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Anonymity and specificity in the chemical communication signals of social insects

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Summary. The chemical communication signals of social insects, like many other insect semiochemicals, are complex mixtures that exhibit considerable variation in molecular composition and in the relative proportions of components. We propose that this variation is often functional, identifying individuals and groups on a variety of organizational levels and making possible a variety of adaptive discriminatory behaviors. Signals may be characterized as anonymous which are uniform throughout a group or organizational level, identifying the signaller as a member of the group but not distinguishing it from other members. Specific signals vary, and identify the signaller as an individual or member of a particular subgroup. These terms are relative; a given semiochemical may be anonymous in one context and specific in another. Specificity may be derived from the biosynthetic 'noise' in an anonymous signal by a process of chemical ritualization. Mechanisms for recognizing both anonymous and specific signals depend on their predictability; recognition of predictable signals may be encoded in a closed developmental program, while those that are unpredictable must be learned. These categories may be usefully applied to a broad range of interactions among social insects, including sexual communication, community structure, and nestmate and kin recognition.

Introduction

Insects are among the principal model organisms in which the composition, production, perception, behavioral ecology and evolution of chemical communication signals have been examined. Perhaps because of the initial emphasis on sex pheromones as mechanisms for reproductive isolation, until relatively recently investigators have tended to treat the chemical signals of insects as species-specific, but uniform within a species. The early discovery of such extremely fine-tuned sexual communication as that of the silkmoth *Bombyx mori* (Schneider 1957, 1969) encouraged the belief that, among insects, each behavioral response is released by a single chemical substance. By contrast, much greater population and individual variability was attributed to the chemical communication signals produced by vertebrates, particularly mammals, in which pheromones often mediate more 'personal' interactions such as individual recognition, dominance ranking and territorial marking (Wilson 1970; Shorey 1976). While the complex chemical composition of mammalian pheromones was examined for functional significance, the same degree of variation observed in an insect pheromone would be ascribed to contamination or biosynthetic 'noise'. It is now clear that such a double standard was, at best, an oversimplification. Most insect semiochemicals have proven to be complex mixtures, and single-compound pheromones are actually rare (Silverstein and Young 1976; Payne et al. 1986). In this respect at least, insects and vertebrates do not differ greatly in the sophistication of their chemical communication systems.

A conspicuous early exception to the dogma of 'one substance, one response' was provided by the social insects, which exhibit colony-specific recognition of nestmates and territorial marking (Wilson 1970; Hölldobler and Michener 1980). Indeed, the specificity of so-called colony odors among ants and bees was well known more than a century ago, long before the ubiquity and importance of chemical communication were generally realized (e.g., Forel 1874). The current interest in kin recognition in a wide variety of organisms, from coelenterates to primates (Holmes and Sher-

Table 1. Organizational levels at which chemical communication may occur among social insects. Anonymous or specific signals may be employed at each of these levels, and signals that are anonymous at one level may be specific at another

Individuals

Sexes
Developmental stages
Castes
Age cohorts

Mating pairs
Mating aggregations

Foundress associations (pleometrotic spp.)
Dominance hierarchies (queens; workers)
Kin cohorts:
  Patrilines (queens multiply inseminated)
  Matrilines (polygynous spp.)
Spatial regions within nests; multiple nests (polydomous spp.)

Daughter colonies (budding and swarming spp.)
Unicolonial populations
Unrelated neighboring conspecific colonies

Multi-species communities:
  Competitors
  Predators; prey
  Slave-makers; social parasites
  Symbionts (myrmecophiles; termitophiles)

man 1983; Fletcher and Michener, in press), has given new impetus to the study of discriminatory behavior based on relatedness-correlated chemical cues. Other recent studies indicate that colony- and kin-specific cues represent only two of many levels at which functional variation may occur in the signals of social insects, ranging from individual-specific trail laying (Jessen and Maschwitz 1986) to interactions between species in ecological communities (Hölldobler 1986).

Though such complexity is probably more widespread in the communication signals of all insects than previously suspected (and doubtless occurs in other sensory modalities in addition to olfaction) the eusocial insects are particularly good subjects with which to address this phenomenon for three interrelated reasons. First, the impressive diversity and ecological dominance of social insects is in large part due to the power of their communication mechanisms, which coordinate the activities of many individuals. Their reliance on chemical communication has in many cases led to highly sophisticated systems for the exchange of complex information. Second, the role of inclusive fitness in the various hypotheses on the origin and maintenance of eusociality (Hamilton 1964; West-Eberhard 1975) suggests that selection should favor discrimination based on variation that is correlated with relatedness. Third and most important, chemical communication serves important functions in a wide range of ecological/organizational levels within and between insect societies, both among individuals and groups (Table 1). It seems highly unlikely that each level would be characterized by its own simple and unique chemical signals, evolved entirely independently of the others.

In the following discussion, we do not attempt a comprehensive review of chemical communication at each of the organizational levels listed in Table 1. Instead, we illustrate some of the diversity of complex signals and their adaptive functions, drawing selected examples from our own work and that of other researchers. We present these cases in a general framework according to the following proposition: That the discriminations made by social insects in different contexts are based on nested levels of variation in chemical signals which feature both *anonymous* and *specific* characteristics.

Anonymity and specificity

The properties of complex semiochemicals[1] may be clarified by drawing an analogy from the field of artificial intelligence, which is concerned (among other things) with programming computers to distinguish among different types of objects. As such discriminations are comparable to those made by insects, this analogy seems not inappropriate. In the technique known as object-oriented programming, objects are characterized by both *class variables* and *instance variables*. Instance variables are specific to each object, while a class variable is common to all members of the same class. In addition, classes may themselves be instances of higher-level classes; e.g., 'my car' is an instance of 'cars' is an instance of 'motor vehicles'. A higher class is characterized by all the class and instance variables contained in its component classes. However, just as each instance differs from the others in the same class, the class variables of each component class differ from those of other members of the same higher class (Winston 1984; Texas Instruments 1985).

