

## Evolution of Insect Communication

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### I. INTRODUCTION

All social interactions involve communication, whether mutual attraction, repulsion, identification of species and kin, courtship and parental care, establishment of dominance and division of labour, mutualistic symbiosis or any other form of coexistence.

But what is communication? It is not easy to draw a line between stimuli produced by animals that are truly communicative signals and others that are not, and the definitions given by different authorities in the study of animal communication vary considerably.

Wilson (1975) defines biological communication relatively broadly as "the action on the part of one organism (or cell) that alters the probability pattern of behavior in another organism (or cell) in a fashion adaptive to either one or both of the participants." This definition is very close to that suggested by Burghardt (1970): Communication "occurs when an organism emits a stimulus that, when responded to by another organism, confers some advantage (or statistical probability of it) to the signaler or its group."

Many authors, on the other hand, use the term communication only when the signalling behaviour is believed to confer an average statistical benefit to both sender and receiver. In these cases, which Marler (1968) calls "true communication", the transfer of information is mutually adaptive to both participants, or, as Otte (1974) expressed it, "most communicative interactions are characterized by positive selection for transmission and positive selection for receptions." These communicative relationships can be exploited by predators and parasites that "intrude" into the signalling system of a prey or host species, either by "illegitimately" decoding signals or by imitating signals and thereby manipulating the prey or host.

Recently, in a provocative paper Dawkins and Krebs (1978) suggested that all animal communication is a form of manipulation whereby communication or "signalling" is "characterized as a means by which one animal makes use of another animal's muscle power." They argue that "natural selection favours individuals who successfully manipulate the behaviour of other individuals, whether or not this is to the advantage of the manipulated individual." Although I do not disagree with their basic thesis, which is primarily based on aggressive display behaviour, I believe the "manipulation hypothesis" does not easily explain the evolution of complex communication systems which do promote true inter-individual co-operation, as so often documented in the eusocial insects.

It seems to me that communication or signalling behaviour in animals is in fact so diverse and its functions and effects so much dependent on social and other environmental contexts that a unified and precise definition is difficult if not impossible to find. Therefore a relatively broad definition of animal communication, as suggested by Burghardt (1970) and Wilson (1975), is probably the most useful one for a general discussion of signalling behaviour.

There are more than one million species of insects living on earth. They not only comprise the largest amount of animal biomass in most terrestrial habitats, but also exhibit the greatest diversity of social organizations in the animal kingdom. It is not surprising, therefore, that in no other animal class do we find communication behaviours nearly so diversified as in the Insecta. It is impossible to give a comprehensive review of the evolution of insect communication in this essay. I have chosen to limit myself to discussing some of the concepts in the study of the evolution of insect communication, stressing examples from the social insects that both have the most complex communication system and are also among the best studied.

We find four major sensory modalities involved in insect communication: visual, air- and substrate-borne vibrational, tactile and chemical communication. Which sensory modalities are chosen depend among other things primarily on the biology and phylogenetic history of the species, the nature of the environment, whether or not the signal has to be durable or quickly fading and whether the signal must be effective over long distances or at close range. Although it is convenient to study communicative systems according to the modality used, in practice there is a high proportion of signals that are compounded from several modalities, and their adaptive significance and evolutionary history can only be understood if the composite signals are studied as a unit.

There are two main themes in evolutionary biology: adaptation and phylogeny. Both themes are best examined by comparative methods. Adaptive strategies can often be deduced from analogous mechanisms found in phylogenetically diverse groups of species. And since we do not have behavioural fossils, the reconstruction of the most likely history or phylogeny of animal communication is based on comparative studies of the organizational levels of communication mechanisms in closely related species.

Many evolutionary biologists have placed all biologically significant questions in two categories: the physiological "how" and the evolutionary "why" questions (e.g. Mayr, 1982). As we shall see, this partition is not very useful in the study of animal communication, because in order to answer the evolutionary "why", we first have to understand the physiological "how". In other words, the comparative analysis of the mechanisms of animal communication provides the basis for understanding the adaptive significance and for reconstructing the evolutionary history of communication behaviour.

## II. SEXUAL COMMUNICATION: REPRODUCTIVE ISOLATION AND SEXUAL SELECTION

Two important functions of intraspecific communication are species recognition, sex recognition, and individual assessment. Species-specific sexual signals mediate reproductive isolation between sympatric populations, while individual components of sexual signals promote mate assessment and mate choice.

### A. Reproductive Isolation

Biologists generally agree that selection for reproductive isolation between two populations that have re-established contact should occur only if the populations have already diverged sufficiently so that hybrid matings lead to less viable offspring. However, the question whether signal differences develop while populations are evolving independently of one another or emerge subsequently as a result of selection against hybridization is still debated. In fact, in insects only a

few well-documented cases of character displacement in sexual communication exist. Wasserman and Koepfer (1977), for example, studying preferences in *Drosophila arizonensis* and *D. mojavensis* with strains that came from either the same or different geographic localities, found almost no discrimination on the basis of geographic origin. There was, however, a stronger preference for conspecific matings when the two *Drosophila* species came from sympatric populations than when they came from geographically separated localities where one or the other species occurred alone. This suggests that pre-mating isolating mechanisms had been reinforced, possibly by character displacement between the sympatric populations of *D. arizonensis* and *D. mojavensis*.

On the other hand, it has been well documented that genetically based variation in mating behaviour exists within and among geographic populations of *Drosophila* species (see Bryant, 1980; Giddings and Templeton, 1983). Powell (1978) has recently extended Carson's theory of insect speciation through founder events and flush-crash cycles (Carson, 1975) to postulate that pre-mating barriers are likely to precede the evolution of post-mating barriers.

Although these distinctions are understood very well in theory, relatively little is known about actual geographic variation in mating behaviour and mating signals among populations of insect species. In a few cases where variation of mating signals in allopatric and sympatric populations has been sought, no evidence was found to suggest reinforcement of signals in sympatric populations (see Walker, 1974). In conclusion we can say that the available evidence suggests that most species apparently had diverged mostly or fully in their mating signals before they became sympatric, although the reinforcement of signal differences ("character displacement") remains a logical possibility to be tested in individual cases (Brown and Wilson, 1956).

