

## The Nest as the Locus of Social Life

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The nests of wasps and bees are among their most distinctive and studyable features. Any treatment of a species' basic biology will usually include a description of the nest, and at least among eusocial species there are now few genera or species groups whose nests are entirely unknown. The central importance of the nest is reflected in the common use of the term *nesting biology* for the behavioral ecology of these insects.

An understanding of the nests of social wasps must begin with those of solitary wasps. Since Evans's landmark paper (1958, expanded in Evans and West-Eberhard 1970), it is generally regarded as a precondition for the evolution of aculeate sociality that the female have a fixed nest to which she repeatedly returns. Behavioral mechanisms for such nest fidelity are well established in solitary aculeates, many of which show extraordinary capabilities of spatial orientation (Baerends 1941, Carthy 1958, Evans and West-Eberhard 1970). For spiders, the web has much the same social-evolutionary importance as a stationary physical nucleus around which a social group *can* form. The known colonial spiders are all web builders (Shear 1970, Buskirk 1981).

Nests of social insects are the locus of colony life in the most literal sense. Interactions between colony members mostly take place at the nest, and in a great many species the individual is effectively a solitary insect while away from the nest. This is certainly true of social wasps, which have no known territoriality, virtually no group foraging, and no demonstrated food-source recruitment, although many swarm-

founding polistines lay odor-spot trails to new nest sites (Jeanne 1981a,c).

The internal relations of any nonclonal society are necessarily a mixture of cooperation and conflict. On the one hand, the members have some overlap of interests on account of shared resources and, usually, high genetic relatedness. On the other hand, because they are not genetically identical, their overlap of fitness interests is incomplete. In my view, it is this very tension that makes sociobiology so interesting, and it is the great accomplishment of kin-selection theory (Hamilton 1972, West-Eberhard 1975, Michod 1982) to have shown how we can make some sense of it.

The nest is the stage on which this drama of cooperation and conflict is played, and what takes place offstage is rarely central to the drama. This chapter describes the uses to which nests are put and the interplay of nest structure with function. For a similar approach to the nests of social bees, see Michener (1974: chap. 7).

## FUNCTIONS OF THE NEST

Wasp nests are constructs, at once light-weight and solid, which serve principally as nurseries for innumerable new generations and have the auxiliary purpose of sheltering the families of artisans which build them. (Saussure 1853-1858:LXIX)

The nest patently originated as a site of brood care and development, or nursery. In this respect, it is very different from the webs of spiders—mentioned above as having an analogous role in the evolution of sociality—which just as patently began as foraging devices. The nest's primary function, then, is to provide a protected microenvironment for the developing brood and its food provisions. Providing food, in turn, is the focus of foraging. Unlike members of many other social groups, such as social ungulates, flocking birds outside of the breeding season, or soldier crabs (*Mictyris* spp.), adult social insects do not forage mainly for themselves but for the brood held in the nest (see Hunt, this volume).

Animal architecture is by no means exempt from the general evolutionary tendency for biological structures to take on new functions (Hansell 1984a). Spider webs, for example, often serve as a substrate for vibratory sexual communication (Barth 1982, Foelix 1982). Comparable shifts of function are also found in the nests of solitary Hymenoptera. For example, while the female of the sphecid wasp genus *Trypoxylon* (subgenus *Trypargilum*) is away foraging, her consort male occupies and guards the newest cell, the physical focus of pair bonding

(Cross et al. 1975, Brockmann 1988). A single empty cell serves as a resting chamber for the female of the eumenine wasp *Calligaster williamsi* (Williams 1919).

Nonetheless, such secondary functions do not appear to be widespread among solitary Hymenoptera, and they probably are rarely important in the nesting economy. In contrast, sociality introduces a new aspect to the nest by virtue of the presence of at least a few interacting adults. Almost unavoidably, the nest thus takes on new roles that may be largely independent of the immediate presence of brood. This is analogous to the way bars, barbershops, and churches have assumed social functions having little to do with refreshment, haircuts, or prayer. There are hints of this point of view in Saussure's statement, quoted above, and in Hansell's (1984a) observation that among aculeates it is only in solitary, presocial, and some primitively eusocial species that the nest shelters only the brood; other species have added specialized structures to shelter the colony as a whole.