We define the *anonymous* properties of a chemical communication signal as those which identify the signaller as a member of a class or organizational level, but do not distinguish it from other

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[1] The functional definition of the term 'pheromone', as a chemical signal which causes a specific reaction in a conspecific receiver, fails to encompass adequately the multiple contexts in which a given signal may be utilized. In most cases we employ the broader term 'semiochemical', designating any chemical that mediates interactions between two organisms (Law and Regnier 1971; Norlund 1981)

instances of the same class or level. Anonymous cues are uniform or invariant among all instances of a class. The *specific* properties are those which vary, identifying the signaller as a particular instance of its class, or as belonging to one class among others which together comprise a higher class. Clearly these terms are relative, and their application depends on the level under examination. As a brief example, consider an ant following a chemical recruitment trail. At the species level, it orients with respect to the species-specific trail substance, and (usually) does not respond to trails of other species. At the colony level, this response may be anonymous, that is, a trail laid by any conspecific will be followed; or it may be colony-specific. At the individual level, no distinction may be made among the anonymous trails of different nestmates, or each individual may specifically recognize its own trail. Similarly, a sex pheromone that is specific at the species level may be anonymous at lower levels, equally (and only) attractive to all conspecific potential mates. On the other hand, it may be specific at the level of kinship, enabling relatives to avoid inbreeding, and variation at the individual level may also function in assessing mate quality.

Properties of anonymous and specific signals

A single-molecule sex pheromone is an obvious example of an anonymous signal, uniform throughout the species; the uniqueness of the molecule produced is the source of specificity at the interspecific level and hence reproductive isolation. Among multicomponent communication signals, however, a variety of chemical properties may differ between the different instances of a class of signals. The exocrine products of social insects exhibit an extraordinary complexity, providing considerable opportunity for such variation. The Dufour's gland secretions of the carpenter ant *Camponotus ligniperda*, for example, include at least 41 compounds (Bergström and Löfquist 1972, 1973). Mandibular glands of the weaver ant *Oecophylla longinoda* contain over 30 compounds, in colony-specific proportions (Bradshaw et al. 1975, 1979a). This mixture appears to regulate a temporal sequence of orientation and aggressive reactions, as different components (hexanal, hexanol, undecanones and octenal) successively diffuse outward from the point of origin (Bradshaw et al. 1979b). A series of farnesenes from the Dufour's glands of fire ants (*Solenopsis* spp.) contribute different parts of a complex trail-following response, and remarkably, the different constituents vary in their degree of species-specificity (Vander Meer 1986b).

The potential information content of a chemical signal is not limited to the products of a single exocrine gland. Several glands may contribute to one behavioral response; e.g., the trails of a number of ant species contain both poison gland proteins and Dufour's gland hydrocarbons. The former are generally anonymous at the interspecific level, while the latter can be species-specific (Morgan 1984). The trails of harvester ants (*Pogonomyrmex* spp.) contain poison and Dufour's gland secretions, to which colony-specific substances may be added by the hindgut (Regnier et al. 1973). Nor is specificity necessarily restricted to exocrine gland secretions. Semiochemicals that contain hindgut material incorporate components derived from the diet (Hölldobler and Wilson 1978). Chemical analysis of the body surface, in particular the outer hydrocarbon layer that waterproofs insect cuticle, has revealed extensive variation among species, and often variation at lower levels as well (Howard and Blomquist 1982; Blum, in press).

What are the properties that provide specificity? Though some or all constituents may be shared among a given pair of semiochemicals, their relative quantities can vary, producing idiosyncratic patterns. These patterns may be specific at the species level, as in the sex pheromones of the tortricid moths *Archips argyrospilus* and *A. mortuanus*, both composed of the same four acetates but in different ratios (Carde et al. 1977). When the set of components of a semiochemical is species-specific, still finer levels of specificity may be attained by varying component ratios. Three nested levels of compositional variation are strikingly illustrated in the Dufour's gland secretions of the halictine bee *Evylaeus malachurum*, characterized by a species-wide profile of lactones, isopentenyl esters and hydrocarbons. The relative amounts of these components are more similar among nestmates than among non-nestmates, and the details of the pattern are also unique to individuals (Hefetz et al. 1986). Honey bee (*Apis mellifera*) queens can be assigned correctly to subspecies by the proportions of five decenoic acids in their mandibular gland 'queen substances' – with the principal inhibitor of worker oviposition, (E)-9-oxo-2-decenoic acid, most prevalent among *A. m. capensis* queens, whose workers lay most readily and may require strong suppression. However, the profiles of individual queens are also uniquely identifiable (Crewe 1982). Colony-specific proportions of cuticular hydrocarbons have recently been shown to provide nestmate recognition cues in *Camponotus* spp. (Clement et al. 1986; Morel and Vander Meer 1986).

In addition, the sets of components that comprise different mixtures can be mutually exclusive or partly so, with specificity resulting from the presence or absence of a particular molecule (rather than differing proportions of components in mixtures composed of the same molecules). Even an alteration in the three-dimensional structure of the same compound may suffice for uniqueness; e.g., species-specificity in the sex pheromones of diprionid sawflies is provided by varying combinations of chiral isomers (Jewett et al. 1976). This form of variation seems to occur most frequently at the species level, where the distribution of diagnostic chemical characters has been utilized by systematists (Bisby et al. 1980), though not all chemotaxonomically useful compounds are necessarily active in determining behavioral responses. The Dufour's gland secretion of *Evylaeus malachurum* is distinguishable from those of three other halictine species by the presence of isopentenyl docosanoate, isopentenyl eicosanoate and nonadecane, and the absence of isopentenyl octadecanoate (Hefetz et al. 1986). The poison gland alkaloids of the introduced fire ant *Solenopsis invicta* include four distinctive piperidines, and lack piperideine and a fifth piperidine found among the native North American species (Vander Meer 1986a). However, populations of a single species may also feature unique components, e.g., of a pair of ipsdienol enantiomers found in the aggregation pheromone of bark beetles (*Ips pini*) in New York, one is absent from Californian conspecifics (Lanier et al. 1980).