High species specificity of sexual signals has been demonstrated in many insect groups. Calling songs of Orthoptera "designate an individual's mating type and are, in effect, used by females to assess the genotype of potential mates" (Otte, 1977; see review of the literature therein). It has been demonstrated in some species of crickets (Bentley and Hoy, 1972; Hoy and Paul, 1973; Hoy, 1974) and grasshoppers (von Helversen and von Helversen, 1975a,b) that the song patterns and neural perception mechanism are genetically controlled. In crickets, for example, the calling song is a procession of sound pulses structured in a very predictable pattern. The sound pulses are produced by "fixed action patterns" consisting of stereotyped rapid closing strokes of the forewings, which bear specialized frictional cuticular devices for sound production. Within a given species the temporal structure of the calling song is rigidly stereotyped, but it varies characteristically among different species. It is the motor system responsible for the production of the "fixed action patterns" which is neurologically controlled (Hoy, 1974). In addition the experimental results obtained with crickets suggest that the sender and receiver mechanisms are "genetically coupled" (Hoy *et al.*, 1977). On the other hand, von Helversen and von Helversen

(1975a,b) found that hybrids between two species of grasshoppers produced very variable songs and hybrid females did not exhibit a particular response specificity towards hybrid and parental songs, indicating that genetic coupling is not a universal phenomenon in the acoustic insects.

Chemical communication is not only the evolutionally oldest form of communication (Haldane, 1955; Wilson, 1975), it is also the most common communication mechanism in insects. As Bergström (1979) pointed out, "there are principally two different ways to achieve specificity with volatile signals. One is a very characteristic chemical structure of the signal, with comparably characteristic acceptor structure. Another is a blend of relatively unspecific compounds, where the combination of them, perhaps in definite proportions, accounts for specificity." [For a discussion of models concerning the encoding of specific pheromonal blends in the receiver, see Steinbrecht and Schneider, 1980.]

Pheromonal blends are of particular significance in maintaining reproductive isolation in several groups of Lepidoptera (for review, see Silberglied, 1977). This has been very clearly demonstrated in the lepidopteran subfamilies Olethreutinae and Tortricinae by Roelofs and his collaborators (Roelofs, 1975, 1979). For example, all tortricine species investigated use 12-carbon-chain compounds as sex attractants. At first sight this seems to indicate that the sexual calling signal is not very specific. Refined investigations have revealed, however, that the individual species "use precise blends of a number of components—some using various mixtures of cis-trans isomers, some utilizing acetate-alcohol or acetate-aldehyde mixtures, and some using mixtures of positional isomers" (Roelofs, 1975).

Similarly, in the aculeate Hymenoptera studied by Bergström and his collaborators species-specific pheromonal blends are very common. For example it has been long known that males of many bumblebee species establish chemically marked flight routes by depositing spots of odorous secretions at intervals along the route. The height and the location of these flight paths differ from species to species (Haas, 1949a,b; Binger, 1973). The marking pheromone apparently does not, as previously assumed, originate from the mandibular glands, but from the cephalic portion of the labial glands. The males of each species have a characteristic chemical composition, made up by a combination of quite simple fatty-acid derivatives and terpenoids (Kullenberg *et al.*, 1973; Svensson and Bergström, 1977). Although the marking secretions are species specific, some species resemble each other more than others. For instance, there is a close chemical resemblance between *Bombus hypnorum* and *B. lapponicus*, even though morphologically these two species are very distinct and behaviourally they are separated by different heights in the flight routes. Conversely, *B. cingulatus* and *B. hypnorum*, which resemble each other very much in habitus, are chemically very different (Svensson and Bergström, 1977).

Males as well as females are attracted to the chemically marked flight paths

(Kullenberg, 1956), and when virgin females venture close enough, males recognize them from their specific female pheromone. This queen odour seems to be important also for inducing copulatory behaviour in the males. Experimental results obtained by Free (1971) suggest that males of *B. pratorum* first respond visually to black objects of the size of their females. Consequently, they also respond to queens of *B. terrestris*. However, at close range *B. pratorum* males do not attempt to mate with *B. terrestris* females, suggesting that specific female signals, presumably chemical (see vonHonk *et al.*, 1978), reinforce the reproductive isolation.

In the honeybee genus *Apis* chemical communication is also important in regulating sexual behaviour, but not much is known about what if any role these signals play in reproductive isolation in areas where several species coexist. In behavioural experiments Butler *et al.* (1967) determined that drones of *A. mellifera* are attracted by mandibular gland secretion of *A. cerana* and *A. florea* queens. Similar results were obtained by Ruttner and Kaissling (1968), who also recorded identical electrophysiological responses from antennal olfactory sense calls (poreplates) in drones of *A. mellifera* and *A. cerana* when they were exposed to 9-oxo-2-decenoic acid (9ODA) (the main component of the *A. mellifera* queen sex pheromone in the mandibular gland) or to the secretion of the mandibular gland of *A. cerana*. It is interesting, however, to note that Ruttner and Kaissling observed *A. mellifera* drones to be somewhat more attracted to queens of their own species than to *A. cerana* queens. In their experiments both species cross-mated, but such queens did not produce viable offspring.

During the mating period honeybee drones usually assemble in large numbers in "congregation places". Every year the same localities are visited for this purpose (Zwarlicki and Morse, 1963; F. Ruttner and Ruttner, 1965, 1968; H. Ruttner and Ruttner, 1972). The specific cues by which these assembling areas are detected by the drones are still a mystery. No evidence exists as yet that pheromones are involved. Although Gerig (1972) reported that extracts from heads of males attract flying males once they have arrived at the congregation places, no one has proved which features of the assembly sites attract the first males. When a virgin female appears, she is immediately pursued by a "swarm" of males, obviously attracted by the 9ODA released from the female's mandibular glands (Gary, 1962, 1963). Where colonies of *A. cerana* and *A. mellifera* were kept in the same area, drones of both species were found in the congregation places, indicating that these congregations areas are not species specific (Ruttner, 1973). Puzzled by this phenomenon, Koeniger and Wijayagunasekera (1976) studied the daily time pattern of the mating flights of three sympatric *Apis* species in Sri Lanka, *A. florea*, *A. cerana* and *A. dorsata*, and found them well separated. Thus it appears that a species specificity in the daily mating flight rhythm serves as the pre-mating isolating mechanism in honeybees.

A similar situation has been found in the harvester ants *Pogonomyrmex*, of

which several species coexist in the same areas in the southwestern United States (Hölldobler, 1976). My investigations demonstrated that the sympatric harvester ant species *P. maricopa*, *P. desertorum*, *P. barbatus* and *P. rugosus* are reproductively isolated in part by their distinct daily nuptial flight rhythm. They are separated even more strongly by the use of communal mating sites, in which chemical communication signals regulate mating behaviour activities.

During the mating season males and females of *Pogonomyrmex* converge to specific mating sites. Some of these sites were found occupied over several successive seasons. The males which arrive at the mating arenas discharge their mandibular gland secretions together. Presumably other males and females are attracted by this pheromone. Sexual behaviour is then regulated by a stimulation pheromone produced in the females' poison glands and by a species-specific surface pheromone which the males apparently perceive only when they approach the female closely enough to make direct antennal contact. This combination of a distinct daily activity rhythm, partial mating site isolation and the ability of males to discriminate conspecific from heterospecific females is adequate to isolate the sympatric *Pogonomyrmex* species from each other reproductively.

