He never completely recovered, and he died on September 20, 1907, while visiting Wisconsin.

Reference

Mallis, A. 1971. *American entomologists*. Rutgers University Press, New Brunswick, New Jersey. 549 pp.

SNOW SCORPIONFLIES. Members of the family Boreidae (order Mecoptera). See also, SCORPIONFLIES.

SOCIAL INSECT PHEROMONES. Social insects are unique in that they have overlapping generations in which adult workers (normally sterile) assist their mother in rearing sisters and brothers. In addition, there are reproductive and non-reproductive castes constituting a division of labor. Our discussion of social insect pheromones will be restricted to the social Hymenoptera (Formicidae, ants; Apidae, bees; Vespidae, wasps) and Isoptera (Termitidae, termites), although there are examples of social thrips and cockroaches.

Regardless of the size of the social insect colony, which can range from tens of individuals to millions, social interactions are required for effective food retrieval, brood and queen care, regulation of caste (sexuals/workers), recognition and exclusion of non-nestmates, and other tasks. There are several sensory mechanisms available to social insects for communication, e.g., tactile and vibratory, however, chemical communication has evolved to a high level of complexity in these insects.

There are advantages to the use of chemical signals as a means of information transfer. The chemicals are relatively small, volatile structures that are energetically inexpensive to biosynthesize and easy to release into the surrounding airspace. In addition, because the signal is detected through space by the sense of smell, it is functional under various environmental conditions. Some disadvantages are that it is difficult to direct the signal at a single recipient unless detection is through direct contact. Also, once released, the signal cannot be changed rapidly or in some cases the signal dissipates before the information has been transferred to all intended recipients. Specific terminology has been developed to define chemical interactions between organisms. We will restrict ourselves to intraspecific chemical communication.

Pheromones are chemicals released by an individual that have an effect on members of the same species. The word pheromone is derived from the Greek 'pheran' meaning to transfer and 'horman' meaning to excite. There are two pheromone subcategories, a) releaser pheromones – produce an immediate response in the recipient individual, e.g., a male moth orienting toward the sex pheromone released by the female moth; and b) primer pheromones – perception triggers the initiation of a complex physiological response that is not immediately observable. Both pheromone types are extremely important in maintaining colony social structure.

Unlike hormones, pheromones must be secreted outside the insect's body via exocrine glands. It is a testament to the importance of pheromones to the success of social insects that they have evolved a very diverse repertoire of exocrine glands – over 70, with 45, 21, 14, and 11 in ants, bees, wasps, and termites, respectively. Some of these glands function to produce wax, other types of building materials, or defensive compounds; however, many exocrine glands have become specialized for the production of pheromones that play major roles in communication and the maintenance of colony social structure. Pheromone-producing glands can be found anywhere on the social insect – from the pretarsal glands of bees to the frontal and labial glands of termites. In addition, the ovipositor of solitary insects evolved into the sting in the aculeate Hymenoptera, bees, wasps, and ants. Most important for this discussion is that the accessory glands associated with the ovipositor evolved into the Dufour's and poison glands. Both of these glands have become very important in pheromone communication in social insects.

The pheromone products have diverse uses among social insects. Recruitment pheromones help guide workers to food materials and in a different context can lead the entire colony to new nesting sites. When a worker ant, wasp, bee, or termite detects an intruder it will release an alarm pheromone that acts to excite and attract nearby workers, which then respond aggressively toward the intruder. Other compounds act as sex pheromones, queen recognition pheromones, territory markers, and brood pheromones, among others. Additional layers of complexity are added because pheromone structure and function varies within the morphological/functional caste system in social insects. Not only is there variability between queens and workers different, but also between the

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different worker castes as well. Sometimes, a single chemical plays different pheromonal roles, depending on the caste releasing it and the context of the situation. With such a plethora of glandular sources and elicited behaviors there appears to be no pattern in pheromone chemical structure or the glandular source relative to behavior elicited. To illustrate the unpredictability of glandular source versus function, trail pheromones in ants have been reported from the Dufour's gland, venom gland, hindgut, pygidial gland, Pavan's gland, and the postpygidial gland. Thus, the glandular source of a pheromone that elicits a particular biological behavior must be determined through bioassay.

