

JOINING AND AVOIDANCE BEHAVIOR IN NONSOCIAL INSECTS

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■ **Abstract** Groups of two or more consensual conspecific adults of many kinds of nonsocial insects have been observed to form at feeding, mating, ovipositional, or sheltering sites. Conversely, adults of these same insects have been observed to avoid joining consensual conspecifics (or their progeny) and to place themselves (or their progeny) at some distance that results in spacing. Examples from various taxa illustrate that mechanisms underlying joining or avoidance behavior differ among species, as do types of benefits and costs to individuals who decide to join or avoid others. Moreover, within a given species, the decision to join or avoid others can be affected markedly by the physiological and informational state of the individual and by contextual response thresholds to resource availability. Decisions that benefit the individual may or may not affect the group in terms of total reproductive output.

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INTRODUCTION

In many kinds of animals, individuals join others of their species (conspecifics), resulting in the formation of a group (38, 53, 78, 85, 88, 132, 214, 217, 223). For the purposes of this review, we define joining behavior as a positive response of individuals to stimuli culminating in an association between two or more conspecifics that endures for more than a fleeting moment. By joining conspecifics, an individual may gain a variety of benefits. If the number of conspecifics composing a group is too large, however, a joiner may suffer various costs that ultimately affect its fitness. To date, reviewers of conspecific interactions in insects have dealt largely or exclusively either with mechanisms leading to and benefits resulting from joining conspecifics (see e.g. 132, 214, 217) or with mechanisms associated with avoiding conspecifics (resulting in spacing) and costs of overcrowding (see e.g. 55, 95, 158, 173, 198).

Our intent is to present a unified treatment of joining and avoidance behaviors in nonsocial insects that embraces underlying mechanisms as well as associated benefits and costs. We begin with a functional analysis of the spectrum of individual responses to conspecifics. We proceed with a presentation of some relevant examples from different orders of insects, recognizing that limitations of space preclude an all-encompassing account. We then offer a more detailed treatment of how a range of variables can have a marked impact on the degree to which joining and avoidance behaviors are expressed. Finally, we deal with population consequences of the joining behavior of individuals. Throughout, we focus on responses of individuals to conspecifics and do not explicitly address intersexual responses. Also, we place emphasis on joining behavior that is elicited primarily by a positive response to stimuli originating from conspecifics rather than behavior that represents a positive response to stimuli from the habitat per se or behavior that is a by-product of grouping of progeny within the same clutch, recognizing that conspecific and habitat stimuli may interact in shaping the course of joining or avoidance behavior.

FUNCTIONAL ANALYSES OF RESPONSE TO CONSPECIFICS

Insects utilize various resources throughout their lives. These include food, mates, oviposition sites, and shelters or resting sites (173). When an individual attempts to locate or exploit a resource item, it may encounter a conspecific also engaged in a resource search or exploitation. The focal individual must then make a simple decision: join the individual or individuals already engaged in resource-search or exploitation or remain independent. The latter decision could include emigration (194, 243), generally referred to as conspecific repulsion or deterrence

(22, 74, 104, 205, 233, 257, but see 115). Functional analyses of this decision consider the fitness implications of the join versus leave options (78, 129). Details regarding assessment and utilization will differ among species and their resources, but the following inequality holds as a general statement:

$$f(VR, c, n) > P_f \sum_{i=1}^T \sum_{j=1}^N P_{VRi} f(VRi, c, n_j) \quad (1)$$

On the left-hand side of Equation 1, the focal individual that chooses to join will receive some payoff as a function of sharing (or usurping) the resource, VR , with local conspecifics, n , via some competition process, c . The right-hand side describes the payoff from a solitary mode that includes the average payoff from discovery of other items that are found at discrete sites. Here, the average expected payoff depends on the likelihood of locating a resource (P_f) or resource-holding sites that range in size from 1 to T , as well as the probable distribution of conspecifics across those resources (187). It should be noted that frequently conspecifics might respond to the arrival of “joiners” by changing to “solitaries” themselves, thus affecting payoff to the focal individual as in classical ideal free-distribution theory. Thus, our analysis of joining/avoiding is strategic, not tactical (i.e. it considers the behavior of others). This kind of analysis falls under the rubric of game theory (145), wherein one seeks the evolutionarily stable strategic response to conspecifics (78). The analysis is further complicated when inclusive fitness is the more appropriate measure and individuals within groups differ in their degree of relatedness to the focal individual [see (195) for an example of among-sib evolutionary games in caterpillars].

When individuals seek resources independently as well as exploit the resource-finding abilities of others, the distribution of individuals within these two classes at any one time is solved as the evolutionarily stable strategic response. Giraldeau & Beauchamp (78) distinguish between two joining games: information sharing, in which these two behaviors can be performed simultaneously [e.g. olfactory search for food and visual search for conspecifics (see e.g. 19)], and producer-scrounger, in which the two types of searches are mutually exclusive. Almost all experimental work has been applied to group-foraging birds (e.g. pigeons), although it could be applied equally well to some insects.

A subset of our model concerns the actions of individuals upon joining a group. For example, given the higher depletion rate of resources at sites foraged by groups, should the focal individual increase its search or handling speed or decrease its level of discrimination? There is some evidence for lower thresholds of acceptance in group settings in parasitoids (242), blackflies (147), and tephritid flies (170, 174, 188). Such a shift in threshold is often referred to as social facilitation (38, 85). Furthermore, although this review focuses on behavioral responses to conspecifics, individuals sometimes accelerate or modify ontogenic processes when grouped with conspecifics (11, 159). For example, Holbrook & Schal (103) showed that male cockroach nymphs developed significantly faster when paired with conspecific conspecifics than when alone. Similar effects have

been demonstrated in a range of orders, including Orthoptera (13), Homoptera (235), Lepidoptera (80), and Diptera (204), although in some cases it is difficult to separate physical effects of grouping (e.g. increased temperature) from a strict response. In addition, morphological and physiological changes may be caused by direct density-dependent factors in locusts (190). The inequality model that we introduced here could easily be applied to physiological or developmental processes. However, as noted, when the fitness from accelerated development depends on the developmental rate of conspecifics, game theory is needed to evaluate fitness payoffs (see e.g. 24, 68).

In addition to join/avoid decisions, we also consider situations in which an individual finds itself at a resource site that is best exploited by several individuals [e.g. *Ephestia kuehniella* larvae (166)]. There may also be costs associated with sharing resources. Thus, the decision now becomes whether to invite others or go it alone. In the examples section, we provide cases of invitation effects across several orders. According to our functional theory, invitations should be extended only when the sender benefits (3). Some cases that support this prediction [e.g. bark beetles (127)] are illustrated.