These examples illustrate that it is not at all universal that sexual signals serve as pre-mating isolation mechanisms, suggesting that the main function of sexual signals has to be explored in a different behavioural context. In fact, recently West-Eberhard (1983, and Chapter 13, this volume) convincingly advanced the hypothesis that the primary function of sexual signals is in promoting sexual competition and mate choice.

The argument is that signals employed in sexual competition can undergo rapid and divergent evolution, because of their paramount importance in determining access to mates and because of the relatively few restrictions to evolutionary change of communication signals. Thus sexual competition can lead to a rapid signal divergence between populations which subsequently can 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."

## B. Male Assessment and Choice

Mating aggregations and communal signalling occur in many insect groups; among the more familiar examples are communal chorusing in cicadas, crickets and katydids (Alexander, 1975; Walker, 1969), synchronous flashing of males by some firefly species (Buck and Buck, 1968; Lloyd, 1971, 1973, 1977, 1983), communal chemical calling in bark beetles (reviewed by Alcock, 1981) and the assemblies of honeybee drones in traditional congregation places, as mentioned above.

In the light of modern evolutionary theory many mating assemblies can ulti-



mately be explained as the result of males competing for access to females at locations where females are most likely to occur, such as emergence or hibernating sites, feeding areas and oviposition sites. But this does not apply to the mating assemblies of harvester ants, the bumblebees or the honeybees. For example, *Pogonomyrmex* males are attracted in large numbers by the mandibular gland pheromone that other males discharge upon arrival at the mating arena, and the females are also attracted from outside by the collectively discharged male pheromone. There is no control by males of resources at the mating arena valuable to females. In fact, after mating the females fly off again, and only upon landing a second time (often hundreds of metres distant from the mating arena) do they break their wings and begin to dig a nest chamber in the soil. There is also no indication that males assemble where nests from which females emerge might be especially dense.

This parallels very much the situation described by Alexander (1975) for some acoustical insects such as the "periodical cicadas." He proposes the following explanation for the evolution of such communal display behaviour in male assemblies: Because of the importance to females of comparing and selecting males at mating time, females are only attracted to areas where males are dense. "Once mating is largely or entirely restricted to male aggregations . . . every male profits from cooperation, such as synchrony in chorus, which increases the number of females attracted to his particular group" (Alexander, 1975).

Sexual selection is generally assumed to operate in two ways: competition within one sex for mates of the other sex (intrasexual selection), or preferential choice of mates by one sex (intersexual selection). In practice it is often difficult to distinguish between the occurrence of intersexual and intrasexual selection. Because males usually far outnumber females in the mating aggregation, male competition for access to females should also be high. This asymmetry, together with "female choice behaviour", should lead to considerable differences in male reproductive success, as reported in bird and mammal mating assemblies (the "leks").

In many aspects the mating system of *Pogonomyrmex* resembles the vertebrate lek system, including the use of traditional lek sites (Hölldobler, 1976). In the mating arena females are numerically underrepresented at any one time, and several males usually struggle for access to the same female. The first males to contact females often do not mate because of the females' initial resistance or interference from other males. We repeatedly observed males being successfully displaced by other competing males, and even if one male was copulating with a female others literally formed waiting lines, vying to get in the best position to be next. Of course, only if multiple inseminations are possible would the males' "waiting in line" be adaptive. Indeed, multiple matings have been documented in all *Pogonomyrmex* species studied (Nagel and Rettenmeyer, 1973; Hölldobler,

1976). Thus, it seems quite important for males to hold on to the female very firmly. In fact, males of some *Pogonomyrmex* species have particularly strong mandibles with heavily developed muscles. I hypothesized that the intense male competition is a major selecting force for the development of these morphological features and that the females' resistance may allow females to select for the strongest or most persistent males. Recent data obtained in field studies with *P. barbatus* and *P. desertorum* support these assumptions (Davidson, 1982).

In order for female preference to develop, a significant variation in male phenotype must exist. Davidson demonstrated that in both species large males gain access to mates more successfully than smaller males, and while all females that alight on the mating ground eventually mate, "there is significant variation in the reproductive success of males and this variation is associated with male size." Furthermore, Davidson found that "large *P. barbatus* females mate with large males more frequently than expected if pairing occurred at random." On the other hand, Davidson found that the mates of small females are significantly smaller in both species studied than those of large females, and she suggests that "female coyness may enhance the frequency of mating with large males by intensifying male-male rivalry." Finally, Davidson provided evidence that large male body size may be a marker of colony fitness. "For six colonies of *P. desertorum* studied in 1980, the positive relationship between total reproductive biomass and mean male body size borders on statistical significance."

Finally, watching females being surrounded by a frenzied cluster of powerful males, one wonders how the mated female can ever free herself in order to depart from the mating lek. We discovered that females which are apparently fully charged with sperm and no longer motivated to mate, whenever they are assaulted by additional sexually excited males, produce stridulation signals (Markl *et al.*, 1977). Our observational data indicate that males depart more readily from stridulating females than from silent ones. This is obviously of advantage to both sexes: Males stop wasting effort on females already loaded with sperm, while females no longer run the risk of being mutilated by the males' mandibular grasp (Hölldobler, 1976) and can leave the lek as early as possible.

From circumstantial evidence reported in the literature, I assume that many of the aerial mating swarms of ants, the communal mating routes in bumblebees and wasps and the congregation places in honeybees are also the result of sexual selection and probably have a function similar to that of the mating leks of *Pogonomyrmex*.

Evolutionary theory predicts that the differences between the sexes in mating behaviour should be strongly influenced by the relative parental investment of the sexes in offspring. In the social Hymenoptera, as in most insect species, females invest considerably more energy and take higher risks in raising off-

spring; they are therefore usually the much more "choosy" partner in accepting mates. This difference also influences the evolution of the dichotomy of pair-forming communication (e.g. Alexander and Borgia, 1979; Thornhill, 1980) and the selection of a particular signalling mode.

In many of the acoustical Orthoptera and cicadas, for example, the cost of the elaborate signalling devices and the higher risk of being detected by predators due to acoustical signalling is borne by the males, whereas the females search silently and choose. On the other hand, in moths the situation seems to be reversed: the females send out calling signals and males are the searchers. Greenfield (1980) has suggested, however, that the extremely low signal intensity (low release rate of pheromone) can be seen to be adaptive in evading predators and in minimizing energy expenditure, but more importantly, might also facilitate sexual selection. The argument is that females

select mates who are "better" searchers by emitting a very weak signal. This modulation of signal intensity may represent a compromise between a release rate sufficiently high to be detected by males, but low enough so that "inferior" searchers seldom reach the emitting females. Thus, signalling females can stochastically implement mate choice analogous to the manner in which searching females are believed to assess male signalling power in many species.