Pheromone glands

Pheromone-producing glands are specialized for the distribution of their secretory products. Besides the biosynthesis of the active pheromone components, the glands must be able to regulate the release of the secretion. The mechanisms of release are not well understood; however, glands that have reservoirs may have specialized musculature at the reservoir opening that controls the release of the gland contents. Interestingly, the act of opening the mandibles initiates the release of alarm pheromones from mandibular glands of some ant species. Where there is no reservoir, glandular products may be released directly to the outside as they are produced. Release may be continuous or synthesis and release could be triggered by exogenous stimuli.

The chemistry of social insect pheromones is very diverse. Releaser pheromones elicit an immediate response in the recipient and are generally detected by the antennae in the air and therefore must be volatile. Primer pheromones elicit physiological change and may or may not be volatile, because they can be distributed to colony members by grooming and/or trophallaxis (passage of regurgitated material from one individual to another). We will briefly go through the major pheromone behavioral categories and their associated chemistry.

Alarm pheromones

Alarm pheromones represent an important evolutionary development for eusocial insects because they enable colony worker resources to be focused at specific colony needs, e.g., nest or food defense. The alarm signals only act to alert other members of the colony. If the alerted workers subsequently find an intruder they will likely respond aggressively by attacking. If they find food they may be stimulated

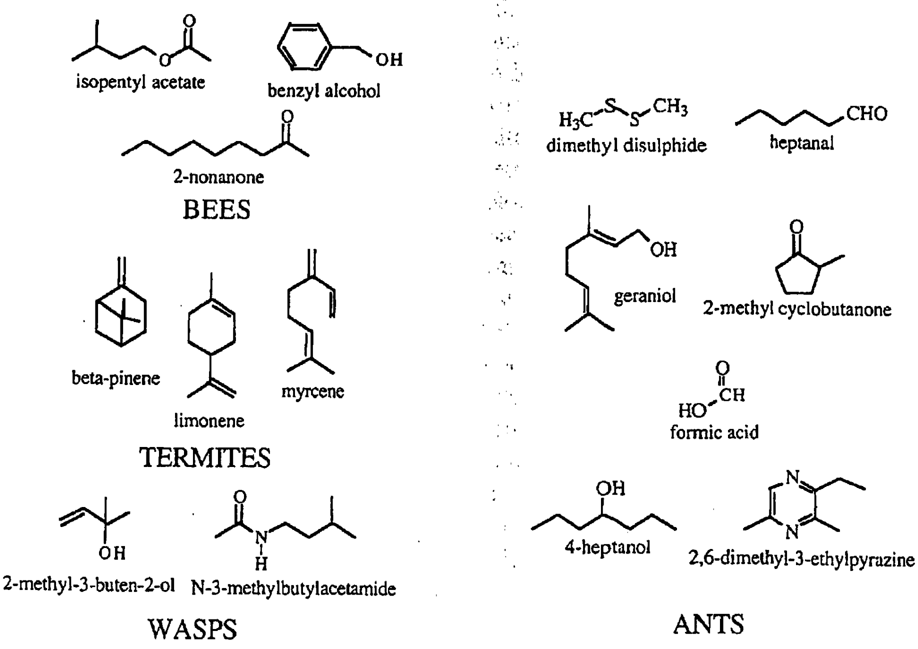

Fig. 933 Representative alarm pheromones identified from bees, termites, wasps and ants, illustrating the diversity of structural types.