Jeanne (1977a) has briefly treated this subject as it applies to eusocial wasps. He defined the primary functions of the nest as those directly related to brood care, and identified four categories of secondary functions: (1) defense against enemies of the brood, (2) maintenance of favorable physical conditions, (3) serving as the main locus of social interactions, and (4) preservation of its own structural integrity. Jeanne's distinction is thus analogous to that between primary and secondary sexual characters. My own concept is much the same, but I find it more useful to treat Jeanne's functions 1, 2, and 4 as primary and to set secondary functions as nearly equivalent to his function 3. As with sexual characters, however, there can be no absolute division between primary and secondary nest functions.

In this chapter, I consider five broad types of secondary functions as they apply to the nests of eusocial wasps. Each of these is also relevant to other eusocial insects, in some of which we can identify particular structural features presumed to have evolved by reference to these or other secondary functions (e.g., Table 15.1).

*Defining colony membership.* As the colony's home, the nest is closely guarded against intrusion by foreign insects. Its perimeter thus sets a sharp boundary to the colony, and residency is nearly equivalent to colony membership. So confident are we of this general principle that in field studies we regularly associate insects collected from the same nest as members of the same colony, even if there is no separate confirmation of such status. Indeed, the term *nestmates* is in general use for what should strictly be called *colonymates*, and I use the latter term only where I wish to emphasize that what is shared is the social group. On the other hand, the frequent use by entomologists of *nest* to signify the colony is confusing and should be discontinued.

**Table 15.1.** Examples of eusocial insect nest features believed to have originated to serve secondary functions

<i>Taxon</i>	<i>Feature</i>	<i>Secondary Function</i>	<i>Reference</i>
Some higher termites (Termitidae)	Thick-walled royal cell near the nest center	Queen's seat of influence: a sort of bunker	Noirot 1970
Dwarf honey bees ( <i>Apis florea</i> )	Broadened top of the comb	Communication: platform for communicative dances	Lindauer 1971
Some stingless bees (Apidae: Meliponinae)	Chamber just proximal to entrance tube	Resting area: chamber for guard bees	Wille and Michener 1973
Bumble bees ( <i>Bombus</i> spp.)	Old cocoons retained in nest	Food storage: honey and pollen	Michener 1974, Alford 1975
Giant honey bees ( <i>Apis dorsata</i> group)	Deep cells in the upper part of the comb	Food storage: honey	Morse and Laigo 1969, Underwood 1986
Leaf-cutter ants (Myrmicinae: Attini)	Fungus gardens	Food production	Batra and Batra 1979; Weber 1979, 1982
Fungus-gardening termites (Termitidae: Macrotermitinae)	Fungus gardens	Food production	Howse 1970, Batra and Batra 1979
Weaver ants ( <i>Oecophylla smaragdina</i> , <i>Polyrhachis</i> spp.)	Auxiliary silk bowers	Shelters for symbiotic homopterans	Degen and Gersani 1989; Starr, unpubl.
Mound-building ants ( <i>Formica montana</i> )	Auxiliary bowers of soil and plant matter	Shelters for symbiotic aphids	G. Henderson, unpubl.
Fire ants ( <i>Solenopsis</i> spp.)	Large, temporary exit holes	Escape of sexuals for mating flights	Lofgren et al. 1975, Starr, unpubl.
Many higher termites (Termitidae)	Temporary tunnels to the surface, sometimes temporary waiting chambers	Escape of sexuals for mating flights	Nutting 1969
<i>Macrotermes bellicosus</i> and some other termites	Peripheral tunnels, sometimes opening at the surface	Nest ventilation	Howse 1970, Noirot 1970

*The queen's seat of influence.* Second to being a nursery for the brood, the nest's most important role is perhaps as the seat of the queen. The importance of this function is reflected in studies of polyethism in polistine foundress groups (e.g., West-Eberhard 1969, Jeanne 1972, Yamane 1985, Röseler, this volume), in which the fraction of time spent on the nest is treated as a key variable. Dominant queens consistently spend less time away from the nest than do subordinates. This tendency may be so marked that it serves as a convenient index for recognizing the dominant queen. Similarly, in all eusocial insects it is the workers who undertake most or all off-nest tasks. We can thus regard the nest in some sense as a personal domain in which the queen holds sway.