The males of several lepidopterous species also release chemical signals during courtship that are thought to be aphrodisiac in role (Pliske and Eisner, 1969; Schneider *et al.*, 1975; Broppé, 1979; Conner *et al.*, 1981). In the arctiid moth *Utetheisa ornatrix* and butterflies of the nymphalid subfamily Danainae, which have evolved a remarkably similar courtship system, the males obtain pyrrolizidine alkaloids from food plants during their larval stage. It has been shown that these compounds both serve as defensive substances in the adult insects and provide the raw material from which the chemical aphrodisiac is manufactured. Recently Conner *et al.* (1981) proposed that the male courtship signal may be used by females to assess the male's ability to sequester defensive compounds.

Finally, in the discussion of sexual selection there is some debate about whether individuals choose their mates on traits that have a genetic basis (see Borgia, 1979; Lambert *et al.*, 1982). Indeed, few attempts have been made to test experimentally whether or not the chosen mate differs genetically from those rejected (e.g. Partridge, 1980), an important prerequisite in the opinion of Lambert *et al.* (1982) for the claim that intersexual selection takes place. In addition, in most of these experiments it is difficult to decide whether mating success is based on intra- or intersexual selection. On the other hand, it has been argued that if particular genotypes are always selected, other genotypes should rapidly disappear, thus decreasing genetic variance. But without genetic variance mate selection based on genetic differences is not possible. For a detailed discussion of these issues see West-Eberhard (1979), Thornhill (1980), O'Donald (1980), and Thornhill and Alcock (1983).

### III. RECOGNITION AND DOMINANCE SIGNALS IN THE SOCIAL HYMENOPTERA

Thus mate choice implies that individual differences can be recognized and the choice is based on the comparison of these differences. Very little is known, however, about how individual differences are recognized and measured.

#### A. Recognition of Individuals

In the primitive eusocial halictine bee *Lasioglossum zephyrum*, males recognize individual differences in female odour and accordingly show differential responses. Females which the males have previously smelled elicit significantly less attraction or "pouncing" behaviour. Even after the males were presented the odours of a number of other females the males still remembered the odour of the female they had courted before. It is assumed that males, by responding differentially to these odours, budget time and energy by avoiding females that may have repulsed them or with which they have already mated (Barrows *et al.*, 1975; Barrows, 1975a,b). Similar results have recently been obtained with *Drosophila* (Ehrman and Prober, 1978; Spiess and Kruckeberg, 1980).

The ability of individual recognition, based on so-called discriminators (genetically determined odour labels, Hölldobler and Michener, 1980), appears also to play an important role in the social organization of primitive eusocial societies in the Hymenoptera. The best studied case is that of *Lasioglossum zephyrum* (see review in Hölldobler and Michener, 1980; Michener, 1982). It is possible that in this species (as perhaps in other primitive eusocial species that form societies of not more than about a dozen individuals) female discriminators involved in mating behaviour are also used in distinguishing nest mates from foreign conspecifics. As Michener (1982) expressed it: "Presumably in an evolutionary sense *L. zephyrum* is taking advantage of attributes of solitary ancestors and using them in an eusocial context."

In a series of ingenious experiments Greenberg (1979) and Buckle and Greenberg (1981) demonstrated that *L. zephyrum* guard bees are able to recognize the degrees of similarity of arriving bees to nest mates and then are more likely to accept close relatives of a nest mate than distant ones. Although the discriminators are genetically controlled, the bee's response to them is based on learning. Discriminators are not transferred among nest mates; each bee separately learns those of every other and accepts an unfamiliar bee if its discriminator matches any one of the separate templates it has stored. In addition the data strongly suggest that the bee does not learn or know its own odour.

In the very large colonies of highly eusocial ants and bees, however, it is unlikely that workers could learn every nest mate as a separate referent. Some

blend of discriminators must form a homogeneous label acquired and learned by all. In these cases two principal recognition mechanisms are likely to occur: Each colony member may produce genetically determined odour labels which are distributed among all nest mates to form a collective colony odour; or the queen may produce discriminators which are distributed to all her workers (Hölldobler and Michener, 1980).

If genetic differences rather than environmental odours play the dominant role in the determination of colony odours in these large societies, the simplest procedure would appear to be for the queen to provide the essential ingredients. In the simplest conceivable case, where 2 alleles influence odour at each locus, only 10 loci would generate  $3^{10}$ , or 59,049, diploid combinations; 3 alleles at 10 loci could yield  $6^{10}$  combinations. Monogyny would make such a system easily operable; polygyny would tend to break it down (Hölldobler and Wilson, 1977).

Carlin and I (1983) have recently obtained the first experimental evidence that transferred queen discriminators serve as recognition cues in monogynous colonies of the ant genus *Camponotus*. These acquired odour labels are sufficiently powerful to cause non-preferential acceptance among unrelated workers of different species, raised in artificially mixed colonies, and rejection of genetic sisters reared by heterospecific queens.

Thus, in contrast to primitive eusocial Hymenoptera such as *Lasioglossum*, highly eusocial species such as the monogynous carpenter ants (*Camponotus*) give at most a subordinate role to the workers' individuality. It might be possible that on the queen's removal, worker egg laying coincides with the uncovering of worker discriminators, and patrilineally related intracolony cohorts may discriminate against one another and compete to raise males. Preliminary results that we obtained with the myrmicine ant *Novomessor cockerelli* indicate that this might be the case. Similarly, the data of Breed (1983) and Getz *et al.* (1982) suggest that in queenless groups genetically controlled discriminators of individual honeybee workers can be effective in forming intracolony cohorts.

In this context the discovery that honeybee workers recognize their own queen and can distinguish her from others on the basis of odours is especially important (Boch and Morse, 1974). The olfactory cues which workers use to identify their own queen could be a blend of odours that the queen has acquired from the hive environment (Boch and Morse, 1981). More importantly, Breed (1981) recently discovered genetically determined discriminators in individual queens, a result confirmed by Boch and Morse (1982). Furthermore, Crewe (1982) found substantial variability in the composition of the mandibular gland compounds of honeybee queens. He confirmed a previous finding that there are significant differences between young virgin queens and mated queens and also discovered that each mated queen produced a unique blend of components. The blend was more similar among inbred sister queens, but even within these cohorts there were considerable differences. As Crewe pointed out, the particular blends of

mandibular gland secretions differ among individuals in a population, are not of extrinsic origin, are obviously genetically controlled and therefore fulfil all the requirements for discriminators.