We expect that payoffs from decisions will be contextual in nature (188) and that the behavior(s) we observe has been molded by natural selection under a suite of ecological conditions (129). For example, the cost of not joining a conspecific at a resource site is probably much higher for insects that forage for ephemeral resources [e.g. some burying beetles (187)] than for species that forage for more readily available items [e.g. many tephritid flies (196)]. Of course, resource availability can be situation dependent [e.g. seasonal effects (197)]. Moreover, the optimal decision could be reversed within the same system. Individuals might be attracted to conspecifics under some conditions but repelled by them under other conditions or at least show an altered magnitude of response (see examples section). In fact, different responses to conspecifics in different contexts would provide the strongest support for the functional concepts described above (see e.g. 89, 162). Unfortunately, few researchers have conducted controlled experiments on such responses.

Thus far, we have described the focal individual as a static entity; in other words, we have ignored such variables as condition, age, and maturity. In reality, the payoff for choosing to join, ignore, or move away from conspecifics is often state dependent (143). Imagine a small predatory insect with high energy reserves (i.e. in good condition). Further, suppose that this insect encounters a large conspecific that has just captured some prey. Should the focal individual choose to join the other, a fight will ensue, and the former is likely to be driven away. A decision to seek other prey will likely provide a higher payoff than would joining, given the likely asymmetry in fighting prowess. By contrast, imagine the small individual as having low energy reserves (i.e. in poor condition). A decision to seek other prey could result in starvation unless alternate prey is located soon. Thus, it may pay the focal individual to attempt to join (usurp resources from) conspecifics even if the chance of success is low. Problems of this sort are best dealt with via dynamic game theory, in which both state dependence and frequency dependence

are considered (101). It is important to realize that different state-dependent effects are commonplace (20, 116, 144).

Beyond physiological state, there is the notion of informational state (144). As pointed out by Robertson et al (188), Stamps (222), and others, encountering a conspecific at a resource site provides information on the state of the environment—for example, the ratio of foragers to resource items or the stability of the habitat (65). Our functional perspective sees insects as nonomniscient Bayesian foragers (see e.g. 94) that update their informational state with each encounter with conspecifics. From this perspective it is very easy to understand why a response to food or other resource items might change after an encounter with conspecifics (see section on variation among studies).

The simple model described here points to the importance of correctly characterizing competition [see (112)]. When an individual attempts to use a resource item that is already being sought or used by a conspecific, its return may be enhanced or reduced, or it may not differ from what it would accrue if it remained solitary. This view of multiple effects of resource competition is at odds with the most commonly held view that increased density has fitness costs (55; but see 113), although the latter is an extension of population dynamics theory at the species level. Furthermore, there are often asymmetries in resource accrual at co-utilized sites. Resource-sharing asymmetries have received considerable attention of late from studies of reproductive skew theory, although most of this work has focused on social insects (40; but see 86, 187). Finally, although we have concentrated on the resource-accrual portion of the fitness payoff, it is also true that the extent of mortality suffered by individuals when solitary may differ from that endured when grouped with conspecifics, as expressed (when grouped) via decreased susceptibility to dehydration (52), increased vigilance (167, 246), a dilution effect (34, 87, 125, 146), increased strength of warning signal in aposematic insects (see e.g. 77), or increased numbers of encounters with parasites or disease agents (see e.g. 29, 91, 97, 181). Increased mortality associated with grouping may include density-dependent responses by plants to herbivores (see e.g. 256).

Several general scenarios can be postulated that describe the range of effects of conspecifics on per capita resource acquisition and/or utilization. In the first, enhancement, the presence of conspecifics actually increases the likelihood that an individual will either locate or exploit resources. In the second, resource location or exploitation is independent of conspecific presence. In the third scenario, individuals perform less well in the presence than in the absence of conspecifics. The exact mechanisms underlying these effects likely differ across species, resources, and contexts. For example, in stink bugs, positive density-enhancement of feeding (39) is due primarily to the increased range of prey sizes that young instars can exploit when they join older instars that have subdued what the former would normally be inaccessible prey. Alternatively, male grasshoppers that join conspecifics may increase their chances of attracting females because the conspecific males have stationed themselves at high-quality sites (155). At present, there are more demonstrations of negative than positive density-dependent effects on

resource accrual, perhaps because of the aforementioned conceptual bias that has led to more interest in the former than the latter.

Finally, before we delve into specific examples, it is important that we distinguish between levels of organization. Throughout the examples that we discuss, we take the perspective of the individual and the possible adaptive nature of response to conspecifics even though effects of such response can be manifested at higher levels of organization. For a simple example, suppose a cockroach experiences pure scramble competition while foraging in a group. Each time another individual joins that group, the focal individual will suffer a concomitant reduction in fitness indexed by reproductive rate, r (this is the classic logistic model):

$$dN/Ndt = r(1 - N/K), \quad (2)$$

where r is the intrinsic rate of increase, N is the number of individuals in the group, and K is the carrying capacity of the resource.

If one were to plot per capita fitness against N , the result would be a linear decrease in r with group size at the resource site. In other words, the focal individual would perform best when alone at the site. An alternate and very commonly applied approach is to plot reproductive performance of the group against group size. In our specific example, this would yield a parabola, not a linear decline. The key point here is that the density of individuals that maximizes individual performance will often differ greatly from the density that optimizes group performance. Because our interest is in the adaptive nature of response and because natural selection is a much stronger force at the individual level (252), our focus is on effects of joining/avoidance on individual performance.

Why should an individual ever join a group? As mentioned, as long as the gain from joining a group is greater than that from being solitary—for example, when solitary sites are hard to find—the optimal behavior is to join the group. Recalling that conspecifics might also respond to the focal individual should it attempt to join, we can, in theory, deduce an optimal threshold(s) for an individual to join a group. By contrast, at the group level, there is an optimal group size that maximizes group productivity; the former and latter will rarely match. Pulliam & Caraco (177) reached similar conclusions for a wide taxonomic range of organisms that regularly associate in groups (e.g. lions, juncos, etc).

EXAMPLES FROM DIFFERENT ORDERS OF INSECTS

Dictyoptera

Numerous species of cockroaches exhibit aggregative behavior as nymphs or adults, particularly when resting (200). Various stimuli are known to elicit joining and/or maintain grouping, including microclimatic factors such as relative humidity, temperature, and light, which may channel individuals toward particular locales; physical stimuli originating from substrate texture or architecture of

selected location; phomonal stimuli originating from roaches themselves, from feces of conspecifics, or from surfaces impregnated with such feces; and antennal contact with conspecifics, providing tactile and chemical stimulation (52). Several adaptive values have been postulated for individuals in aggregations of cockroaches (224, 254), one of which has substantial experimental support. It involves a greater ability to reduce water loss and survive hostile dry conditions when individuals are in groups than when isolated, as occurs in nymphs of *Blattella germanica* (52) and adults of *Gromphadorhina portentosa* (258). This advantage results from overlap in diffusion fields of water vapor in grouped individuals giving rise to reduced steepness of the water vapor gradient between the body and the surrounding atmosphere (52). Some cockroaches exhibit an enhanced rate of development and/or a greater weight gain when in groups than when isolated, as occurs in nymphs of *Periplaneta americana* (249) and *Diploptera punctata* (103) and in adults of *B. germanica* (102). The inclusion of an individual insect in a group is thought to result in diminished brain inhibition of juvenile hormone production, leading to more rapid growth or sexual maturation (76, 102). Rather than being a benefit to individuals attributable to selection operating on joining behavior, these physiological changes may be simply a response to aggregation per se.