*Communication.* The signals that pass among nestmates are almost entirely chemical and tactile, so that sight and (airborne) sound have little part in social insect communication (Hölldobler 1977). Given the prominence of tactile signals, we might expect to find that the nest is used to transmit vibrational signals to nestmates. Both adults and larvae of some social wasps use the nest in this way (see Communication and Nest Structure, below).

*A resting area.* Anyone who spends time watching social insects soon realizes that much of the time they do nothing (Wheeler 1957). It is mainly at the nest where they do nothing, or at least nothing in particular, so that the nest is a resting area as well as an area of activity.

*A mating site.* There are two fairly obvious foci for sexual interactions in aculeate hymenopterans, because there are two places where males could expect to find females: at the nest and at food sources. Compared with the sexual behavior of solitary wasps (e.g., Evans 1966a, Alcock et al. 1978, Thornhill and Alcock 1983), that of social wasps is still quite poorly known (e.g., note the paucity of references to the subject by Thornhill and Alcock 1983). Present knowledge suggests that most species mate away from the nest. There is some indirect evidence of at-nest mating in some polistines and within-nest mating in temperate vespines (reviewed by Ross and Carpenter, this volume), and it may be significant that males of tropical vespines and a few polistines and stenogastrines are rarely found away from the nest (Starr, unpubl.). Still, it remains to be seen in which groups, if any, the nest is the primary site of courtship and mating.

This listing by no means exhausts the range of known or putative secondary functions of social insect nests, as indicated in Table 15.1. Not all known secondary functions of nests appear to be significant for most social wasps, and I will comment on two that are not. First, the nests of many social insects serve as a food-storage facility in a manner quite different from the mass provisioning of most solitary aculeates and a few social species, in which the amount needed for complete

larval development is served into a single cell along with the egg. Use of the nest as a food-storage facility is especially prominent in the highly eusocial bees (Michener 1974, Roubik 1989), honeypot ants (Wilson 1971: fig. 14-6), and fungus-gardening ants and termites (Sands 1969; Batra and Batra 1979; Weber 1979, 1982). *Polistes* and some other wasps often store droplets of honey in cells (Marchal 1896b, Rau 1928, Evans and West-Eberhard 1970, Strassmann 1979), but only the polistines *Protonectarina sylveirae* and two species of *Brachygastra* are reported to regularly stockpile large quantities of honey (Buysson 1905, Zikán 1951, Naumann 1968, Evans and West-Eberhard 1970, Richards 1978a). I have found *Polybia* nests with cells stuffed with prey, but that is exceptional among wasps (see also Gobbi 1984). The evident reason is that dismembered prey, unlike pollen and some other social insect staples, is not readily preserved.

Second, while the nest clearly has a key defensive role, especially in protecting the brood from predators (Jeanne 1975a), it does not stand as a refuge for individuals threatened away from the nest. When independent-founding polistines are disturbed at the nest, they often retreat to the far side of the comb. Similarly, in social insects with enclosed nests, individuals at the nest entrance or inside the nest often respond to outside disturbance by backing deeper into the nest (e.g., *Pseudochartergus fuscatus*: Jeanne 1970c). In this limited sense, the nest is a refuge. One might further expect a wasp threatened in the vicinity of her nest to flee into it, much as a marmot or fiddler crab runs to its burrow. However, I have never seen that happen, even in species that nest in impregnable hollows or burrows, nor have I found it mentioned in the literature.

## THE ELEMENTS OF NEST STRUCTURE

Here I name and briefly discuss the main features of the nests of social wasps. For detailed analyses of their materials, design, and evolution, see Jeanne (1975a) and Wenzel (this volume).

Unlike the nests of most termites and ants and many social bees, those of all social wasps are free-standing structures formed by the accumulation of material. Many vespines nest in ready-made cavities in the soil. Although they may enlarge the cavity (Spradbery 1973a, Akre et al. 1980, Edwards 1980), such excavation is not itself an enlargement of the nest, but simply gives room for nest building to proceed. As noted by Malyshev (1968), this structural independence of the nest from its environment should allow considerable freedom in the development of the overall structure and final size, and in fact social wasp nests seem relatively unconstrained by the substrate.