These chemical findings are also in agreement with Breed's (1981) results, which show that even in inbred lines only 35% of the queens are able to replace each other without being attacked by the worker bees. This acceptance rate is still significantly higher than that obtained with outbred sisters (12%), whereas non-sister queens were all rejected.

Although no direct evidence yet exists that honeybee queen discriminators are transferred onto the workers, thereby creating a homogeneously labelled group of nest mates, it is entirely conceivable that genes responsible for colony odour determination are only switched on in the reproductive individual, and that non-reproductive individuals are imprinted on the queen odour shortly after eclosion. It has been convincingly documented that multiple inseminations are the rule in honeybees and that they are much more common in monogynous, outbred ant colonies than previously assumed. This means that the average relatedness between individual sisters can be lower than the one-half relatedness between a queen and her offspring and that the worker groups are relatively heterogeneous genetically. It is reasonable to speculate that only by the unifying power of the queen odour can the social integrity of the worker groups be maintained (Hölldobler and Michener, 1980). These considerations support the parental manipulation theory, according to which selection acts on queens to produce manipulated worker castes whose major tasks are to secure nest sites and other essential ecological resources and to assist the queen in raising her reproductively fully competent offspring [for a review and critical evaluation of "offspring consent theory" and "parental manipulation theory" in social evolution, see Starr (1978) and Bartz (1983)].

## B. The Maintenance of Dominance

It is well known that in a honeybee colony the queen inhibits both workers' ovarian development and the rearing of additional queens through the release of pheromones from her mandibular glands. The principal inhibitory component of this "queen substance" is 9ODA. According to recent results the queen's inhibitory signal can be transferred by workers who had contacted the queen to other workers unable to contact the queen. Seeley (1979) found that workers "that have made extensive (> 30s) queen contact appear to behave as 'messengers' dispersing queen substance. They walk more rapidly, antennate nestmates and receive inspections more frequently, and perform fewer labor acts in the 30 min following queen contact than do randomly chosen broodnest workers of the same age." The observational evidence strongly suggests that the messenger bees disperse the queen substance via antennal contact (Seeley, 1979; Ferguson and



Free, 1980; Juska *et al.*, 1981). It is entirely conceivable that in the same process queen odour labels or colony discriminators are also transferred from the queen to the workers.

Control of workers by queens seems to be a major principle in the organization of highly eusocial, monogynous insect societies, and consequently the queen appears to be a logical source for the colony odour. In the evolutionary primitive stage of eusociality, such as *Lasioglossum*, recognition and dominance signals are clearly separate. But in the highly evolved eusocial systems, such as the large monogynous societies of honeybees and many ant species, queen recognition and queen dominance signals, while not necessarily identical, are nevertheless closely integrated. In the latter case the queen not only inhibits the reproductive activity of the worker nestmates, but may also "mask" the workers' individuality with her own recognition label.

These considerations are in close agreement with the suggested evolutionary pathway of pheromonal queen dominance in social insects. It has been proposed that dominance was first established and maintained by direct physical aggressiveness and egg eating. In the next step, aggressive superiority was linked to individual discriminators, thus enabling nest mates to identify the dominant individual and thereby avoiding costly frequent physical conflict. This situation seems to be represented by *Bombus* (Free, 1953), where the queen first establishes reproductive dominance by physical aggressiveness towards workers, which later learn to identify the queen on the basis of odour and tend to avoid her. This stabilizes the social dominance order. In the final step "direct interactions could then become increasingly rare or completely supplanted by a (chemical) signal of the queen's presence" (West-Eberhard, 1977).

As a result of queen control of reproductive activity in insect societies the difference in reproductive success between an egg-layer and non-egg-layer is tremendous. Recently West-Eberhard (1982) argued that dominance signals involved in queen control should show a striking species-to-species variation, because the difference in reproductive success between an egg-layer and a non-egg-layer is so great that strong selection should act on those traits determining reproductive success. This can be expected to lead to a rapid divergence of dominance signals in isolated populations and closely related species. West-Eberhard supports her argument by describing the remarkable diversity of dominance rituals in *Polistes* and oviposition rituals in stingless bees.

But, as far as we know to date, these considerations are not supported by the apparent uniformity of the pheromonal dominance signal in the honeybee. As pointed out earlier, in all species and races of *Apis* 9ODA has been found to be not only the major attractive compound in the female sex pheromone (Butler *et al.*, 1967; Ruttner and Kaissling, 1968; Koeniger, 1976), but also the most effective dominance and inhibition signal of the queen. In fact, most of those honeybee workers that become egg-layers after removal of the queen also produce 9ODA in their mandibular glands, thereby inhibiting ovarian development

in sister workers (Ruttner *et al.*, 1976; Crewe and Velthuis, 1980). Nevertheless, it would be interesting to follow up West-Eberhard's suggestion and conduct a comparative study of the whole signal complex of dominance in honeybee races and species. As we know from investigations by Velthuis (1970), a queen-substance effect can also be caused by abdominal secretions of honeybee queens. Furthermore, some results obtained by Butler (1966) indicate that mandibular gland extracts of *A. cerana* queens, although effective as inhibitors in cross-specific tests, appear to be less powerful in *A. mellifera* workers than extracts of conspecific queens.

As pointed out earlier there seems to be a close relationship between recognition and dominance in the evolution of queen control signals. In reconstructing the evolutionary pathway of chemical dominance signals in honeybees, Velthuis (1977) suggested there is also a close link in sexual signals and dominance signals. Indeed, in *Apis* both secretions from the mandibular glands and abdominal tergal glands (which are unique to the queen caste) serve as sex pheromones (Renner and Vierling, 1977), while inside the hive the same secretions function as attractant and entourage pheromones and as inhibitors of the workers' reproductive activities. Velthuis suggests that workers may select virgin queens on the basis of the attractive power of their abdominal secretions and that those queens may be correspondingly attractive to males in the mating congregation places. However, recent evidence suggests that the queen selection by sister workers might be based on queen discriminators indicating the degree of relatedness to worker cohorts (Getz *et al.*, 1982).

#### IV. WORKER COMMUNICATION AND DIVISION OF LABOUR IN SOCIAL HYMENOPTERA

Because of the division of labour, insect societies can conduct numerous activities at the same time rather than having to perform them sequentially. The co-ordination and assignment of tasks depends heavily upon communication.

The division of labour in reproductive and non-reproductive castes is regulated by a variety of communication signals which can be effective either as physiological primers or as behavioral releasers, according to the distinction by Wilson and Bossert (1963). Often it is not easy to draw a clear line between the primer effect and releaser effect. In fact, the honeybees' queen substance can function both as a primer and as a releaser pheromone.