to ingest the food. So, while the alarm reaction is usually associated with defensive behavior, it is subsequent stimuli that often dictate what happens next. The release of alarm pheromones may be initiated by the physical disturbance of an individual worker or by the chemical recognition of an intruder. Once the alarm response is initiated, its release may be 'telegraphed' to other nearby workers. This helps explain anecdotal accounts that hundreds of nestmate bees or wasps respond to the accidental disturbance of a single bee or wasp. Similarly with fire ants, people report that worker ants will sneak up their leg, then when in position all of them will sting in unison. Actually the ants simply go undetected for a period of time, until a movement disturbs one ant that then releases an alarm pheromone, quickly activating nestmates in the area. While the mandibular gland is the most common source of alarm pheromones they have also been reported from the pygidial gland, Dufour's gland, Koschevnikov's gland (associated with the sting apparatus of bees), and other glands.

There are many reported behaviors associated with alarm pheromones. In ants for example, attraction to the alarm pheromone source, increased speed of movement, frenzied running, aggression, raised head and more have all been reported as alarm behaviors. More complicating is that the context in which the alarm pheromone is released can affect worker response, e.g., colony disturbance, an encountered intruder, age of the colony, etc. Consequently, it is important for the researcher to clearly define the alarm behavior being investigated.

The requirement for a quick response to the alarm pheromone, as well as for its rapid dissipation after the perceived need has passed suggests that alarm pheromones should be small volatile compounds. While in some instances only one component is reported, e.g., 2-methyl-3-buten-2-ol for the hornet (*Vespa crabro*), it is expected that many more potentially active compounds will be isolated and identified. For example, initially only isopentyl acetate was isolated from Koschevnikov's gland in honey bees (alarm pheromone source); however, subsequent analysis has identified at least 22 additional compounds. Many ant alarm pheromones have been isolated and identified. Considering the necessity that alarm pheromones must be highly volatile, the variety of structural types pays homage to the biosynthetic versatility of the social insects and ants in particular.

Future work in this area should focus on the precise definition of the alarm behavior, development of a behavior-specific bioassay, and then the bioassay-driven isolation of the active compounds.

Recruitment pheromones

Recruitment pheromones are compounds involved in bringing colony workers to a particular location

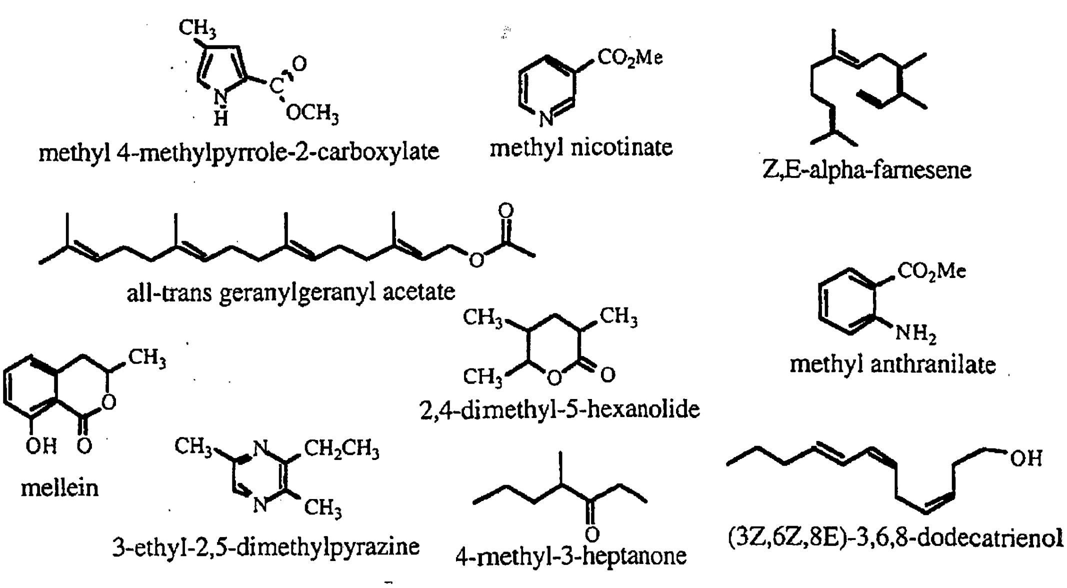

Fig. 934 Representative recruitment pheromone structures illustrating the diversity of structural types.