Can joining conspecifics be of adaptive value to individual cockroaches regardless of the size of group? Evidence from at least one study, on *P. americana*, suggests that beneficial effects for individuals decline when groups are too large, possibly because of increased cannibalism among early-instar nymphs (249). Mechanisms contributing to avoidance have been studied in *B. germanica*; crowded adults release a pheromone, eliciting dispersal by conspecifics (199). A fuller appreciation of factors constraining large group size in cockroaches and circumstances associated with benefits versus costs to individuals of joining groups of various sizes awaits detailed investigation.

Orthoptera

Cricket In part, male crickets "sing" to attract females as potential mates. In several species, such acoustical-calling behavior also stimulates distant males to join callers, thereby resulting in grouping of males within a locale (266). Grouped males have a higher probability of encountering females than do comparatively isolated males, especially when the overall population density is low (28, 96). There are limits, however, to the density of individuals in a group. Indeed, spaced-out gregariousness, a condition in which a male does not tolerate close proximity of another male, is commonplace in crickets (31, 266). Detection of proximate males, and ensuing initiation of agonistic behavior leading to local avoidance and spacing, likely involves responses to a combination of visual, olfactory, auditory, and tactile cues from nearby or encountered males (2, 31). Males are much more prone when at high densities than at low densities to engage in singing as a consequence of encounters with other males. The more a cricket sings, the greater its chance of being discovered by acoustically orienting parasitic flies and predators

(29, 202, 265). The extent of grouping conducive to maximum fitness of individual males may differ according to habitat and resource structure (75) and prior experience of individuals (2).

Grasshoppers Mating in most species of grasshoppers involves scramble competition among males for females (81). In the genus *Ligurotettix*, however, males respond positively to acoustical calls made by conspecific males and move preferentially to bushes occupied by such males (155). Bushes with several males attract (through sound) and accumulate more females per capita than bushes with only a single male (211). Grouped males usually average more matings per capita than males that are sole occupants of bushes (82). The most highly prized bushes apparently are those that males assess as being of greatest food value to themselves, with females (which emerge after males) apparently using the presence of males as a partial sign of a quality host (81). Factors limiting densities of *Ligurotettix* adults on single bushes have not been well studied but presumably involve energetic costs resulting from excessive agonistic encounters among males and potential negative consequences of high apparency to natural enemies.

Among various species of grasshoppers in which individual females are known to join groups of conspecific females (106), one of the most fascinating is *Zonocerus variegatus*. As reviewed by Chapman et al (34), a single shrub may contain hundreds of mature females and males and hundreds to thousands of egg pods laid by grouped females. Observations suggest that joining originates in a manner similar to that described for *Ligurotettix* grasshoppers, although male odor, rather than male sound, may be the most important stimulus attracting females. There appear to be two principal advantages to individuals grouping as adults: enhanced defense against predation as a consequence of being distasteful and having aposematic coloration, and enhanced developmental rate and size of nymphal progeny compared with individuals feeding in isolation. Although adults, eggs, and young nymphs can reach rather astonishing densities in a shrub, middle-aged and older nymphs do disperse in response to as-yet-undetermined stimuli. Should their density remain high, they could be highly susceptible to food shortage and epidemics of disease, which are less likely to occur during drier times when adults and young nymphs are active. High levels of parasitism of grouped adults have been observed, but apparently parasitism is not an important selective constraint on group size owing to its initiation after most females have already laid their eggs.

Locusts Perhaps the most extensively studied single species among all insects that form large groups is the desert locust, *Schistocerca gregaria*. In the field, females have been observed to deposit egg pods at densities approaching 1000/m² (192, 238). Stimuli from certain plants attract gravid solitary-phase females (18a), whereas pheromones emitted from froth encasing egg pods deposited in sand by conspecifics attract both solitary- and gregarious-phase females (18a, 203). These stimuli, along with more local tactile stimuli (232), elicit oviposition in the immediate vicinity. Grouped egg laying ensures that hatching nymphs are in close

proximity to one another. Whereas solitary-phase nymphs emerging from widely spaced egg pods deposited by solitary-phase adults tend to avoid one another, gregarious-phase nymphs emerging from clumped egg pods laid by gregarious-phase adults are attracted to one another (122, 191), promoting enhanced "gregarization" as a consequence of effects of combined tactile, visual, and pheromonal stimuli received from nearby nymphs (67, 190). In addition to olfactory stimuli from eggs and nymphs, pheromones emitted by gregarious-phase males (but not solitary-phase males) may also play a role in drawing solitary and gregarious adults of each sex to "gregarizing" groups during early stages of group formation (156).

Benefits to individual desert locusts that join large groups or swarms are not well understood but, in at least some circumstances, apparently include a reduced risk of predation. Solitary-phase juveniles are typically green, whereas gregarious-phase juveniles are black with contrasting yellow or orange body parts. When gregarious-phase juveniles consume plants that are toxic to vertebrates, predators such as lizards learn quickly to avoid aposematically colored gregarious-phase juveniles but do not avoid solitary-phase juveniles (229). Costs to individuals associated with joining a swarm must involve at least some risk of not obtaining enough food to support optimal development when the food supply is limited. Computer simulation models rooted in and verified by field observations and experiments strongly suggest that the structure of the resource habitat (particularly the degree to which plants as food resources are clumped) has a major influence on the degrees to which solitary-phase individuals avoid each other and gregarious-phase individuals react positively to each other (42, 216). The more concentrated the resource, the greater the probability of grouping and eventually swarming.

Homoptera

Aphids Aphids feed on phloem fluid of plants and are known to aggregate in tight or loose groups that sometimes comprise tens of thousands of individuals (227). Three tendencies can lead to aphid aggregations: a tendency of aphids to select only certain parts of a plant for feeding (density-neutral), a tendency of young nymphs (wingless) to remain close to their parent (density-neutral), or a propensity of aphids to join or interact positively with conspecifics (density-positive) (109, 124, 150, 152, 250). Several kinds of stimuli lead to grouping in aphids, including physical or chemical properties of particular plants or sites within plants favorable for aphid feeding (150, 167, 250), an attractive or arresting odor emitted from feeding aphids themselves or plant tissue undergoing feeding by aphids (30, 120, 150, 165), visually attractive characters of conspecifics (108, 120, 124), and tactile stimuli in the form of antennal contact with conspecifics (123). Advantages to individual aphids of joining a group may include gaining greater access to plant nutrients as a result of redirection of nutrient flow toward sites occupied by grouped individuals (247), a potential for becoming larger and hence realizing a greater fecundity (247), and an enhanced probability of escaping predation (32, 123, 125, 236) mediated by response to alarm pheromone emitted by nearby aphids (167) or bodily contact with threatened aphids (125).