**Fig. 15.1.** Nests of eusocial wasps, illustrating main features and some of the gross variation. (a) Naked comb of *Mischocyttarus labiatus* suspended from a centric petiole (petiole central on comb). (b) Naked comb of *Polistes erythrocephalus* suspended from an eccentric petiole (petiole near edge of comb). (c) Nest of *Ropalidia horni* comprising three combs, each with an eccentric petiole. Although the two larger combs appear coalescent, they are discrete. (d) Nest of undescribed *Parischnogaster* species, a series of cells arranged approximately linearly along a substrate, with no true petiole. (e) Cross-section of *Vespa affinis* nest, showing the parallel combs connected by petioles and surrounded by an envelope (stelocytarus calyptodomous arrangement). (f) Cross-section of *Brachygastra augusti* nest, without petioles between the parallel combs, which are extensions of the envelope (phragmocytarus arrangement). Note single hole through the lower comb. (g) External aspect of *Synoeca septentrionalis* nest, the envelope perforated by a single entrance hole. See Jeanne (1975a: fig. 9) and Wenzel (this volume: Fig. 14.47) for the internal structure.



The accumulated nesting materials of most social insects can be grouped into four categories: (1) plant matter, (2) mud and feces, (3) silk, and (4) wax and resins. Social wasps build with plant material, mud, or a mixture of the two, often with some admixture of glandular material. Most social wasp species appear to use little or no mud. Rather, the nest consists of plant material chewed into a pulp and in most parts of the nest drawn into a thin sheet, which dries to form a variably strong, flexible material known as carton.

The fundamental unit of all wasp and most bee nests is the cell, the fixed chamber in which an individual develops from an egg into an adult. For present purposes, we can take this as a given. As Jeanne (1977a) has pointed out, though, the very interesting question of why wasps and bees segregate the brood in individual cells, while ants and termites do not, has yet to be answered.

Almost all social wasps compactly arrange a group of cells into a comb by orienting the cells in parallel, with a high degree of wall sharing between adjacent cells (Fig. 15.1a-c; see Fig. 15.1d for an exception). If the number of cells becomes very large, there comes a point at which a single comb is no longer the most compact arrangement. Most species with mature colonies of more than about 100-200 adults (Jeanne 1977a) and with roughly 1000 or more cells characteristically build two or more combs in parallel, most commonly one above the other (Fig. 15.1e-f; Wenzel, this volume: Figs. 14.2, 14.43, 14.54). A few polistines build concentrically arranged combs (Vecht 1966, Evans and West-Eberhard 1970: fig. 91; Wenzel, this volume: Figs. 14.1, 14.38). Adjacent combs are separated by a more-or-less regular wasp-space, a separation sufficient to allow a wasp to walk between them. Such a nest thus has a hierarchical structure, in which the cells are grouped into combs, which are grouped in turn into a parallel set.

It is conceivable that an additional layer might be added to this hierarchy through the construction and use by a single colony of several distinct nests. Many ants and some termites have such polydomous (= polycalic) colonies, but they are unknown among social bees. The nesting arrangements of some wasps could be regarded as polydomous, although none achieves the sort of dispersion that we usually associate with the term (see *The Boundary between Colony and Non-colony*, below). The flightlessness of ants and termites is probably sufficient to account for this difference. The apparent absence of accurate food-source communication in wasps and most social bees is undoubtedly due to the fact that they fly from one site to another, so that they cannot recruit by means such as odor trails and tandem running (see Hölldobler 1977). It is thus hard to see how social cohesion could be maintained among dispersed nests if newly emerged workers cannot easily learn their locations.

The first (or only) comb may be either sessile—i.e., sitting directly against the substrate—or attached by a slender petiole (stalk or pedicel) (Fig. 15.1a–c). If there are several combs, they often are connected across the wasp-spaces by comparable petioles (Fig. 15.1e). No species of Stenogastrinae builds a petiole, though many achieve a similar effect by building a sessile nest on a slender vine or twig (Fig. 15.1d; Wenzel, this volume: Fig. 14.7).

Vespines and most swarm-founding polistines nest in compact cavities and/or surround the comb(s) with a sheetlike envelope (Fig. 15.1e–g). The envelope is usually continuous except for a single narrow entrance hole (Fig. 15.1g). Many instances of nests with more than one hole are known (Starr 1989b), but only in the genus *Protopolybia* do multi-holed nests appear to be a regular architectural feature (J. Wenzel, unpubl.). An envelope thus sets a very definite perimeter to the nest, with the entrance hole as the point of communication between the exterior and interior. Many social insects alter or plug entrance holes in response to disturbance (e.g., Khoo and Yong 1987) or open temporary new holes for massed mating flights (e.g., Nutting 1969). However, social wasps have never been reported to make such alterations, so the nest's size and form can be treated as nearly constant in the short term.