where they are needed. An ant trail between the colony's nest to a dead insect or other food material is a familiar sight to most people. The trail is the end result of a complex process; but since it is easily observed this pheromone system is sometimes referred to as the trail pheromone. Nestmates may be recruited to gather food resources, or to defend their territory against invasion, or recruitment pheromones may be used to guide the migration of the colony to a better nest site.

The terrestrial ants, of necessity, have evolved a wide variety of recruitment mechanisms and glandular sources of recruitment pheromones. In ants the Dufour's gland, poison gland, the pygidial glands, and sternal glands, hindgut, and rectal gland have been reported as sources of recruitment pheromones. Pheromones from these sources can be readily envisioned being deposited on a solid substrate. Similarly the sternal gland is used in several genera of termites as a source of trail pheromones. Thus far this gland is the only known source of termite trail pheromones. The flying social insects also have a need to recruit a worker force to food supplies and/or to guide colony members to new nesting sites and hence recruitment pheromones can also play a role. Social wasps do not commonly recruit to food sources but do recruit to new nest sites. During this process workers drag their gasters on a substrate to deposit sternal gland secretions, which then guides the migrating colony to a new nest site. Stingless meliponine bees deposit mandibular gland products at intervals on the ground while the Nasanov gland in honeybees is a source of marking pheromones. Most investigations of recruitment pheromones have focused on ants, primarily because they form readily observed trails on the surface and bioassays have been relatively easy to develop.

The red imported fire ant, *Solenopsis invicta*, is a good model to illustrate the behavioral components of the recruitment process. The process begins when a foraging scout worker discovers a food source too large for it to carry back to the colony. During the foraging process the scout keeps track of its position relative to a light source (sun, street light, etc.) and is able to navigate pretty much straight back to the colony. As it makes its way back, it periodically deposits minute amounts of Dufour's gland products to the substrate. The Dufour's gland is attached to the base of the sting apparatus and the products exit through the sting. Thus, in this case, the sting is periodically extended to touch the substrate. When the scout returns to the nest Dufour's gland products are used to attract other workers toward the scout and activate them to follow the very weak initial trail. The attracted and activated workers detect and respond to the trail by following it to the food source. The movement back and forth along the trail is called orientation. The newly recruited workers ingest some food, stimulating them to reinforce the trail with additional recruitment pheromone as they return to the nest. More workers are recruited until the food source is covered with fire ants and additional workers cannot get to the food and do not reinforce the trail. As the food source diminishes fewer workers reinforce the trail and because of its volatility, the concentration of the deposited recruitment pheromone weakens until the food is gone and the trail evaporates completely. The recruitment process can be broken down into several sub-categories. a) Initial trail laying by the scout ant; b) attraction of additional workers to the scout ant; c) activation (induction) of the workers to follow the trail; d) trail orientation. Separate behavioral bioassays were developed for each of the categories and used to guide the isolation of the responsible pheromone components. Z,E-α-farnesene appears to be solely responsible for orientation, but does not attract worker fire ants. A mixture of Z,E-α-farnesene and a bicyclic homofarnesene account for 100% of the Dufour's gland activity in an olfactometer (attraction) bioassay. Remarkably, when this mixture is presented to foraging ants as a trail they do not orient along the artificial trail! This illustrates that the workers first need to be activated or put into a more alert state. In some ant species the scout worker will physically agitate perspective recruits, whereas the fire ant can do the same job with Dufour's gland products. This activation requires virtually a reconstitution of the complete chemical profile of the Dufour's gland.