What are the properties that provide anonymity, given that the complexity and the potential for specificity of multi-component semiochemicals is so great? The chemical compositions of all instances of a class of signals might be identical, with all constituents shared in precisely equal ratios. However, though this may occur in some cases, anonymity requires only that the various instances appear indistinguishable to the insect, i.e., the difference in components to which the receiver is behaviorally responsive must not exceed its threshold for discrimination. O'Connell (1975) proposes that the perception of complex semiochemicals involves many sensory receptor types, each sensitive to different ranges of constituents; specificity of particular blends is encoded by the overall pattern of receptor firing. If a series of similar, but not identical, blends evokes the same across-fibre pattern in the receptors (or, more likely, in the central nervous system where receptor firing patterns are integrated), this set will be perceived as a single anonymous signal. Getz and Chapman (in press) model discrimination among such sets in an *n*-dimensional 'odor space', where the dimensions are different chemical compounds and the projection along each dimension represents the concentration of that compound.

As demonstrated by the Dufour's glands of halictines, it is not inconsistent for a semiochemical to be anonymous at one organizational level and specific at another. A bee may sometimes be sensitive to the specific proportions of components, for example in determining whether to admit a nestmate into the burrow entrance. In another situation, when choosing a conspecific mate, it may respond only to the anonymous presence of species-wide compounds in the *same* secretion and fail to discriminate (or choose not to respond to) the available variation. From the viewpoint of the nervous system, then, two similar subsets of the Dufour's gland odor space could stimulate distinctive firing patterns in a nest guard, but evoke identical patterns during mate selection. Such context-dependent responses to chemical stimuli are well known from many studies of insect olfactory mechanisms (Payne et al. 1986). Thus anonymity may be as easily achieved through alterations in perception as by resemblance of the semiochemicals. Unfortunately, this means that functionally anonymous signals will not always appear indistinguishable when analyzed in the laboratory. Consequently, behavioral and physiological bioassays remain essential for elucidating communication mechanisms.

Modulation and chemical ritualization

Not all constituents of chemical communication signals need have the same functional significance. In many cases, one or several major components act as key stimuli, triggering a basic anonymous response, while additional components add specificity. Undecane, for example, is apparently the active alarm signal in most ant species of the subfamily Formicinae, and is usually the most abundant product in formicine Dufour's glands. However, other hydrocarbons are also present, and the total mixture is often species-specific (Morgan 1984). In *Oecophylla longinoda*, further specificity is added by droplets originating from the rectal bladder, used in colony-specific territorial marking (Hölldobler and Wilson 1978). As rectal marking alters the probability of winning territorial conflicts – ants are more aggressive on ground that they have previously marked, and less so on ground marked by another colony – it fulfills the criteria for a *modulator* of the alarm response (Markl 1985). To date the rigorous investigation of modulatory communication signals, defined as those which do not themselves release behavioral responses but which influence reactions to other signals, has been limited to cases in which one signal modulates another of a different modality (Markl 1983, 1985; Hölldobler 1984). However, different elements of cues in a single modality can also interact in this fashion; thus the paradigm also applies to multi-component semiochemicals in which the additional information of specificity may be seen as modulating the response to an anonymous chemical releaser.

If specificity is considered as a form of modulation, and assuming that modulatory functions presuppose the existence of the behavior being modulated, a possible evolutionary route to signal specificity can be proposed. The production of simple semiochemicals, releasing simple, anonymous reactions, is subject to the inevitable imprecision of all biosynthetic processes. The resulting degree of variation may well be perceptible to the receiver's sensory system, but will ordinarily have no effect on the response to the signal. However, should an adaptive advantage happen to correlate with any of the available variants, selection will favor individuals which respond differentially on the basis of these specific characteristics – i.e., modulation of the original response. To continue the previous example, other Dufour's gland hydrocarbons will be released along with undecane. If, say, genetically-similar colony members tend to produce similar hydrocarbon patterns, then the signal may come to be modulated by this added specificity, informing workers whether nestmates or aliens are releasing the alarm. Once the presence and/or proportions of additional components significantly affect the response to the basic releaser in an adaptive manner, selection is expected to improve their distinctiveness and stereotypy.

This process of chemical ritualization, driven by inclusive fitness, sexual selection, avoidance of hybridization or inbreeding, or other selective pressures, could derive increasingly functional specificity from the 'noise' in an ancestral anonymous signal. Ritualization of specific variation is likewise possible in chemicals that initially were uninvolved in communication. Species-specific trail pheromones from the poison glands of myrmicine ants are generally the metabolic byproducts of venom synthesis (Morgan 1984), while the Dufour's gland hydrocarbons of formicines, sprayed together with formic acid, may enhance its spread and penetration (Howse et al. 1986). In addition, variation that modulates a response in one communicative context could become ritualized for use in another, as in nestmate recognition cues of the halictine bee *Lasioglossum zephyrum*, which apparently played a prior role in outbreeding (Michener 1982). Thus the context within which specific variation in a given signal originated, and the selective pressures involved, may later be obscured; e.g., West-Eberhard (1983, 1984) suggests that species-specific signals that now provide reproductive isolation are often secondarily derived from sexually-selected specificity at the level of intraspecific competition (see below).

Ontogeny of perception and expression

Gamboa et al. (1986) point out that nestmate recognition consists of both perception and expression components, and that the ontogeny of both must be included in a complete explanation of the recognition system. Their observation applies equally to discrimination among the instances of any class of communication signals. For variation in semiochemicals to be functional, an individual must have some criteria for determining whether, or in what way, to respond to a given variant. These decision-making rules may be innate or learned – or, to use less problematic terminology, determined by closed or open ontogenetic programs (Mayr 1974). The extent to which discriminatory behavior results from genetically and/or environmentally determined factors has been addressed by a number of authors, largely in the context of kin recognition (reviewed by Hepper 1986).