Even very large nests are usually about as compact overall as substrate conditions will permit. That is to say, combs tend to be roughly circular and of such a number and arrangement that the total nest volume and outer surface area are not much beyond minimal for that number of cells. Such compactness is consistent both with economy of building materials (Jeanne 1975a, 1977a) and with maintenance of social cohesion. Where we find strong departures from this general rule of nest compactness, it draws attention to the social significance of within-colony dispersion of individuals. In a very elongate nest or one that separates into branches or lobes, some sets of individuals may have little physical contact with some others, with probable social consequences. Similarly, it is reasonable to think that any barriers between occupied parts of a nest may affect social cohesion, especially in matters of reproductive competition and other conflicts among nestmates.

#### THE BOUNDARY BETWEEN COLONY AND NONCOLONY

As stated above, residency on the nest and colony membership are very nearly one and the same. Given such a distinct criterion, the dividing line between one colony and another should be plain to members of each, and we should expect stable membership, with little drift-

ing of individuals between colonies. This expectation is for the most part upheld in eusocial insects (Wilson 1971). *Polistes* foundresses have an unruly tendency to switch nests (West-Eberhard 1969, Pratte 1980, Gamboa 1981, Noonan 1981, Itô 1984a), but nest switching is almost entirely confined to the earliest part of the colony cycle. The attention given to nest switching is testimony to its uncommonness among social insects, and evidently occasioned Gamboa's (1981:153) remark that "*Polistes metricus* . . . exhibits considerable nest infidelity."

Itô and Higashi (1987) studied a population of wasps under circumstances where a breakdown in colony boundaries might be expected. A very dense aggregation of the independent-founding species *Ropalidia plebeiana*, occupying some thousands of combs, is known to have persisted for several years in one place in New South Wales, Australia. Richards (1978b) had suggested that groups on different combs were not independent colonies but together constituted one or more "super-colonies," in the manner of some ants of the *Formica rufa* species group (e.g., Higashi 1978, Rosengren and Pamilo 1983). Nonetheless, observation of marked individuals showed very little drifting between combs from one day to another (Itô and Higashi 1987).

Given this general identity between the nest and its colony, tolerance of a new individual on the nest is the same as accepting her into the colony, and physical expulsion is a simple, unequivocal means of ostracism. A *Polistes* queen seeking to join an established foundress group, for example, may land nearby and remain at the margins of the nest, sometimes for days, awaiting an opportunity to insinuate or force herself into the colony by taking up physical residence (West-Eberhard 1969, Gamboa et al. 1978).

The converse of this process often takes place in pleometrotic *Polistes* colonies soon after the first workers emerge: active hostility among adult females escalates until the subordinate queens are driven off the nest and out of the colony (Pardi 1942a, 1947; West-Eberhard 1969; Gamboa et al. 1978; Reeve, Röseler, this volume). A comparable event happens in the colony cycle of the swarm-founding *Metapolybia aztecoides* and *M. docilis* (West-Eberhard 1973, 1978b). Fletcher and Blum (1983) suggest as a general rule in social Hymenoptera that it is the workers that do the culling in such situations. Unfortunately, little direct attention has been given to the question of which members of social wasp colonies are responsible for the ousting of supernumerary queens, but the implication has been that, for *Polistes*, the workers remain largely aloof from a battle between queens. The lack of worker involvement in the reduction of queen number would be consistent with our general conception of queen control as relatively direct and physical in these wasps. It seems likely, on the other hand, that the elimination of males from the colony is always carried out by workers.

The periodic violent expulsion of male honey bees by workers is well known (Morse et al. 1967, Free and Williams 1975, Winston 1987), and similar occurrences are known or suggested in some *Polistes* (West-Eberhard 1969, Kasuya 1983a).

Much the same processes of social acceptance and ostracism (through "peripheralization") are known from primates (e.g., Box 1984, Jolly 1985: chap. 15), the difference being that there is no unambiguous physical boundary such as the nest furnishes. Do social insects recognize the nest edge in particular as the boundary? It is hard to believe that they do not, yet I am not aware that the question has been addressed.