The fire ant provides one example; however, in some ant species the scout attracts and escorts a single nestmate back to the food source and in others the scout physically activates nestmates who are then able to independently follow the trail. Social insects occupy virtually all ecological niches and have evolved a myriad of mechanisms to accomplish tasks such as recruitment to bring nestmates to a point in space where extra legs and mandibles are needed. The chemistry of many recruitment pheromones has been determined.

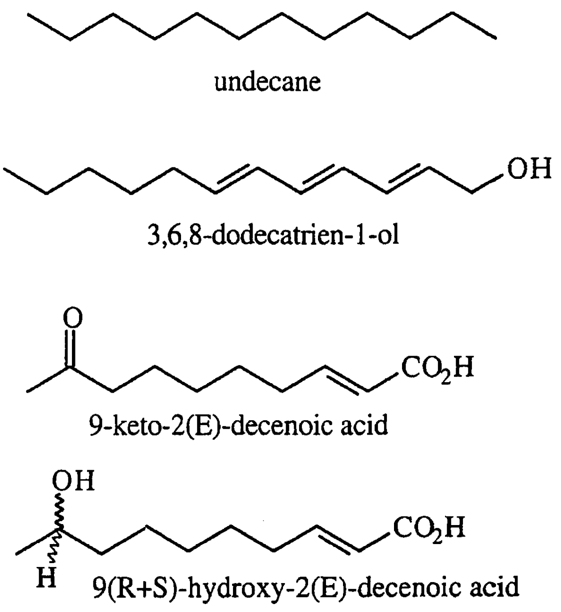

Fig. 935 The structures of known social insect sex pheromones.

Sex pheromones

Sex pheromones are substances that are emitted by males or females that function to attract the opposite sex for the purpose of mating. Most commonly the female attracts the male(s) to her. There are many examples among solitary insects, especially lepidopteran species, of both the associated behaviors and the chemistry of the pheromones involved. However, few sex pheromones have been reported in social insects, probably because of the difficulty in developing appropriate bioassays. Most social insects, including the terrestrial variety (ants and termites), mate during 'mating flights'. The mating flights are usually triggered by specific environmental conditions, so laboratory assays are difficult to establish and observations of the natural phenomenon have been rare. For example, the red imported fire ant, *Solenopsis invicta*, may send off hundreds of thousands of male and female winged sexuals, with males taking flight approximately 30 minutes before the females. The males and females find each other, presumably through sex pheromones, and mate about 100 to 200 meters in the air, then the females come down to attempt to start a colony. No one has yet seen a mating pair of fire ants and no one has been able to get them to mate successfully in the laboratory!

The honey bee 'queen substance' produced by the mandibular glands is used in the context of an established colony to control the production of female sexuals. These same glandular products are used by virgin queens to attract male drones for mating. While there are many compounds produced by the mandibular glands, only two compounds appear to play a sex pheromone role: (E)-9-oxodec-2-enoic acid and (E)-9-hydroxydec-2-enoic acid. The other two examples of sex pheromones in social insects are also pheromones that have different behavioral effects depending on the context of their use. In termites 3,6,8-dodecatrien-1-ol is a trail pheromone, but has also been implicated as a sexual attractant for two termite species: *Pseudacanthotermes spiniger* and *Reticulitermes santonensis*. The one and only sex pheromone from an ant species was isolated from *Formica lugubris*. The pheromone undecane was isolated from the mandibular glands and accounted for 100% of the sex pheromone bioassay activity. This compound is also used by workers as an alarm pheromone.