From the present perspective, the perception rules for both anonymous and specific signals can be either genetically encoded or acquired by experience, depending on the predictability of signal expression. When the expression of a semiochemical is highly predictable, the genome of the receiver can 'know' in advance what characteristics to expect, and can program an efficient, hard-wired neural mechanism for recognizing them. This is clearly true of anonymous sex pheromones, detected by tuned specialist receptors that respond principally or solely to a single molecule (Schneider et al. 1964). Learning to react to such a pheromone would provide no advantage; since all instances are the same, males can learn nothing from previous experience that will improve their ability to recognize conspecifics in the future. Strong selection against failing to respond correctly to the first female encountered should favor a closed developmental program. Some forms of specific variation are also predictable, and the criteria for discriminating them can also be hard-wired. Thus mate selection based on individual differences in sexual signals could be accomplished via an innate perception mechanism which responds more strongly to the 'better' variants, with no experience required.

Conversely, when the expression of a semiochemical is unpredictable, the receiver's genome cannot dictate a perception mechanism in advance, and the criteria for responding must be derived from experience. Nestmate recognition cues, for example, appear to be learned shortly after eclosion in all social insects studied (e.g., Carlin and Hölldobler 1986). A new worker eclosing into a colony whose queen mated more than once cannot know what heritable recognition signals to expect among its half siblings, and in addition, any cues that are acquired from other colony members and/or the external environment must also be learned. Masson and Arnold (1984) and Gascuel et al. (1986) suggest that young adult honey bees learn to recognize odors in an imprinting-like manner due to timing of olfactory center development in the brain, which would admirably fit Mayr's (1974) definition of an open ontogenetic program. The correlation between perception rule ontogeny and predictability of expression need not be restricted to intraspecific signals. A colony of the ant *Pheidole dentata* learns to recognize and respond aggressively toward any ant species that frequently intrudes into its territory, as the identity of neighboring colonies is usually not predictable in advance (Carlin and Johnston 1984). However, *P. dentata* colonies also innately recognize their most serious and ubiquitous competitors, species of the genus *Solenopsis* (Wilson 1975; Carlin and Johnston, unpublished results; discussed below).

Anonymous and specific signals in the social insects

Sexual communication

Sexual communication signals serve three important functions: Attraction of the opposite sex, species recognition and mate assessment. The first function may be accomplished by an anonymous semiochemical, but the latter two require specificity on some level. Species-specificity, mediating reproductive isolation between sympatric populations of different species, is the best known form of sexual signal variation in many insects. However, this does not preclude variation at organizational levels other than that of the species, which serves the third function of assessing mate quality. While some sex pheromones may anonymously identify all conspecifics of a given sex, many also contain chemical components that vary among kin lineages and permit inbreeding avoidance or optimization, while variation among individuals can also promote intersexual selection, i.e. the choice of mates that possess a variety of desirable characteristics which may be passed to their offspring.

Species-specific semiochemicals play an important role in the reproductive behavior of many social Hymenoptera. In the well-studied bumblebee genus *Bombus*, for example, males of many species establish chemically-marked flight paths, depositing chemical secretions at intervals along the route. The heights and locations of these flight paths differ from species to species (Haas 1949; Binger 1973), and the secretions of each species have a characteristic composition of fatty acid derivatives and terpenoids (Kullenberg et al. 1973; Svensson and Bergström 1977). Bees of both sexes are attracted to the marked routes, where males recognize and respond to the specific pheromones of virgin females that venture close enough (van Honk et al. 1978). Although the secretions are species-specific, those of some species (e.g. *Bombus hypnorum* and *Bombus lapponicus*) bear a close chemical resemblance to one another, even though these bees are morphologically quite distinct. Reproductive isolation in this situation is apparently accomplished behaviorally by differing heights of the flight routes (Svensson and Bergström 1977).

Less is known about the role of chemical communication signals in reproductive isolation among sympatric honey bee (*Apis*) species. In behavioral experiments, Butler et al. (1967) determined that drones of *A. mellifera* are attracted to the mandibular gland secretions of queens of *A. cerana* and *A. florea*. Similar anonymous responses were obtained by Ruttner and Kaissling (1968), who also made electrophysiological recordings from the antennal olfactory cells of *A. mellifera* and *A. cerana* drones. Both exhibited identical responses to 9-oxo-2-decenoic acid (the main component of the mandibular gland sex pheromone of *A. mellifera* queens) and to the mandibular gland secretions of *A. cerana*. Interestingly, though, these authors reported that *A. mellifera* drones were somewhat more attracted by conspecific queens than by *A. cerana* queens. Both species cross-mated in their experiments, but did not produce viable offspring (post-mating reproductive isolation).

Thus the sexual communication signals of honey bees seem to be largely anonymous. Species-specificity in the rhythm of mating flights may serve as the major pre-mating isolating mechanism in this genus. In field studies in Sri Lanka, Koeniger and Wijayagunasekera (1976) observed that *Apis cerana, A. dorsata* and *A. florea* mate at different times of day. Some sympatric ant species also exhibit only partial or no species-specificity in their sexual signals, but are effectively isolated by specific ecological parameters such as the timing or location of mating (Hölldobler and Bartz 1985). As these examples illustrate, species-specificity is by no means universal in sexual semiochemicals, and behavioral mechanisms of reproductive isolation may be common. If species-level chemical anonymity is widespread and, apparently, does not hinder reproductive isolation by other means, then the principal function of those sexual signals that *are* species-specific may lie elsewhere than in the prevention of interspecific hybridization.