Despite the strong tendency toward intraspecific grouping seen in many aphid species, spacing of individuals within a group (spaced-out gregariousness) also occurs (123). If individuals within a group become too dense, the consequence may be reduced growth and developmental rates or even death (33, 56, 152, 250) as well as an enhanced probability of becoming infected by fungal pathogens (32). Stimuli triggering dispersal of individuals from groups at densities perceived as being excessive include slowed nutrient flow to feeding sites or changes in food quality (33, 56, 99), odor (but not alarm pheromone) emitted from nearby conspecifics (30, 165) or from plants attacked by high-density aphids (179), and frequent tactile encounters with conspecifics (124).

In at least one aphid species, *Phorodon humuli*, properties of compounds making up the blend of semiochemicals released by alates feeding on host leaves change according to aphid density, and this change is accompanied by a corresponding shift from attractiveness to repellency of the blend to other alates as colonizing aphids build from low to high density (30). Density-dependent variation from attraction to repulsion of individuals responding to aphid-associated stimuli has also been observed in other aphid species, with variables such as stage of development (nymphs versus adults), age of adults, and morphology of individuals (alates versus apterae) playing a decisive role in the nature of the response (56, 108, 150, 165).

Cicadas Adult periodical cicadas often reach densities of several hundred per tree or bush (62, 253), resulting primarily from attraction of males and females to sounds produced by initial males (61). Mating occurs in leks, after which females leave and oviposit elsewhere (139). Advantages to individual males of being in a group of conspecifics during courtship and mating may include reduced interference from nearby males of related species (61, 138), a greater probability of encountering a female in general and especially one whose receptiveness to mating has been enhanced by repeated auditory and visual stimulation from other males (138), and a greater probability of escaping predation by birds (this is true also for females grouping at oviposition sites) (118). The principal cost of joining a group to individuals of either sex may be an increased probability of being infected by fungal pathogens and thereby losing reproductive capability (253). In the bladder cicada, *Cystosoma saundersii*, again both sexes are attracted to the sound of calling males; but at close range (≤ 0.5 m) an individual male no longer moves toward calling conspecifics but rather travels away from them, thereby reducing acoustic interference arising from nearby callers and allowing females to discriminate better between the individual male and its neighbors (57). Males grouped in this fashion achieve more matings per capita than isolated males (58).

Heteroptera

Grouping of eggs, nymphs, or adults is common in many subsocial species of Heteroptera (71, 153, 230). We draw attention here to the asocial species *Perillus*

bioculatus, a stinkbug that often feeds in groups on leaf beetle eggs and larvae. Older but not younger nymphs succeed in overcoming defensive reactions of large prey, with young nymphs frequently observed to join one or more older nymphs at large prey (39), apparently in response to a pheromone released by older nymphs (4). Benefits to younger nymphs include access to otherwise unobtainable prey, while older nymphs may benefit from the aid of younger nymphs in subduing large prey (39). Presumably, there is an upper limit to the number of nymphs aggregating on a single prey beyond which benefits to individuals of grouping level off or decrease, but this has yet to be examined for *P. bioculatus*.

Coleoptera

Bark Beetles The most thoroughly studied insects with respect to characterization of ranges of group size conducive to high-level fitness of individuals are bark beetles. Bark beetles feed directly on subcortical (xylem and phloem) tissues of woody plants and span a variety of host use patterns, ranging from saprophytic (with feeding being confined to dead trees) to facultatively parasitic (normally saprophytic but capable of parasitizing stressed live trees) to obligately parasitic (colonizing only living trees) (182). The type of host use pattern has a marked impact on performance of individuals across a range of group sizes.

In at least one species of bark beetle, *Dendroctonus micans*, which feeds almost exclusively on living trees, the ultimate infestation of a host may involve arrival of just a single female, which lays a large clutch of eggs in a single cavity (228). Hatching larvae emit a pheromone that elicits joining and results in larval grouping (83). Individual larvae associated with groups grow faster and larger than solitary larvae, with individuals in larger groups having an advantage over individuals in smaller groups in overcoming host secretion of toxic resin and plant secondary chemicals as defenses against larval feeding (228). Individuals in very large groups of larvae, however, may experience slower growth (228), probably owing to effects of competition for food or space (201).

In most species of bark beetles, infestation involves colonization of single trees by hundreds or thousands of adults, which feed, mate, and oviposit after arrival (127, 182). For some species (e.g. *Tomicus piniperda*), volatile attractants from host trees alone are sufficient to elicit arrival of adults (27). But in most species in the genera *Dendroctonus* and *Ips*, group colonization arises from the release by pioneer beetles of attractive pheromone that, by itself or in conjunction with host or microbial volatiles and tree visual stimuli, elicits joining (127, 182). A pioneer beetle presumably benefits from release of pheromone by attracting potential mates, but an equally important benefit involves overcoming host defenses. Thus, both sexes may respond positively to pheromone released by either sex of pioneer adult, with increasing numbers of adults being increasingly capable (either by themselves or aided by phytopathogenic fungi which they inoculate) of outpacing defense responses of host trees (127, 157, 182). Failure of bark beetles that infest living trees to overcome tree defenses by group attack is likely to result in the

death of most or all individuals. Even so, it is not appropriate to invoke group selection as operative in bark beetles because the initial response of an adult to pheromone emitted by a pioneer beetle is presumed to be a reaction to the pioneer as a potential mate or, in the case of a consensual response, to information indicative of a potentially suitable host tree.

Despite a large fitness advantage to individuals associated with group colonization of host trees in many bark beetles, there are costs to individual fitness when groups become excessively large. Among adults, intraspecific competition during gallery construction can reduce gallery length and numbers of eggs per gallery in *Dendroctonus* and *Ips* species (184, 189, 264). Perhaps the most significant negative consequences of competition are to larvae, which, unlike adults, are constrained to remain within established galleries and may suffer reduced size and high mortality when overcrowded (6, 127, 201). In addition to the direct negative effects of excessive population density, indirect negative effects may occur as a consequence of the increased ability of predators and parasitoids to detect bark beetles as prey when the latter are at a high density (181). Individuals at densities approaching the upper limit of population productivity may produce an array of stimuli (especially acoustical and chemical) that generate negative responses in would-be colonizing conspecifics, leading to termination of aggregation and to avoidance (27, 127, 182). Involvement of chemical stimuli ranges from production and release of specific inhibitory compounds (e.g. brevicomin, frontalin, and verbenone) in *Dendroctonus* to release of a pheromonal component that is attractive at low doses but repellent at high doses in *Pityogenes* (205) to reduction or cessation of production of certain components of an attractive pheromone in *Scolytus* and *Ips* (27, 127).