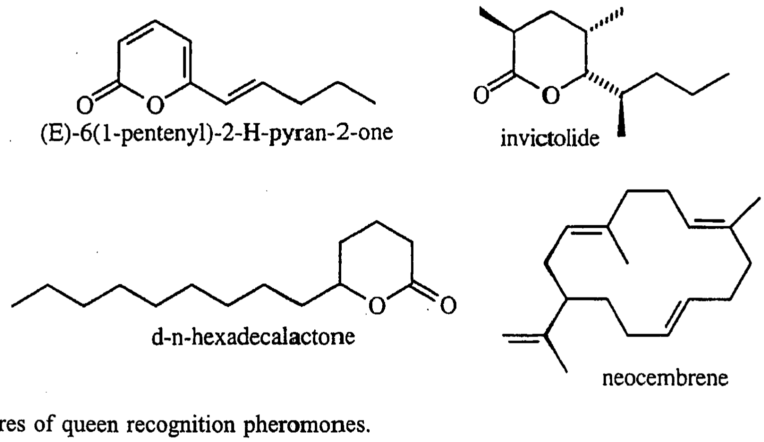

Fig. 936 The structures of queen recognition pheromones.

Queen pheromones

Queen recognition pheromones or more simply 'queen pheromones' are exocrine gland products released by the queen that usually attract workers to her, eliciting care and protection. Most queens of social insects have the ability to attract workers, so the behavior is well documented. Again, various glands serve as sources for the queen pheromone, from the mandibular glands in the head of honey bees to the poison sac in the abdomen of fire ants. The queen benefits from the attention of the workers, and the workers may also use the pheromone signal to gain information about the queen. For example, the release of poison sac contents is directly linked to queen egg laying, thus workers may be able to assess the fecundity of their queen based on the amount of pheromone released into the colony.

The chemistry of these pheromone systems has been elucidated in only a few systems. In the fire ant *Solenopsis invicta* the source of attractant pheromones was found to be the queen's poison sac. Two lactones have been identified as the active pheromones. The pharoah's ant, *Monomorium pharaonis*, produces a macrocyclic compound, cembrene A, in its Dufour's gland that elicits worker attraction. Ejection of the sting and possible deposition of Dufour's gland products on the eggs has also been reported for this species. The honey bee queen pheromone is produced by the mandibular gland and has turned out to be a very complex mixture of compounds that by themselves are only slightly active but when taken together act as synergists, reproducing the activity from the mandibular gland itself. Unusual for pheromones, most of the compounds are found in tens of µgs. In spite of the large quantity of pheromones produced, the synergistic effects of the components complicated the isolation of the active compounds. No queen pheromones have been isolated and identified yet from termite species. Only one compound, δ-n-hexadecalactone, has been isolated as a queen pheromone from a wasp species. It was isolated from head extracts and affect worker behavior.

Releaser and primer pheromones

As mentioned earlier there are two broad categories of pheromones, releaser and primer pheromones. The above discussion centers around releaser pheromones whose detection yields an immediate observable behavioral change. Thus, bioassay development is easier and results can be obtained quickly. This area of social insect pheromone communication has foraged ahead rapidly, while primer pheromones have lagged far behind. This is because they trigger the initiation of complex physiological responses that are not immediately observable. It may take days or more to obtain results. Bioassays have been developed that demonstrate the existence of primer pheromones, but the chemistry has not been forthcoming, except for the honey bee.

The honey bee, *Apis mellifera*, is one of the most extensively studied social insects, in part because of its economic importance and the ready availability of colonies. Interestingly, the queen's mandibular pheromone blend of five components acts as both releaser and primer pheromones. The blend attracts workers to the queen as in 'queen recognition' and therefore has releaser pheromone effects. It acts as a primer pheromone by inhibiting queen rearing by workers. Additionally, it retards the build up of