West-Eberhard (1983, 1984) has convincingly argued that the primary contexts in which sexual communication signals function are the promotion of intrasexual competition and mate choice. According to this hypothesis, semiochemicals employed in sexual competition are under strong selection, since they are of paramount importance for determining access to mates; at the same time, there are relatively few restrictions on the evolutionary change of such signals. Thus sexual competition can lead to a rapid divergence of signals between populations, which can subsequently lead to speciation. West-Eberhard concludes that 'many species-specific signals heretofore attributed to selection for species recognition are probably instead products of sexual selection'. Supporting this model, Phelan and Baker (1987) have recently provided strong empirical evidence that male courtship pheromones in five families of Lepidoptera have evolved through sexual selection.

While potential mates may be attracted by signal components that are anonymous at the species or genus level, components that vary at finer levels may be used to assess their quality and determine whom to mate with. Chemical cues that differ among the individuals in a population, and are not of extrinsic origin, have been called 'discriminators' by Hölldobler and Michener (1980). The response to individual-specific discriminators may be either genetically programmed or learned, depending on their predictability. One case in which learning of discriminators has been demonstrated is the mating behavior of the halictine bee *Lasioglossum zephyrum*. A male bee recognizes odor differences among individual females and exhibits significantly less attraction toward females (or filter paper impregnated with the odor of females) which it has previously contacted than toward an unfamiliar female. Even a male that has been successively presented with the odors of up to eight different females remembers the specific cues of each for at least an hour afterward. Mated females ordinarily reject further courtship, and males that learn to avoid those with which they have already attempted to mate avoid wasting time with unreceptive individuals (Barrows 1975a, b).

L. zephyrum males are also less attracted to the kin of a female which they have previously encountered. Smith (1983) found that the attractiveness of an unfamiliar female is negatively correlated with her genealogical relationship to a familiar one. He proposed that males select females on the basis of intraspecifically-variable, polygenically-controlled sex pheromones, and avoid kin of familiar individuals 'by mistake'. Since the variation that provides specificity to the females' semiochemicals is correlated with relatedness, outbreeding would also be promoted if males learn to recognize the signals of sisters in their natal nests, as well as those of mates during courtship. It is possible that signal specificity that functions in the selection of unmated females and in inbreeding avoidance (both of which are adaptive in solitary as well as social species) provided the original varying cues on which other discrimination systems were subsequently built. Michener (1982) and Smith (1983) suggest that *L. zephyrum* females may use the same individual-specific female signals in nestmate recognition that males use in mate choice.

Among the ants, there is considerable diversity in mating strategies and the specificity of mating preferences. Wesson (1939) reported that males of the slave-raiding species *Harpagoxenus americanus* prefer to mate with non-relatives, while in *Pogonomyrmex californicus*, no such preferences have been found (Mintzer 1982). However, the mating strategies of these two genera are markedly different. Ants of the tribe Leptothoracini (to which *Harpagoxenus* belongs) are characterized by the 'female calling syndrome', in which females remain relatively stationary and attract males by means of sex pheromones released during specialized calling behavior (Buschinger 1968; Hölldobler and Bartz 1985). The female calling syndrome, which tends to occur in species that produce relatively few reproductives annually (including some phylogenetically primitive species and some with small colonies (Hölldobler and Bartz 1985)), may prove to be characterized by signal specificity. *Pogonomyrmex*, by contrast, exhibits the 'male aggregation syndrome' (Hölldobler 1976a, Hölldobler and Bartz 1985). Thousands of males from many colonies gather at mating sites, usually designated by conspicuous landscape features, to which females fly to mate. Males compete strenuously for access to females, and the chance of a given male encountering a nestmate female is low. Under such conditions, specialized discrimination behavior to either avoid or promote inbreeding would be of little use, and anonymity of sexual signals may generally be associated with large aggregations of males.

A similar situation may exist in the social wasp *Polistes fuscatus*. When paired with nestmate and non-nestmate females, males seem to choose their mates without regard to previous familiarity (Larch and Gamboa 1981; Post and Jeanne 1983). As this species also mates in aggregations, it is probably under little or no selection pressure to discriminate former nestmates during mating (Post and Jeanne 1983). However, Ryan and Gamboa (1986) determined that previous experience with males affected the preferences of virgin females in the laboratory; those never exposed to any males mated significantly more frequently with non-nestmate males than with nestmates, while those previously exposed to males exhibited no discrimination. On the other hand, virgin females of another social wasp, *Vespula maculifrons*, prefer to mate with male nestmates rather than non-nestmates (Ross 1983). Further study may enable us to attribute biases favoring kin or non-kin among different species to their differing life history strategies. Still, whatever the significance and extent of inbreeding or outbreeding in wild populations, relatedness-correlated specificity in sexual cues (i.e., discriminators) must underlie either form of mating preference.

Community structure

On the broader level of ecological interactions among populations and species, social insects tend to coexist in highly structured communities. Colonies are usually more or less fixed in space, and often exhibit intricate competitive interactions, primarily involving other social insect species. Studies of ant communities, in particular, provide considerable evidence that intra- and interspecific competition is crucial in determining complex community structures, and that the resultant partitioning of resources is largely dependent on chemical communication, employed in territorial and recruitment behavior (Hölldobler and Lumsden 1980; Levings and Traniello 1981). There is currently much dispute among ecologists over the extent to which such community interactions are the result of coevolution. One approach to this problem would be to examine the mechanisms of communication involved. From the present viewpoint the question arises: Do 'enemies' in social insect communities recognize one another specifically, or treat one another anonymously?