Density ranges conducive to maximum population productivity have been characterized for several bark beetles, including *D. ponderosae* (180) and *Ips cembrae* (264), which infest living trees. Especially interesting are species such as *Ips pini* that infest primarily dead and defenseless trees and that aggregate on such trees despite suffering high individual costs of competition even when at very low densities (189). Could aggregation in such species be a remnant behavior from species that colonize living trees (189)? Group sizes favoring maximization of population productivity in bark beetles may differ substantially depending on the structure of the resource habitat (nearness of neighboring hosts), the physiological state of potential hosts, and the physiological and informational states of bark beetle adults (157, 182).

Burying Beetles Adult silphid beetles in the genus *Nicrophorus* bury small vertebrate corpses in soil as food for their offspring (66). Although in some cases all females involved in burying a corpse are closely related, in other cases they are unrelated (234). There may be two to several females as well as several males initiating burial, depending on the size of the corpse (208). The odor of a decaying carcass, alone or in conjunction with a pheromone released by males, attracts

females (66). On a small corpse, benefits from grouping (if any) may accrue only for a single dominant female, whereas on a large corpse, benefits accrue for every female (187). Such benefits may include an enhanced ability to bury a large carcass more quickly and thereby reduce its apparentness to interspecific competitors (66), defend progeny against predators and congeneric intruders (207), or maintain a carcass in a state suitable for larval development (234).

No matter how large it is, a carcass is still a limited resource. If overcrowded, larvae could suffer severely from intraspecific competition were it not for infanticide carried out by parents and conspecific adults in the form of killing and eating eggs and young larvae in advance of competition (17, 66). There appear to be no cues by which a parent can distinguish its progeny from unrelated progeny; larvae appearing on a carcass outside a certain time window are consumed by adults (66). Burying beetles represent an intriguing example of an environmental variable (size of carcass as a larval resource) playing a key role in a delicate balance between benefits and costs to individuals of grouping (187, 208).

Tenebrionid Beetles Both sexes of adults in several different genera of tenebrionid beetles (e.g. *Orzaephilus*, *Prostephanus*, and *Tribolium*) aggregate at food and oviposition site resources in response to pheromones released by pioneer males (69, 168, 245). When resources become crowded, thereby increasing the risk to progeny, adults or larvae release other pheromones that repel would-be colonizers (69, 168, 245). Although fitness costs associated with larval crowding in these genera have been well studied, benefits from grouping, other than enhancement of the probability of frequent copulation and resultant higher fecundity (see e.g. 164), have not. *Tenebrio molitor* larvae respond positively to volatile components of frass released by conspecific larvae at sites providing food or safe refugia, resulting in larval grouping; when such sites become crowded, (a situation accompanied by increased amounts of volatile fatty acids released by feeding larvae), dispersal of larvae to alternative sites commences (248). *Parastizopus armatriceps* adults dig burrows into desert sand beneath host plants. Under moist conditions, it is common for a burrow to have one or two adults, but during dry conditions, adults congregate in groups and thereby reduce body water loss (183). Apparently, grouping in this species is a dynamic phenomenon whose occurrence fluctuates rapidly depending on the availability of food and water (183).

Other Beetles Several other kinds of beetles have been observed in aggregations of hundreds or thousands of individuals. Notable are large aggregations of light-flashing lamyrid males (especially Asian species) in trees (26), coccinellid beetles at overwintering sites (44, 141), gyrinid beetles in ponds (246), and scarabaeid beetles on plants (134). Although stimuli eliciting aggregation and benefits to individuals of clustering have been studied or theorized for each of these groups, costs to individuals associated with differing levels of aggregation have not been examined in detail.

Lepidoptera

For many butterflies (214, 215, 219) and some moths (237, 255), males aggregate in groups of from 2 to ~20 individuals. Grouping (lekking) of males may originate via attraction of males to physical or chemical cues of host plants of females, male-emitted pheromone, or a variety of non-resource-based landmark stimuli, such as hilltops or patches of sunlit earth in otherwise shady areas (132, 135, 214, 215). In concept, male grouping offers several potential selective advantages to individual members, including enhancement of signal apparency to females, reduction of the probability of predation, and establishment of proximity to particular “hot shot” males that may increase mating opportunities (214). For the butterfly *Melitaea cinxia* there is good evidence that an increase in male density from very low to low or moderate results in a greater proportion of females being mated and a reduced risk of population extinction (130). Why groupings of lepidopteran males infrequently exceed ~20 individuals (214) is uncertain but may be related to a decrease in the probability of obtaining a mate coupled with an increase in energy expended in defense against additional intruding males (49, 135, 251).

Although a majority of lepidopterans deposit eggs singly, there are some species whose females deposit clusters containing hundreds of eggs (37, 93, 220), resulting in aggregation of early-instar larvae. Clustering of eggs may arise also from a positive response of one female to another, resulting in deposition of adjacent egg masses (1, 142). Advantages to individual eggs of being in clusters (and hence to fitness of females that laid them) include a reduced overall probability of mortality from desiccation and parasitoid attack (because most eggs are hidden beneath exposed surface eggs) and enhanced protection against predators (especially in species whose eggs are toxic and aposematically colored) (37, 220). The main cost to individual eggs of being in a cluster may be greater detectability by parasitoids (221). Regardless of the benefits or costs to individual eggs of being aggregated, it is important to recognize that the female parent determines egg placement and may or may not realize the benefits or costs corresponding to those of its egg progeny.

Lepidopteran larvae hatching from clustered eggs are aggregated initially and may remain so through early and possibly later instars. In most cases, the dominant stimulus facilitating larval aggregation is pheromonal, but in some species, visual and substrate-transmitted vibrational stimuli may play a role (47). Numerous studies have revealed multiple advantages to individual lepidopteran larvae of joining conspecific larvae to form groups (36, 47, 54, 73, 133, 220, 259). Among these are an enhanced probability of finding suitable food, an increased ability to overcome host plant physical or chemical defenses, induction of a nutrient sink, an enhanced frequency of feeding, increased thermoregulatory ability leading to a faster growth rate, and a decreased probability of predation (either through aposematism, dilution, or group creation of shelters such as silken webs). As larvae become larger, they may reach a size at which the benefits of grouping during early instar stages are offset by the costs of intraspecific competition and food

depletion, necessitating movement to new hosts (36). Also, pathogens spread faster among densely grouped larvae than among moderately grouped or solitary larvae, placing a further constraint on group size (97, 186).