##### A. Efficiency of Division of Labour

Primer pheromones may also play a significant role in the regulation and maintenance of the physiological and behavioural homeostasis in insect societies and in the endocrine control of polyethism and polymorphism in the worker



castes (Lüscher, 1976; Nijhout and Wheeler, 1982; DeWilde and Beetsma, 1982). The evolutionary adaptive significance of these regulatory sociophysiological mechanisms can, however, only be understood by a comparative investigation of the ergonomics of castes and division of labour in insect societies (e.g. Oster and Wilson, 1978). For instance the complex physical caste system of *Atta sexdens* is devoted primarily to the processing of leaves and other fresh vegetation into a form that can be utilized by the ants' symbiotic fungus. Wilson (1980a,b) found that an assembly line is employed, with medias cutting and retrieving the vegetation and successively smaller workers processing it through several stages up to and including the placement of tufts of fungi on the newly laid boli. Finally, the smallest workers of all care for the growing fungus and assist in dispensing it to other members of the colony.

In his ergonomic analysis Wilson discovered that the size-frequency distribution of leaf cutters in *A. sexdens* conforms closely to the optimum predicted by the energetic efficiency criterion for harder vegetation; that is, *Atta sexdens* commits precisely those size classes to the leaf cutting that are energetically the most efficient, by both the criterion of the cost of making new workers and the criterion of the cost of maintenance of workers.

The efficiency of division of labour in insect societies also depends on the correlation of the task assignment and the age of the workers. In the honeybees and ants it has been well established that interior workers belong to a younger age class than exterior workers (for a review, see Oster and Wilson, 1978). In the harvester ant *Pogonomyrmex owyheeii*, Porter and Jorgensen (1981) recently demonstrated that the large population of interior workers, which are long-lived and have high energy reserves, represent a reservoir of both social energy and forager replacements. In contrast, foraging workers are physically worn and drained of most energy reserves. Predation and enemy pressure on foragers is high, but since foragers are old and most of their stored energy has been used up, they are low-cost investments in food gathering; they are a "disposable caste".

The "disposable caste" also seems to play an important role in the efficiency of territorial defence in ant societies. Many ant species establish and maintain territories, the design of which depends on the patterns of resource distribution (Hölldobler and Lumsden, 1980). Territories of ant societies are defended co-operatively by the usually sterile worker castes, and because of the division of labour between reproductive individuals and the workers, fatalities caused by territorial defence have a different qualitative significance for social insects as compared to solitary animals. The death of a sterile worker represents an energy and labour debit, rather than destruction of a reproductive agent. As I have recently discovered in the weaver ant *Oecophylla smaragdina*, even this energy debit is minimized by engaging primarily the old workers, which are drained of social energy reserves, in the territorial defence. These workers are housed in special barrack nests on the periphery of the territory, and they are the first to

respond to key stimuli which signal a territorial invasion (Hölldobler, 1983). Thus, worker death might more than offset its cost by bringing or maintaining resources and colony security.

## B. Caste and Modulated Responses to Communication Signals

Different worker groups and castes of the society also show different response behaviours to communication signals. For instance in the ant *Pheidole dentata* the soldier caste is known to respond particularly aggressively to the alarm recruitment signals of workers (Wilson, 1975). Cammaerts-Tricot (1974) has shown that there is a differential response to pheromones by different temporal castes in *Myrmica rubra*. In several ant species it has been found that young workers react to an alarm signal by retreating into the nest, while old workers move out and display aggressive behaviour. Furthermore, the workers' response behaviour also varies in time and space. For example, if an alarm signal is discharged close to the nest, it releases aggressive behaviour in workers; but at greater distance from the nest it elicits escape behaviour (Maschwitz, 1964). Also, the signal itself can be varied; if the alarm pheromone is presented to *Pogonomyrmex badius* workers in low concentrations it merely attracts nest mates, but in high concentration it releases aggressive behaviour. If the high concentration persists, the attracted workers start to dig where the concentration is highest. It was demonstrated that this "high concentration signal" elicits rescue behaviour in *Pogonomyrmex*, for example when workers are buried under sand after a cave-in of their nest (Wilson, 1958). Similar cases of multiple functions of, and responses to, communication signals are known in other social hymenopteran species (see review in Hölldobler, 1977).

These examples indicate that communication in complex social systems is seldom if ever characterized by a direct "all or none" response. In fact, as Markl and Hölldobler (1978) pointed out, communication is not always a deterministic releasing process, but sometimes plays a different and more subtle role in behaviour. For example, in a group of social insect workers very subtle influences caused by communication signals suffice to adjust the behaviour of group mates towards one another in an optimal manner. In such a case, we would expect to find quite low information content for communicative interactions, leaving the group members a large degree of freedom to tune their behaviours according to many other simultaneous necessities in addition to group interactions. In this view, "low-efficiency" communication systems serve different but no less important purposes than more highly deterministic systems. They gradually and smoothly influence the behaviour of receivers, not forcing them into determined behavioural channels, but slightly shifting the probability for the performance of other behavioural acts. We have called this kind of communication system

“modulatory communication”. In it, signals do not release specific behaviour patterns, but rather modulate the probability of reactions to other stimuli by influencing the “motivational state” of the receiver. We should expect such “modulatory communication” to be most frequent in complex animal societies, where a large number of members perform many different tasks at the same time and where an economically efficient organization of behaviour requires that the work force distribute its energy investment among the different tasks through an optimum pattern of division of labour.

In some respect a primer signal might be considered to belong to this category of communication. However, its effect on the receiver's physiological state is usually much more profound and long lasting and therefore quite different from what we call “modulatory communication”.

Typical examples of modulatory communication in ants are the drumming behaviour in *Camponotus herculeanus* and *C. ligniperda* (Fuchs, 1976) and the stridulation signals in *Novomessor cockerelli* and *N. albigulosus* (Markl and Hölldobler, 1978). In these species, the modulating signals serve to facilitate a behavioural change in the receivers. The direction and distribution of the changes are not controlled by the modulatory signal itself but by auxiliary stimuli. Hence, in *Novomessor* stridulation does not modify the production of specific behaviours but only the readiness to react to other stimuli impinging on the receiver at the same time. Modulatory signals are devices for shifting the threshold for the releasing effectiveness of other stimuli, thus amplifying (or attenuating) the behavioural response to them.