Recent research indicates that a number of social insect species respond to their natural competitors and predators with specific aggressive or defensive actions. Weaver ants of the genus *Oecophylla*, for example, are highly aggressive toward territorial intruders of many ant species. It appears, however, that *Oecophylla* colonies react with mass defense recruitment only to alien conspecifics and to certain other species, such as *Pheidole megacephala*, that are potential predators or serious competitors for essential resources (Hölldobler and Wilson 1978; Hölldobler 1979, 1983b). The ecitonine army ants, which prey heavily on other social insects, have induced the evolution of highly specific defense tactics in a number of ants and wasps, including aggressive recruitment and nest evacuation (Chadab 1979; Droual 1983; La Mon and Topoff 1981; Topoff 1987). Soldiers of a neotropical termite, *Nasutitermes costalis*, are strongly recruited in response to conspecific intruders, while other congeneric species are less effective and other genera are ignored (Traniello and Beshers 1985). Some ants direct specialized interference behavior at particular competitors, e.g. *Conomyrma bicolor* and *Iridomyrmex pruinosum* interfere with the foraging of *Myrmecocystus* spp. by preventing workers from leaving the nest (Möglich and Alpert 1979; Hölldobler 1982).

This phenomenon of 'enemy specification' has been studied in sufficient detail in the myrmicine ant *Pheidole dentata* that the anonymity and specificity of the semiochemicals and responses involved may be addressed. Scouting workers of the fire ant *Solenopsis geminata*, an important sympatric competitor, initiate mass recruitment on discovering a *P. dentata* nest. Wilson (1975, 1976) discovered that colonies can counter the invasions of fire ants, which could easily evict or exterminate them, by the early interception of scouts. *P. dentata* minor workers react to the presence of only a few fire ants by alarm recruitment of large major workers which rapidly eliminate the intruders. Minors recruit majors following either contact with the venom or the body surface odor of an *S. geminata* worker, though the chemical cues must also be accompanied by movement. The stimuli eliciting recruitment to only a few invaders proved to be specific to *Solenopsis*, but anonymously invariant among members of this genus. Wilson (1976) found that even tiny thief ants (belonging to another *Solenopsis* subgenus, *Diplorhoptrum*) evoke this behavior. Other *Pheidole* species have also been reported to exhibit defense responses specifically to *Solenopsis* spp. (Buren et al. 1977; Feener 1986) and to army ants (Droual 1983).

Naive *P. dentata* colonies reared in the laboratory, or colonies collected from localities free of fire ants, react positively on first encountering *Solenopsis* spp. workers. This demonstrates that the genus-specificity of their response is indeed genetically programmed, though experience with fire ants also increases the intensity of recruitment (Carlin and Johnston 1984 and unpublished results). Innate enemy specification implies that long-standing ecological interaction among these species has resulted in coevolved interspecific recognition, and that competition from fire ants, of sufficient impact to provide significant selection pressure, is predictable to the *P. dentata* genome. The species-level anonymity of the chemical cues recognized by *P. dentata* has also provided a considerable, though presumably fortuitous, advantage since the introduced fire ant *S. invicta* must now be a principal competitor in many areas (e.g., Philips et al. 1986).

Superimposed on the genetically-mediated specification of fire ants, *P. dentata* colonies also learn to recognize other ants with which they frequently interact, though far fewer majors are recruited than would be to *Solenopsis* spp. (Carlin and Johnston 1984). Even allopatric species will evoke a response after several introductions. The cues utilized appear to be anonymous at least on the species level, as preliminary results indicate that *P. dentata* workers previously exposed to one colony of an allopatric intruder react equally to conspecifics from other nests (Carlin and Johnston, unpublished). The flexibility of learned specificity makes possible an additional effective defense against the unpredictable competitors with whom a colony happens to share territorial borders. In the further investigation of phenomena of ecological coevolution, it would be worth determining whether similar innate and learned responses to the chemical characteristics of specific competitors and predators are general features of ant community interactions, or unique to the defense recruitment system of *Pheidole*.

Recognition of competitors is also strongly implied by the 'mosaic' spatial distribution and overdispersion of ant colonies (Hölldobler 1983a). How do ants determine which other species should be avoided and which can be tolerated nearby? The partitioning of foraging areas among sympatric species of harvester ants in the genus *Pogonomyrmex* illustrates the involvement of both anonymous and specific semiochemicals in inter- and intraspecific territorial exclusivity. Workers recruit nestmates to new seed patches by means of chemical trails, originating from the poison gland. This relatively short-lived recruitment signal is, so far as is known, invariant among *Pogonomyrmex* species. In addition to these anonymous recruitment trails, persistent trunk routes are established by clearing vegetation and marking with Dufour's gland secretions, which contain species-specific mixtures of hydrocarbons (Regnier et al. 1973; Hölldobler 1976a, b, 1978). The trunk routes also contain colony-specific chemical markers which, together with the species-specific cues from the Dufour's gland, serve to channel the foragers of neighboring nests in diverging directions, effectively partitioning limited food resources.

Interestingly, nearly identical hydrocarbon profiles are found in the Dufour's glands of *Pogonomyrmex barbatus* and *P. rugosus* (Hölldobler 1986; Regnier and Hölldobler, unpublished). Though this similarity might be attributable to the close phylogenetic relationship between these species (Cole 1968), it is also possible that the anonymity of their trunk route signals, which clearly separate the other members of the genus, is an example of character convergence in the sense of Cody (1969). Colonies of *P. barbatus* and *P. rugosus* have very similar ecological requirements and, where they are sympatric, behave as competitively toward one another as toward conspecifics. Their nests are overdispersed, and workers exhibit strong intra- and interspecific defense of their territories (including trunk routes). Thus the anonymity of their Dufour's gland hydrocarbon profiles, whether derived from their common ancestry or by convergence, functions in interspecific competition and resource partitioning. A similar situation has been observed in ants of the genus *Myrmica*, which produce relatively anonymous recruitment signals originating in the poison gland, and species-specific mixtures of hydrocarbons in the Dufour's glands that are used as home range markers (Morgan 1984; Attygalle and Morgan 1985).