Two intriguing cases of grouping involve the moths *Ephestia kuehniella* and *Plodia interpunctella*, whose larvae infest stored products. Females of both species are attracted to and oviposit preferentially in food infested by conspecific larvae via responses to pheromones emitted by larvae during larval encounters (7, 46, 166). Benefits to individual larvae of group feeding may include increased release of nutrients from food, a better ability to regulate microbial growth on food, and better protection from predators through larger mattings of silk (166). However, high larval density can lead to a shortage of food, reduced larval weight, increased cannibalism, and an increased risk of parasitism and death (45, 169). At high larval densities, the amount of larval pheromone emitted is sufficiently large to stimulate larval dispersal and cause adults to seek alternative egg-laying sites (46, 166). As suggested in our functional analyses, the availability of alternative sites affects threshold levels at which adults respond negatively to larval pheromones (166).

Like coccinellid beetles, some butterflies aggregate as adults when seeking shelter. Perhaps the most spectacular example is the monarch butterfly, *Danaus plexippus*; millions of adult monarchs form dense clusters on trees in central Mexico during winter (25). Benefits to individual monarch butterflies of being in very large groups include a reduced probability of predation and an increased probability of staying dry (and hence withstanding lower temperatures) during winter storms (8, 72). Costs include an increased probability of being infected by protozoan parasites (240).

Diptera

Drosophila Groups of a dozen or more conspecific *Drosophila* males are commonly observed, often occurring near discrete and patchily distributed larval food resources such as tree exudates and decaying fruits or mushrooms (100, 214). Groups are formed principally through responses of individual males to a combination of an attractive pheromone emitted by other males and the attractive odor of the resource itself (15, 90, 132). *Drosophila mycetophaga* males in groups have a greater per capita probability of encountering receptive females than do isolated males, but this probability levels off when group size reaches ~20 males (12). The larger the size of the group, the more frequently individual males of *D. mycetophaga* engage in aggressive encounters with other males, although actual costs to individuals of such aggression have not been examined critically (12). *Drosophila grimshawi* females are more likely to visit and mate within leks of moderate size (4–8 males) than in those of larger size (12 males) (60).

Pheromone of male *Drosophila* attracts females, which (for some species) transfer the pheromone to oviposition sites (14), thereby enhancing the attractiveness of such sites and leading to grouping of eggs deposited by different females (35). Grouped larvae are better able than isolated larvae to reduce levels of harmful mold

on surfaces of larval food (98). When overcrowded, however, *Drosophila* larvae not only may exhibit reduced size and higher mortality but also may give rise to smaller adults having lower fecundity (84). Also, the more females ovipositing at the same site and the greater the amount of pheromone deposited, the larger the number of larval parasitoids that may be attracted to the site (91), an additional cost of crowding. Marking pheromones eliciting dispersal of ovipositing females from potentially crowded resources are unknown in *Drosophila*, but in concept, females may reject unacceptable occupied sites by sensing the presence of larvae or the declining condition of a resource (this remains to be studied carefully). The distribution of resources within a habitat strongly affects the degree of *Drosophila* aggregation at individual sites (114).

Mosquitoes Although males of many species of mosquitoes gather in swarms for mating (217), our focus here is on the oviposition behavior of females. Among different species of mosquitoes there is a wide range of densities of conspecific eggs or larvae observed in aquatic habitats and major differences in the manner in which ovipositing adults respond to the presence of conspecifics. For example, gravid females of several *Culex* species are attracted to pheromone emitted by conspecific eggs, resulting in grouping of eggs [reviewed by Bentley & Day (20), Jones (116), and McCall & Cameron (146)]. Conversely, gravid females of several *Aedes* species respond either neutrally or negatively to the presence of conspecific eggs but respond positively to odors associated with the presence of conspecific larvae [reviewed by Bentley & Day (20) and Jones (116)]. Benefits to individual larvae of inclusion in a group include an increased ability to keep water surfaces free of scum [which reduces oxygen availability (65)] and possibly also reduced predation through dilution (146), although the latter has not been well studied.

There is evidence suggesting that, for the pitcher plant mosquito *Wyeomyia smithii*, maximal oviposition occurs in pitchers containing an intermediate density of larvae and less oviposition occurs at lower and higher larval densities (89). Similarly, in the treehole mosquito *Aedes triseriatus*, larval survival under some habitat conditions is greater at intermediate than at lower or higher densities (136). High larval density can result in reduced growth and survival of individuals, sometimes involving cannibalism (110, 136, 185). Females of several species refrain from ovipositing at sites containing high densities of eggs or larvae through responding negatively to substances emitted by conspecifics and possibly also by microorganisms that reproduce to a high density in association with a high larval density (20, 116). At high densities, *A. triseriatus* larvae release a substance that inhibits hatching of recently laid eggs (137). The physiological state of female mosquitoes (20, 116), the presence of natural enemies (263), and the structure of the resource habitat in space and time (65, 136, 262) can profoundly affect the degree to which females respond to the presence of conspecifics.

Other Diptera Positive responses of individual males to visual, pheromonal, or acoustical stimuli associated with the presence of other males, culminating in

the formation of groups of conspecific males, are known to occur in a variety of other dipterans [reviewed by Landolt (132), Shelly & Whittier (214), and Sivinski & Petersson (217)]. Similarly, other individual female dipterans are attracted visually to the presence of conspecifics at feeding sites (e.g. muscid, calliphorid, and sarcophagid flies) (43, 218) or by pheromonal or microbial odor stimuli associated with conspecific females at feeding or oviposition sites (e.g. simuliid, psychodid, calliphorid, and anthomyiid flies) (18, 59, 117, 148, 206). Conversely, after oviposition, females of tephritid, agromyzid, and other anthomyiid species deposit host-marking pheromone, which deters repeated egg laying at sites that can support only a limited number of larvae (158, 178, 198). Only for the tephritid *Ceratitis capitata*, however, is there good evidence that individual females respond either positively or negatively, depending on the conditions, to the current or past presence of other females (see section on variation among studies for further information).

Hymenoptera

Parasitoids Among parasitoids of insects, grouping of adults in nature has been observed primarily only when males are responding to an attractive pheromone of females (79), although agonistic encounters do occur between females at oviposition sites (70, 107). Some investigators, however, have created groups of females artificially (by combining them together in cages) and have found that in both mated *Leptopilina heterotoma* parasitoids of *Drosophila* larvae and virgin *Monoctonus paulensis* parasitoids of aphids, females held in groups but subsequently foraging alone laid more eggs per already-parasitized host than did isolated females (i.e. they superparasitized more often) (151, 244). This same pattern occurred for *L. heterotoma* females foraging together for hosts versus alone (242). Both of these parasitoids are solitary, with only one larva emerging per host, and could incur a fitness cost by overloading a host with progeny (79). Many solitary-parasitoid females deposit a host-marking pheromone as a cue for avoiding self-superparasitism (79, 239). Even so, superparasitism is predicted to enhance female fitness under certain ecological conditions (79, 241) and, as is shown in these examples, can be influenced by the reaction of females to a perceived presence of conspecific females in the habitat.

