the aggregating behavior or the frequent associated rot, fermentation, and pathogenesis due to these insects that causes significant damage to crops and goods. Including evolutionary and ecological aspects of aggregation pheromones may lead to novel insights for the design and implementation of biological control (3, 102, 133).

The use of aggregation pheromones evolves under a constantly changing selection regime, owing to the changing environment and (co)evolution of resources, conspecifics, and natural enemies. After the initial evolution of an aggregation pheromone, the biology of the insect undergoes many changes owing to natural selection. Hypotheses on the primary function of an aggregation pheromone in the existing literature have invoked a plethora of uncorroborated, speculative arguments, frequently including group selection arguments. Furthermore, significant profits are often obtained only after reaching a certain group size, whereas significant costs at smaller group sizes might form a considerable evolutionary hurdle. An Allee effect, kin selection, and "viscous systems" (i.e., no panmixis but greater interactions with direct neighbors) can create a starting point from which a chemical compound can evolve into an aggregation pheromone. Otherwise, the situations must be those in which the initial costs of group living are relatively small, for example, in the case of high abundance or ephemerality of food (101), or in which the compounds serve (initially) another function, for example, as with sex pheromones, courtship inhibitors, or defensive secretions (20).

Some authors have proposed that aggregation pheromones are just an alternative or a derivative of sex pheromones (72). This speculation seems too broad for many species. The response to aggregation pheromones is only rarely affected by mating status (63), and the generally low specificity of the pheromone (i.e., the frequent cross-attraction of other species) argues against a primarily sexual role. Other studies restrained functional explanations of aggregating to a single hypothesis on predator avoidance or defense (59, 120). In reality, the implications of the use of aggregation pheromones for the individual are much wider, and sometimes unrelated to any sexual function or predator interaction. Still, sexual interactions are obviously facilitated in many cases, simply because the two sexes are near one another. This precisely illustrates that it may be short-sighted to assign a single function to the use of an aggregation pheromone for an insect. Each individual bears all advantages and disadvantages of being part of an aggregation, and for aggregation pheromones to persist, the benefits must outweigh the costs. Thus, the statement by Borden (23) that aggregations serve for "protection, reproduction, feeding, or a combination thereof" seems only fitting. Furthermore, costs and benefits of aggregation pheromones vary largely, depending on the characteristics of the biotic and abiotic environment and on individual condition (102, 106). Therefore, it should be expected that the use of and the response to aggregation pheromones often will be adjusted in relation to the prevailing conditions, and studying behavioral plasticity may provide a means to explore functional hypotheses (100). Optimality and game theory approaches are needed to appreciate how all costs and benefits balance within the setting of the organism's ecology (87), but such approaches have yet to be undertaken in research on aggregation pheromones.

The use of aggregation pheromones affects individual insects as well as higher ecological and evolutionary processes. The shortage of integrated studies on ecological, functional, and evolutionary aspects of the use of aggregation pheromones severely hampers our perception of the significance of this communication behavior. Additional field studies are indispensable, because the complexity of communication by pheromones can only be fully elucidated by studying them in the ecological web of interactions. Furthermore, the exciting expansion of chemical ecology into the areas of functional and population ecology can succeed only if nonrandom distribution patterns and individual-level decisions are carefully taken into consideration (138). The existing extensive descriptions on mechanisms should now be accompanied by rigorous investigations of the functions. By comparing the different insect taxa, we revealed some general patterns that may serve as a starting point to initialize further integrated approaches to the study of aggregation pheromones.

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