The absence of species-specificity in chemical recruitment trails has been reported in a number of ants (Wilson 1962; Blum et al. 1964; Hangartner 1967; Torgerson and Akre 1970; Barlin et al. 1976). The cross-species trail following that is often observed may derive from shared anonymous components in the recruitment cues, though some species appear to specifically recognize chemically dissimilar trails of others in order to exploit them (e.g., Wilson 1965). Vander Meer (1986b) reports that the principal trail pheromones produced in the Dufour's glands of *Solenopsis invicta* and *S. richteri* are Z, E-alpha-farnesene and tricyclic homosesquiterpenes, respectively. However, each species is somewhat sensitive to the Dufour's gland secretions of the other and will follow the other's trails in a bioassay. The response to an as-yet unidentified primer component, also from the Dufour's glands, is species-specific in *S. richteri*, but *S. invicta* exhibits the primer reaction to extracts of either species.

Resource partitioning by means of specificity in recruitment trails also occurs at the intraspecific level, which is hardly surprising given that a colony's strongest competitors are usually conspecifics. The trunk routes of *Lasius neoniger*, for example, are marked with colony-specific cues originating in the hindgut (Traniello 1980). Colony-specific marking of territories and nest material are also well known (Hölldobler and Michener 1980). A still finer level of specificity has recently been demonstrated even among individual colony members – a surprising finding, given the prevailing view that individual differentiation among social insect workers is weak. Individual-specific orientation trails have been discovered in the ants *Pachycondyla tesserinoda* (Jessen and Maschwitz 1985, 1986) and *Leptothorax affinis* (Maschwitz et al. 1986). Thus, in at least some species, functional individual variation in semiochemical composition appears to improve the exploitation of resources, perhaps by facilitating division of labor among nestmates which independently search for food and nest sites.

Nestmate and kin recognition

In most social insects, interactions between conspecific adults from different colonies are quite aggressive. Such behavior is considered to be adaptive, as workers obtain inclusive fitness benefits from aiding kin and defending against non-kin, and nestmates are usually more closely related to one another than to members of neighboring colonies. The semiochemicals involved in recognition at the colony level are simultaneously specific and anonymous. That is, workers are able to discriminate between nestmates and intruders, but also tend to treat all nestmates as fellow colony members, irrespective of their true relatedness. This anonymity among genetically-varied nestmates (the 'fellowship concept' of Jaisson 1985) does not preclude specificity at the within-colony level, as described below. Generally, though, it appears that workers encountering one another in the context of territorial defense or nest guarding respond to chemical labels that indicate colony membership, rather than directly indicating kinship.

An individual worker might distinguish nestmates based on heritable variation in the semiochemicals utilized for recognition, which are shared among colony members as a result of common ancestry. Such 'discriminators', discussed above in the context of inbreeding avoidance, have been well documented in the nestmate recognition mechanisms of bees (*Lasioglossum zephyrum*, Greenberg 1979; *Apis mellifera*, Getz et al. 1986). Several models have been proposed by which workers might recognize nestmates of predictable relatedness, via a closed program that dictates the criteria for recognizing kinship directly (Crozier and Dix 1979; Getz 1981). Learning one's own genetically-determined cues or 'self-matching' would constitute an equally effective closed program (Holmes and Sherman 1983; Crozier, in press). More often, though, an open learning program is a necessity since nestmate recognition labels are unpredictable, due to low relatedness within the colony (as when multiple queens are present or queens are multiply inseminated, both of which are quite common in social insects), and/or the acquisition of labels originating extrinsically with respect to the individual worker. Unpredictable extrinsic cues, acquired by all colony members in the shared nest environment, may derive from the diet, nest material, other workers and/or the queen (see flow-diagram model of Carlin and Hölldobler 1986).

The sources of nestmate recognition signals in social insects have recently received a great deal of attention from a number of investigators (cited in Gadagkar 1985; also Breed 1986; Carlin and Hölldobler 1986; Gamboa et al. 1986; Getz and Smith 1986; Obin 1986; Provost 1986; Stuart 1987). While these studies revealed a bewildering diversity of systems, a general pattern is beginning to emerge. When genetically heterogeneous colonies are sufficiently small, as in the primitively eusocial sweat bee *Lasioglossum zephyrum*, the specific discriminators of each nestmate can be learned separately by all (Buckle and Greenberg 1981); there is also evidence that intrinsic cues can suffice for nestmate recognition in some additional cases (Mintzer and Vinson 1985; Stuart 1987). Nevertheless, as far as is known, most species with larger colonies are characterized by a more or less homogeneous recognition signal or 'colony odor' derived at least in part from shared extrinsic cues. Specific between colonies but anonymous throughout each, acquired labels superimpose uniformity on the varied discriminators of different matrilines and patrilines.

In carpenter ants (*Camponotus* spp.), for example, nestmates are distinguished by chemical labels acquired from a variety of sources, functioning in a hierarchical order of significance (Carlin and Hölldobler 1983, 1986, 1987). Workers removed as pupae from a single colony and reared separately, in the absence of queens, are relatively tolerant of one another, but exhibit stronger aggressive behavior toward non-relatives. Diet differences slightly enhance aggression among separately-reared kin. If a queen is present, however, workers attack both unfamiliar kin and non-kin with equal violence, a response which is unaffected by food odors. Cues derived from healthy queens with active ovaries are sufficient to label all workers in large colonies, while the workers' own discriminators become more important when their queen is infertile. Effects of queens on worker recognition have also been reported in *Leptothorax lichtensteini* (Provost 1986) and interspecific mixed colonies of *Myrmica* (Brian 1986). Recent work by Clement et al. (1986) and Morel and Vander Meer (1986) indicates that the acquired recognition cues of *Camponotus* spp. workers consist at least in part of colony-specific relative proportions of cuticular hydrocarbons. In addition, preliminary evidence from interspecific mixed colonies suggests that workers which interact very aggressively with unfamiliar kin acquire some of the hydrocarbons characteristic of their adoptive queen, while kin that interact relatively unaggressively exhibit less 'contamination' with queen-specific patterns (Vander Meer and Carlin, unpublished results).