Sawflies Aggregation of eggs laid by different females is commonplace for diprionid sawflies on conifers and for shoot-galling sawflies on willows (23, 41, 50). For both, there is no evidence of a positive response of ovipositing females to stimuli from other females or from eggs. Rather, in diprionid sawflies, egg grouping apparently arises as a result of a limited availability of suitable oviposition sites (23, 41). In shoot-galling sawflies, it arises via the influence of developing larvae, whose feeding leads to an increased, vigorous local shoot growth highly favorable for further oviposition (50). Individual diprionid larvae benefit from aggregation via enhanced physical and chemical defense capabilities against predators

(41) and a better ability to overcome plant defenses (149). For shoot-galling sawflies, there is no apparent benefit (such as generation of a nutrient sink) or cost (such as resource competition) associated with conspecific larvae co-occurring on the same shoot (50). Costs of grouping in diprionid sawflies may be enhanced egg conspicuousness to parasitoids, an increased rate of infective viral transmission among larvae, and increased competition among larvae (41). In *Neodiprion autumnalis* there appears to be a range in larval group size maximally conducive to balancing benefits and costs (149). Even though eggs frequently are aggregated, a pheromone emitted from eggs deters oviposition in areas immediately adjacent to existing eggs in some diprionids (231), resulting in a well-spaced grouping of eggs. In shoot-galling sawflies, previous oviposition scars deter females from ovipositing on shoots on which all potential oviposition sites bear such scars (50).

Other Hymenoptera Owing to space limitation, we do not deal with bees or wasps (solitary or social) or ants.

VARIATION AMONG STUDIES IN FINDINGS ON JOINING AND AVOIDING

Our description of joining or avoidance behavior resulting in grouping or spacing given in examples in the preceding section does not convey a robust sense of how differences in experimental approach, geographic region, or conditions under which studies are conducted can give rise to differing (even opposing) findings. Here, we deal briefly with studies (including our own) of joining and avoidance behavior of males (associated with mating behavior) and females (associated with oviposition behavior) of the Mediterranean fruit fly, *Ceratitis capitata*.

Male medflies form leks (171) whose locations within a habitat, formative mechanisms, size, and suggested benefits or costs differ considerably among published reports. For example, under conditions in which mature wild-origin males were released into patches of artificial trees in a field cage, males formed leks preferentially on trees baited with ripe fruit and responded positively to a pheromone emitted by caged males serving as pioneers (119). Conversely, census data on the distribution of wild medflies among dozens of trees at a field site revealed that males formed leks preferentially on trees bearing unripe fruit, even though various host trees bearing ripe fruit were present (212). Moreover, lab-cultured males released into the field showed no positive response to a pheromone emitted by caged males serving as pioneers (209). Most investigators do concur, however, that in nature, medfly leks tend to form on leaves in sunlit areas within densely foliated tree canopies, with no more than one male occupant per leaf and with nearly all matings attributable to lekking rather than nonlekking males (260). Numbers of observed males composing a lek have ranged from 2 to 20 depending on the locale and on involvement of feral or released flies (64, 209), with amounts of carbohydrate and protein available to males and the degree of hunger of these flies potentially having

strong effects on the sizes and numbers of leks formed (261). Although it remains to be determined whether per capita acquisition of female medflies increases with increasing lek size (up to some maximum), it is known that, at least in one geographical region (southern Europe), individuals in leks are highly susceptible to predation by vespid wasps attracted by male medfly pheromone (92). In Hawaii, such predators rarely are seen attacking medflies (210). It is unknown whether lek size is shaped by differing probabilities of predator attack.

Female medflies are attracted by the odor of host fruit and deposit clutches of eggs in the fruit flesh (175). In three recent studies in Hawaii, mature wild-origin females were released into field cages containing host plants and fruit and were observed for their propensity to join conspecifics. In one study, in which real host fruits were punctured before use, females showed no tendency to alight on fruit occupied by another female (R Dukas, R Prokopy, D Papaj, & J Duan, unpublished data); but in two other studies, in which fruits were visual but not odor mimics of real host fruit, females did alight preferentially on occupied fruit (172; J Rull, R Prokopy, & R Vargas, unpublished data). Neither fruit size nor egg load appeared to play a role in the differences between findings. To a potential joiner, the presence of a conspecific female on a fruit may convey the valuable information that the fruit is of acceptable quality. So also might preexisting fruit punctures, made by conspecifics or other agents, convey the valuable information that the fruit is in a state suitable for oviposition. Indeed, preexisting fruit punctures may benefit medfly females by reducing the time needed to bore into fruit flesh (hence reducing exposure to predators) and by enhancing the probability of larval survival (158, 161). In the study by Dukas et al, the value of information from preexisting fruit punctures may have overridden the value of information from the presence of conspecifics, resulting in no response to the latter.

In a study in Hawaii by Prokopy & Duan (170), examining post-alighting behavior on punctured fruit (170), more medfly females initiated boring in the presence of a conspecific female on a fruit than in its absence, suggesting the occurrence of socially facilitated oviposition. Three subsequent experiments in Hawaii by Dukas et al using punctured or artificial fruit and a protocol similar to that used by Prokopy & Duan (170) failed to corroborate this initial finding for unknown reasons. Yet in a fourth subsequent experiment in Hawaii conducted by J Rull, R Prokopy & R Vargas (unpublished data) under a different protocol than that used by Dukas et al (with a long period of observation of a group of females allowed to arrive ad libitum on artificial fruit in a tree rather than a short period of observation of a single focal female placed by the observer on a fruit), the results supported the initial finding. Again, fruit size and egg load were similar among all studies, with fruit (as in the above-described studies of the propensity of females to join conspecifics on fruit) being of sufficient size to support larvae from at least two clutches of eggs without cost from larval competition (170).

Following oviposition, medfly females deposit a host-marking pheromone by dragging the ovipositor on the fruit surface (176). The presence of such a pheromone may have several effects on alighting females, including a reduction of

the propensity to oviposit (163, 176). There exists, however, a dynamic threshold (affected by fruit size and ripeness) at which the propensity to exploit preexisting punctures is balanced by the propensity to refrain from risking negative effects of competition with existing occupants (160, 162). Therefore, depending on the context, an alighting female may or may not refrain from ovipositing in a pheromone-marked fruit.