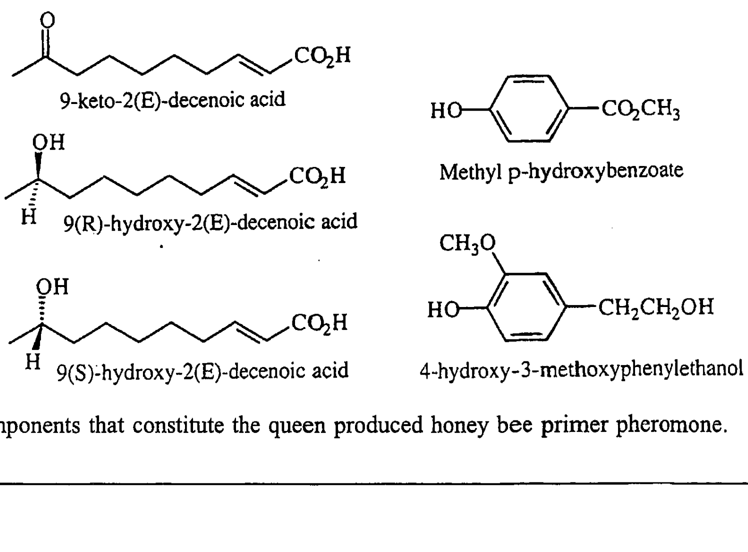

Fig. 937 The five components that constitute the queen produced honey bee primer pheromone.

juvenile hormone titer in worker bees, which effectively acts to slow the developmental progression of workers from brood tending to foraging. These effects clearly represent changes in the physiology of honey bee workers.

Most, if not all, social insect primer pheromones are produced by the queen and function in some way to prevent reproductive competition. Another example comes from the fire ant. The fire ant queen has been demonstrated to produce several primer pheromones that function to: (a) inhibit ovary development in female sexuals; (b) suppress egg production by mature queens in polygyne colonies; (c) inhibit the production of female sexuals; (d) regulate nestmate recognition sensitivity, such that newly mated queens are executed by workers. Unfortunately, the structures of these interesting primer pheromones are still unknown.

We have discussed the main behavioral categories of pheromones in social insects; however, there are other categories, such as territorial marking and brood pheromones, a discussion of which can be found in the references. In addition, there are nestmate recognition cues that are on the surface of individuals that allow members of one colony to distinguish members of another colony of the same species. While the effect is conspecific, the behavioral response is different for nestmate and non-nestmate; acceptance or attack, respectively. Nestmate recognition cues may be acquired from the environment, inherited, or derived from a combination of the two sources. Thus, nestmate recognition cues do not quite fit into the realm of pheromones.

We have demonstrated the complexity of social insect pheromones – their sources, associated behaviors, and chemistry – and hope that readers will be stimulated to delve deeper into the literature to further uncover the beauty and intricacies of this fascinating subject.

See also, PHEROMONES, SOCIALITY IN INSECTS.

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SOCIALITY OF INSECTS. The social insects represent a major evolutionary success story. Their cooperative nest-building, prey capture, and recruitment for food have captured the attention and fueled the imaginations of humans. This cooperation also has contributed to the numerical abundance and ecological dominance of social insects in many habitats. For example, in tropical forests and savannahs, ants and termites outweigh the impressive and very conspicuous mammalian fauna. In all but the coldest environments, ants are the predominant predators of other insects, and they are also major dispersers of seeds of numerous plant species. Social bees pollinate a large proportion of the flora throughout the world, both because they are abundant and because many of them have efficient recruitment tactics such as the remarkably complex dance language of honey bees. Termites are the primary decomposers of wood and other materials containing cellulose in the tropics. Termites and ants together move more soil than earthworms in all tropical habitats, and even in temperate regions, have a major role in mixing nutrients in the soil and creating topsoil. From these examples, it is evident that the social insects figure prominently in nutrient cycles and energy flow in the biosphere.

The majority of all insects are solitary. For solitary species, the most social point in their life cycle is often the interaction between mates, after which females go about their business of reproduction without cooperating with other members of their species. Parasitic wasps lay eggs in their hosts, grasshoppers oviposit in the soil, and butterflies seek out larval host plants on which to lay their eggs. The common thread among these diverse solitary groups of insects is that their offspring develop into adults without interaction with their mothers.