Although in only a few cases has a statistical information analysis of modulatory communication been carried out (Fuchs, 1976; Markl and Hölldobler, 1978), circumstantial evidence suggests that modulatory communication is widespread in insect societies. For example stridulatory behaviour occurs in several ant subfamilies; behavioural studies of its function in several species suggest that it mainly serves modulatory communication (Markl, 1973, 1983). Many ant species that do not stridulate produce vibrational signals by shaking their bodies or drumming with their bodies against the substrate. In those cases where these behaviours have been analysed quantitatively it turned out that they do not release a specific response in nest mates, but rather affect the response threshold for other signals (Fuchs, 1976; Hölldobler and Markl, in preparation).

As pointed out, modulatory communication is usually non-specific. It is possible that in an evolutionary sense it is a primitive form of communication in both ants and other social insects. Other communicative motor patterns in ants, such as short fast runs, jerking or wagging motions employed during recruitment communication to summon nest mates to food sources, to nest sites or to the defence of territories (for review, see Hölldobler, 1978), may in part have evolved from motor displays that originally served as general modulators. They have since been ritualized into specialized signals employed in specific contexts, usually in combination with other signals such as trail or alarm pheromones.

### C. Ritualization

The evolutionary process of ritualization appears to have played an important role in the evolution of diverse modes of communication behaviour in social insects. Several examples will be provided below.

Chemical alarm communication probably evolved from chemical defence behaviour. Like many solitary insects, social insects also use chemicals to repel enemies and predators. In social insects, however, defensive reactions are closely connected with alarm communication, and quite often both substances serve both functions.

A comparative study of the trail recruitment communication in formicine ant species that use hindgut contents as trail pheromones suggests this behaviour might have evolved by a gradual ritualization of the defecation process. We can speculate that in the first stage hindgut material became an important cue in home-range orientation and was then transformed into a more specific orienting and stimulating signal used during recruitment behavior. In special cases, such as the weaver ants of the genus *Oecophylla* (Hölldobler and Wilson, 1978), where the hindgut contents serve as a colony-specific territorial marker, a special glandular invagination at the rectum has developed to function as a separate trail pheromone gland.

In an attempt to understand the evolutionary pathways that led to the sophisticated dance communication of *Apis mellifera* von Frisch (1967), Lindauer (1971) and their associates searched for more elementary forms of communication in other bee species, including the stingless bees (Meliponini). They concluded from their findings that the waggle dance communication behaviour in honeybees is a miniature and highly ritualized replica of the flight to the target area. Simple motor displays, mechanical signals and chemical cues of some stingless bees presumably represent the more primitive mechanisms from which the waggle dance originated. One can hypothesize that in bees, which fly long distances routinely, chemical recruitment is less accurate and therefore has become less significant. This led to the development of the highly sophisticated, ritualized waggle dance, which not only stimulates nest mates, but also transmits relatively accurate information about the location of the target area (for further discussion, see Wilson, 1971; Hölldobler, 1977).

The reverse is true for ants: Although cumulative studies have made clear that motor displays and mechanical signals play an important role in recruitment communication in many ant species (for review, see Hölldobler, 1977, 1978), it appears that during the evolutionary “design” of more efficient recruitment techniques, such signals became less important as the chemical recruitment system became more sophisticated.

The so-called chemical mass communication system is certainly a highly advanced recruitment method in ants. It was first analyzed in the fire ant *Solenopsis invicta* (Wilson, 1962). In this system the number of workers leaving the

nest along a chemical trail is a linear function of the amount of trail substance discharged by workers already on the trail. This means that under natural conditions the number of workers being recruited can be adjusted to the actual needs of recruits at the food source. This phenomenon is called mass communication because it entails the transmission of information that is meaningful only with reference to large groups and cannot be exchanged between mere pairs of individuals.

#### D. Evolution of Recruitment

Comparative analyses of the organizational levels of recruitment techniques employed by different ant species do not necessarily provide direct evidence of the evolutionary pathways of recruitment behaviours. However, they permit us to develop models of the evolutionary steps leading to the highly sophisticated stage of mass communication.

I will now present two illustrations of the comparative analyses of the evolution of more sophisticated recruitment techniques in ants.

The so-called tandem running behaviour is generally considered to be one of the most primitive recruitment methods. Only one nest mate is recruited at a time, and the follower has to keep close tactile contact with the leader ant. This behavior has been described in a phylogenetically scattered array of species, but appears to be most common in the primitive subfamily Ponerinae (for review, see Hölldobler, 1981).

Even some ponerine species that are exclusively solitary foragers employ tandem running recruitment during nest relocations. In fact, it is possible that tandem running recruitment, like social carrying, first evolved as a means to lead strayed nest mates back to the nest. Many ponerine ants construct relatively simple nests in soil, so that it is likely that parts of the nest occasionally cave in. It would be of distinct advantage to be able to guide nest mates to the intact portions of the nest. Colonies might also abandon nests that become unsuitable and move to new nest sites. On such occasions tandem running and social carrying have been found to be a common recruitment technique in ants.

Several species of the ponerine genus *Pachycondyla* employ tandem running communication when recruiting nest mates to new nest sites. In *P. obscuricornis* the recruiting worker "invites" a nest mate by a stereotyped motor display that leads to the formation of the tandem pair (Traniello and Hölldobler, 1984). The nest mate is then led to the new nest while keeping close contact with the hindlegs of the leader. Whenever this contact is interrupted, for example when the follower accidentally loses the leader or is removed experimentally, the leader immediately stops. Only after it receives the tactile signal on its hindlegs or gaster does it again continue to travel towards the target area. During tandem running, secretions from the pygidial gland (located between the sixth and sev-

enth abdominal tergites) released by the leader ant provide a chemical bond between it and the follower (Hölldobler and Traniello, 1980b).

*Pachycondyla obscuricornis* is a solitary forager; it uses tandem running only during nest emigration. In contrast *Pachycondyla laevigata* is an obligate predator on termites, and conducts massive group raids when foraging. The raids are organized by a powerful trail pheromone discharged from the pygidial gland by scout ants (Hölldobler and Traniello, 1980a). The shift in diet from evenly dispersed to strongly clumped food sources (termites) apparently led to the use of the pygidial gland secretions in mass communication and the evolution of the pheromones as stimulatory and orienting signals (Traniello and Hölldobler, 1984).