This account suggests that a broad range of variables, including the genetic origin and the physiological and informational states of the insect, the state of the resource environment, the geographical region, and the nature of the experimental protocol, can have a marked influence on the degree to which an individual expresses a tendency to be positive, neutral, or negative with regard to joining a group or adding progeny to occupied sites. Recognizing and developing concepts for coping with the kinds of variation discussed here are essential for progress toward understanding the dynamic nature of joining/avoidance behavior, grouping/spacing outcomes, and facilitation/inhibition phenomena in insects and other organisms.

POPULATION PERSPECTIVE

When individuals are either attracted to or repelled from resources by conspecifics, the distribution of a population across resources will deviate from random. In the former case, individuals in populations will be underdispersed (or aggregated), but in the latter they will be overdispersed or spaced out. The consequences of such patterns can be addressed via models of population dynamics in which division of resources depends on the distribution of individuals among those resources plus the form of competition (i.e. interference versus contest). Lomnicki (140) provides an excellent introduction to the effects of resource division on population growth.

There are two major issues associated with individual responses to conspecifics. In the first, the nonuniform distribution of individuals among resources is the principal focus. In the second, increases or decreases in expression of particular behaviors (here we include growth and maturation rates) can generate density-dependent effects at the population level. Thus, we return to the important but often confusing concept of individual versus population phenomena. That is to say, processes that benefit the individual may or may not affect population productivity.

We illustrate the potential importance of behavioral responses to population- or community-level phenomena by focusing on a few areas of applied population biology: medical entomology, conservation biology, and insect control via release of sterile males. Due to space limitations, we concentrate on those situations in which individuals are attracted to conspecifics.

Medical Entomology

The epidemiology of many insect-vectoring diseases can vary as a function of biting heterogeneity (i.e. the distribution of bites across hosts) (9, 63). Early work on the population dynamics of diseases such as malaria assumed a uniform distribution

of bites across hosts; in other words, it was assumed that all hosts were equally susceptible. More recent work has demonstrated that a disproportionate number of bites on some hosts can affect the stability properties of epidemics as well as absolute numbers of infected hosts (126). If individuals are attracted to hosts that are already serving as blood sources for conspecifics, biting heterogeneity will ensue. There is evidence for this "invitation" effect in blackflies (147), midges (21), and sandflies (206), with host-seeking females being attracted to already-feeding conspecifics. Interestingly, while the number of bites on attacked hosts increases under such an invitation, the per capita rates of host-mediated feeding success may decline as the density of biting individuals increases (121). To understand why a female would be attracted to conspecifics, one must consider the payoffs that individuals might accrue by joining an already-feeding female(s) against the expected payoffs from seeking a different host (10).

The Allee Effect and Conservation Biology

Most insect populations exhibit a minimum viable size below which extinction is highly probable. At such densities, populations are particularly susceptible to stochastic demographic events (131) and in some cases to negative density-dependent processes (depensation) (226). When the latter effects are applied to individuals, they are known as Allee effects (5).

Stephens et al (226) recently defined an Allee effect as a positive relationship between any component of individual fitness and either numbers or density of conspecifics. As noted earlier, there are a number of mechanisms that could cause such an effect, including positive density-dependent vigilance (246), reduced per capita capture as prey via dilution effects (246), aposematism (77), and mate attraction (154). Thus, the Allee effect is essentially "a shortage of (positive) interactions among conspecifics at low density" (48). How do individual responses to conspecifics enter into our discussion? The key here is that attraction to conspecifics increases the number of interactions above that expected from straight density considerations. Thus, the Allee effect would be mitigated by attraction. Conversely, avoidance of conspecifics would exacerbate an Allee effect. Thus, minimal viable population size in species with positive interactions must take conspecific attraction/repulsion into account. This concept provides an important interface between behavior and conservation biology (51, 193, 225). A potentially intriguing but complicating aspect of this concept is the notion that attraction/repulsion is a flexible trait. The question then becomes: How is the response to conspecifics expressed at low population densities?

Sterile-Male Technique

Pest control via the sterile-male technique has been applied successfully on a number of occasions (16). In a sense, it is an application of the Allee effect in that the impact of release of sterile males increases as the target population decreases in size (48). In the simplest models for estimating the impact of sterile-male release, the habitat has no spatial structure and heterospecifics encounter one

another randomly (128). Attraction of individuals to conspecifics is important in two ways. First, upon release, sterile males may locate females more readily by associating with fertile conspecifics if the latter have secured positions where females are likely to frequent, as suggested by Shelly & Whittier (213). Second, for species whose males associate in leks, determination of the probability that a sterile male will copulate with a fertile female is much more complex than it is for nonlekking species. Unfortunately, much of the sterile-male release theory assumes that females encounter and mate with males randomly (111). Here, we expect that the degree to which males are attracted to conspecifics will impact the efficacy of sterile-male releases. Horng & Plant (105) developed an elegant model for the Caribbean fruit fly, *Anastrepha suspensa*, and showed that lekking behavior has a nonlinear effect on the efficacy of sterile-male releases. Their model assumed that arrival at leks was a Poisson process. We speculate that nonrandom arrival rates at lek sites will further complicate the situation.

CONCLUSIONS

Our review of the literature demonstrates that many kinds of nonsocial insects respond to the presence of conspecifics; in some cases there is clearly joining, whereas in others there is clearly avoidance. The former leads to grouping and may involve facilitation, while the latter leads to spacing out of individuals and may lead to inhibition. Furthermore, the literature suggests that the mechanisms and the circumstances that determine how such responses are expressed, and the types of associated benefits and costs, differ widely. Our functional analysis suggests that the majority of such responses can be explained by selection at the level of the individual. This is true whether the focal organism engages in apparently cooperative or agonistic behavior (3).

In many of the cases we have reviewed, the payoff to the individual for joining or avoiding conspecifics depends on (a) the response of conspecifics to such actions and (b) the physiological and ecological context within which such decisions are made. To date, few insect-based studies have been conducted in either realm even though insects often are excellent subjects for such endeavors. For example, over the past 5 years, according to *Current Contents*, only 10 papers have dealt explicitly with ideal free distributions of insects, compared with 34 for fish, whereas publications on fish in general outnumber entomological papers by less than 2:1 ($P < 0.05$, chi-square test). One can only speculate on the reasons for this taxonomic bias.

Finally, we encourage others to consider carefully the fitness consequences to individuals of being solitary or grouped and, furthermore, to study several areas in which our knowledge of joining/avoiding is weak:

1. Empirical measures of fitness at the individual level for joining or avoiding conspecifics;
2. Application of game theory models to insect foraging problems;

3. Experimental work on contextual responses of individuals;
4. More empirical measures of possible Allee effects.

Taken together, studies of responses of individuals to consensual conspecifics offer insights into both pure and applied entomology at both the individual and population level.

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