The queen is by no means the only source of shared extrinsic recognition cues. The discriminators produced by each worker may be transferred among them all, resulting in a 'gestalt' or mixed label, as originally proposed by Crozier and Dix (1979) and demonstrated by Stuart (1986) in leptothoracine ants. In addition to heritable cues from other workers and/or queens, variation originating in the diet, or other environmental differences external to the colony, also contributes to nestmate recognition in several ant genera (*Acromyrmex octospinosus*, Jutsum et al. 1979; *Solenopsis invicta*, Obin 1986; *Leptothorax curvispinosus*, Stuart, in press). The wasps *Polistes fuscatus* and *Dolichovespula maculata* acquire and learn chemical recognition cues, which include both environmental and heritable components, from nest material (Gamboa et al. 1986). Breed (1986) reports that honey bee (*Apis mellifera*) workers acquire extrinsic recognition cues in the presence of queens and environmental odors, though there is some dispute over the possible formation of collective gestalt labels among queenless workers (Breed et al. 1985; Getz and Smith 1986; Getz et al. 1986).

Social insects may in fact be programmed to respond to odor differences without regard to ultimate origin (Gamboa et al. 1986). Thus, though the acquisition of unifying extrinsic labels seems common, the particular sources involved (or their hierarchy of importance in recognition) may vary widely as a function of the relative strengths of ambient odors available to each species, determined by its general biology, ecology and social organization. Among ant genera, for example, it may prove significant that *Camponotus* exhibits greater queen-worker dimorphism and stronger queen suppression of worker oviposition than does *Leptothorax*, and that *Solenopsis* workers do not require queen suppression, since they lack ovaries. Similarly, one might predict that termites, which like *Polistes* wasps construct nests from processed environmental materials, will prove to derive colony-specific cues from their nest.

The common occurrence of multiple insemination and polygyny not only require a mechanism for anonymously identifying all nestmates as colony members, as opposed to intruders. In the context of interactions among colony members, especially the rearing of reproductive brood, intracolony genetic heterogeneity also poses a problem for the inclusive fitness model of hymenopteran eusociality (Hamilton 1964). Indiscriminately helping to produce half sisters (patrilines) or the offspring of other queens (matrilines) fails to yield the proxy reproductive success that haplo-diploid workers obtain by rearing 3/4-related full sisters. Kin recognition has been invoked as a solution to this difficulty, maintaining eusociality by kin selection despite low relatedness within colonies (reviewed by Gadagkar 1985). Alternatively, even if eusociality is maintained by other means (e.g. parental manipulation), workers that find themselves among nestmates of varied relatedness would nonetheless improve their inclusive fitness by discriminating on the basis of kinship. In either case, sufficient kinship-correlated cue specificity must be retained within colonies' level to permit discrimination of full sisters from other patrilines and matrilines, if 3/4-related cohorts are to cooperate preferentially.

Within-colony discrimination among workers has been relatively little investigated to date. Three studies have examined patriline interactions in honey bees (*Apis mellifera*): Getz et al. reported segregation of worker patrilines during swarming, Evers and Seeley (1986) observed aggressive discrimination between patrilines in queenless colonies containing ovipositing workers, and Frumhoff and Schneider (1987) found that workers preferred to groom and exchange food with full sisters rather than half sisters. All of these investigators used genetic color markers to identify the patrilineal cohorts, which were produced by artificial insemination. However, recent results indicate that these color markers exaggerate the specificity of half sisters' discriminators (P. Frumhoff, pers. comm.). Though discrimination among patrilines has not been tested in ants, Carlin et al. (1987) found that *Camponotus floridanus* workers, originating from unrelated colonies and adopted into mixed nests, persistently antennated non-kin rather than kin, but failed to discriminate consistently in food exchange and grooming.

Kin-biased rearing of queens by honey bees has also been addressed experimentally. Breed et al. (1984) found no preference for nestmate queen larvae over unrelated non-nestmate larvae. Page and Erickson (1984) observed a preference for nestmate larvae that were full sisters (3/4-related) over approximately 1/4-related larvae from another colony. However the latter may have been more distinctive due to their origin in a different nest. Brood was also transferred from different colonies by Visscher (1986), but he controlled for nest-specific cues by presenting workers with non-nestmate unrelated and non-nestmate related eggs, and obtained preferences for siblings (mixed full and half sisters) over non-kin. Noonan (1986) performed the only reported test of worker interactions with queen larvae of different patrilines, all originating in the same nest, and found that workers significantly preferred to visit, inspect and feed full-sister larvae. Unfortunately, these results might also have been influenced by genetic color markers used to identify the patrilines. In sum, evidence is accumulating that the kinship-correlated signal variation necessary for within-colony kin recognition does exist alongside the cues used in between-colony discrimination. Whether this specificity is utilized in adaptive nepotistic behavior under natural conditions remains to be conclusively demonstrated.

Conclusion

Identification and discrimination are major features of biological systems, from embryogenesis and immune responses to communities and ecosystems. All forms of recognition require distinguishable signals, whether antigens or colony odors, varying in ways that correlate with evolutionary advantages. As the preceding discussion demonstrates, the complex patterns of variation in social insect semiochemicals are often functional in this manner. Anonymous and specific signals, which identify individuals and groups on a variety of organizational levels, make possible a variety of adaptive discriminatory interactions. The present paper covers only some examples of these categories, which can be as easily applied to many of the other organizational levels exhibited by social insects, listed in Table 1. Our intent is to provide a unified framework in which to treat such disparate phenomena as sexual communication, community structure, and nestmate and kin recognition, as a contribution to the gradually emerging sociobiology of chemical communication.

The rapidity with which information is accumulating in this field is illustrated by the recency of many of the citations, and any final conclusion at this point would be premature. There is enormous potential here for interdisciplinary interaction, and as techniques improve, still further integration between behavioral ecology, natural product chemistry, and sensory physiology and neurobiology can be expected. Indeed, this collaboration has already brought us far beyond the original conception of an insect sex pheromone as a single, simple molecule releasing a simple response.

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