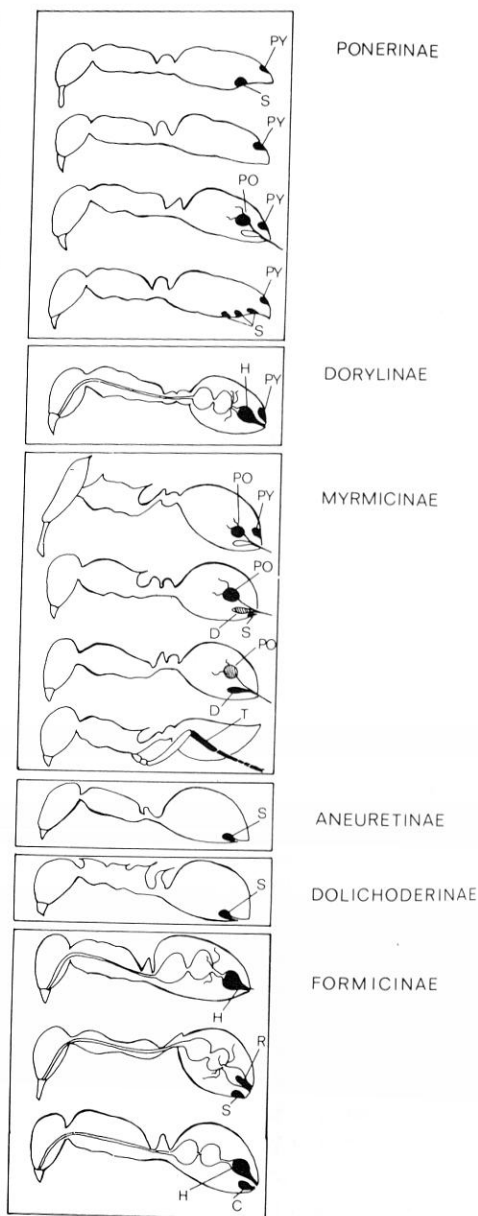
Almost identical modes of recruitment communication have been discovered in other ant subfamilies. But since the anatomical origins of the pheromones are different, we have to assume that the patterns themselves, however, outwardly similar, have evolved independently several times. The parallel is especially striking between the Ponerinae and the Myrmicinae. In the myrmicine genus *Leptothorax* the so-called tandem calling pheromone originates from the poison gland of the sting apparatus (Möglich *et al.*, 1974; Möglich, 1979), while in most other myrmicine species secretions of the sting glands (Dufour gland and poison gland) function as recruitment trail pheromones. During tandem calling a recruiting *Leptothorax* worker raises the gaster into a slanting position, simultaneously exposing the sting and extruding a droplet of poison gland secretions. Nest mates are attracted by the volatile pheromone in the material. When the first ant arrives at the calling ant, it touches it on the hindlegs or gaster with its antennae, and tandem running starts.

It seems very plausible that the highly sophisticated chemical mass recruitment performed by *Solenopsis* and several other myrmicine ants was derived from a more primitive "tandem calling behaviour" of the *Leptothorax* mode. An intermediate mode is perhaps represented by the so-called group recruitment employed by several myrmicine species. In this case a recruiting leader ant lays a short-lived trail with secretions from one of the sting glands, which stimulates a group of nest mates to follow closely behind the recruiting leader ant.

The tandem calling behaviour is also relevant to the evolution of sex pheromones in myrmicine ants. In those species studied the sex pheromone originates from the sting glands (see review in Hölldobler, 1978). It is interesting to note that in species in which wingless ergatoids attract males for mating, for example *Harpagoxenus sublaevis* (Buschinger, 1971), the females display sexual calling behaviour identical to the tandem calling behaviour of *Leptothorax*. This discovery supports the hypothesis that in at least some myrmicine ants sex attractants and recruitment pheromones had the same evolutionary origin. In fact, in some cases the same substance may function in specific situations as sex pheromones and in others as recruitment signals. Again, the parallel to the Ponerinae is



**Fig. 1.** Diversity of trail and recruitment pheromone glands in ants. Representative species in each subfamily are listed from top to bottom. Ponerinae: *Onychomyrmex hedleyi*; *Pachycondyla laevigata*; *Leptogenys chinensis* or *Cerapachys (?) turneri*; *Paltothyreus tarsatus*. Dorylinae: *Eciton hamatum*. Myrmicinae: *Orectognathus veriscolor*; *Pogonomyrmex badius* or *Myrmica rubra*; *Solenopsis invicta* or *Monomorium pharaonis*; *Crematogaster ashmeadi*. Aneuretinae: *Aneuretus simoni*. Dolichoderinae: *Monachis* or *Iridomyrmex*. Formicinae: *Lasius* or *Formica*; *Oecophylla*; *Camponotus ephippium*. C, Cloacal gland; D, Dufour gland; H, hindgut; PO, poison gland; PY, pygidial gland; R, rectal gland; S, sternal glands; T, tibial gland. All sternal glands are labelled "S"; however, the morphology and anatomy of these organs are very diverse. Circumstantial evidence reported by Cammaerts-Tricot (1982) suggests that secretions obtained from the seventh abdominal sternite serves as an auxiliary trail pheromone in *Myrmica*. Most myrmicine ants possess a sternal gland in this region; therefore, I have tentatively marked this area with an "S". In several species it has been demonstrated that more than one gland are simultaneously involved in trail and recruitment communication. For example, in *Pogonomyrmex* the Dufour gland secretions appear to serve as long-lasting species-specific orientation cues, while the poison gland secretions function as stimulating, short-lasting (not species-specific) recruitment signals. A similar situation has been found in *Myrmica*. The literature on which this survey is based has been discussed in Hölldobler (1978, 1982).



striking: here the pygidial glands appear to have functional repertory identical to that of single glands in the Myrmicinae. Depending on the species and behavioural context, the secretions of the ponerine pygidial glands can function as tandem running pheromones, as recruitment trail pheromones or as sex pheromones (Hölldobler and Haskins, 1977).

Comparative studies of the kind I have discussed reveal some of the possible convergent pathways in the evolution of mass communication in ants. Recent morphological and behavioural findings indicate, however, that communication by chemical trails in ants is considerably more diverse than previously assumed (for review, see Hölldobler, 1982). As illustrated in Fig. 1, no fewer than 10 different anatomical structures have been identified in ants as sources of trail pheromones; in the Ponerinae alone 4 different trail pheromone glands are now known. Obviously trail communication has evolved many times independently. Even in the same subfamily the mechanisms and anatomical substrates for trail communication have diverged considerably. Moreover, we have only begun to relate these differences to ecological parameters such as resource distribution, nesting patterns, partitioning of foraging space and territorial defence. But we already know that these ecological factors play a major role in shaping recruitment communication in ants and in other social Hymenoptera (e.g. Oster and Wilson, 1978; Hölldobler *et al.*, 1978; Hölldobler and Möglichen, 1980; Hölldobler and Lumsden, 1980; Hubbell and Johnson, 1978; Johnson, 1982; Pasteels *et al.*, 1982; Visscher and Seeley, 1982; a.o.). Indeed, we have only begun to unravel the complexities of social insect communication, and our interpretation of their evolutionary pathways and adaptations must be regarded as quite tentative.

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