Consistent with this hypothesized relationship between nest and colony boundaries is the observation that the process of colony fission, as far as we know, always involves a change of site for at least one of the daughter colonies. We do not find two or more colonies of any species occupying a single nest. However, colony fission need not entail a shift into unfamiliar habitat for either group. For example, new colonies of stingless bees tend to be established well within the mother colony's foraging range (Lindauer 1971, Sakagami 1982, Wille 1983). The "satellite nests" of *Polistes exclamans* represent an elaboration of the colony cycle in which some females leave the nest to found daughter colonies before the usual end of the season (Strassmann 1981b,d). Although these are usually established nearby, it appears that they do not long remain auxiliaries of the mother colony but are soon independent.

Quite a different situation is presented by individual colonies of those *Polistes* and independent-founding *Ropalidia* species that often or characteristically construct a series of separate combs (Jeanne 1979a, Hook and Evans 1982, Kojima 1984b) (Fig. 15.1c). Although these are by definition unequivocal examples of polydomy, I doubt that they have much in common with the polydomy of many ants and termites. Combs within a group are "independent" (Kojima 1984b) in the physical sense that they neither support nor impede each other, but in the examples I have seen they are far from spatially independent. Rather, they are grouped close together and often show quite regular nearest-neighbor distances (Fig. 15.1c). More important, there is no indication that they are socially any more independent of each other than are different combs within a vespine nest, for example, so that the term *satellite combs* (Kojima 1984b) may be misleading. It is fortunate that Strassmann (1981b) has drawn a clear distinction between this sort of polydomy and a satellite nest situation.

Should such a division of the cells among several distinct combs affect social cohesion? If it is possible for wasps to be "associate members" of a colony, this seems like a good place to look for it. To date, this question has only been partially addressed in one species. Where

*Polistes canadensis* builds multiple combs, queens do not restrict their activities to one comb or another and seem to treat the entire nest much as if it consisted of a single comb (Jeanne 1979a). However, this species (where it builds multiple combs) has the anomalous tendency to utilize each comb for only one brood cycle and to keep moving down the line, like the Mad Hatter and his guests, so it makes little sense to generalize from it to other species. The possibility remains that fragmentation into several open combs breaks up the coincident outlines—from the wasps' point of view—of the nest and the colony.

If this is so, might the extreme elongation of a single open comb have a similar effect? I very much doubt it, just because such nests seem always to be quite small, even where they consist of just one or two rows of cells. Accordingly, there is no part that could be considered an outlying zone, nor is there opportunity for nestmates to become strangers to each other.

## COMMUNICATION AND NEST STRUCTURE

The durable cohesion of a social insect colony demands a flow of information from the queen and brood to the active workers, in order that the colony's status and requirements can be monitored. Except in the simplest colonies, it also requires considerable transfer of information among workers. On a simple level, such exchange is unavoidable, as workers respond to changes in nest features brought about by themselves and their nestmates. There is no indication, though, that such stigmergic responses (Wilson 1971: chap. 11) go beyond just keeping the nest in order to the point of affecting social organization. It is thus more pertinent to ask whether there is a connection between variation in nest structure and the more direct forms of within-colony communication.

Two types of chemical communication are known in eusocial wasps. At least some vespines have queen pheromones that seem to act much like those of honey bees (Ikan et al. 1969, Landolt et al. 1977, Edwards 1980), and chemical alarm is inferred in some polistines (Jeanne 1981b, 1982b) and vespines (Maschwitz 1964a,b, Edwards 1980, Heath and Landolt 1988). The relative development of such communication is evidently related to colony size and complexity, but I see two reasons to doubt any close connection with nest structure.

First, there is no indication that the slow-acting (primer) queen pheromones cannot be distributed just as thoroughly in one kind of nest as another. If this were not the case we would expect poor queen control in the weaver ants *Oecophylla smaragdina* and *O. longinoda*, whose huge colonies are each dispersed among many discrete nests, often over sev-

eral trees (Way 1954, Hölldobler and Wilson 1978, Starr, unpubl.). Yet all examined colonies of these species have been monogynous, and worker egg laying is unknown in queenright colonies.

Second, it is not yet known whether airborne alarm pheromones take significantly longer to reach *responsive* colony members in some kinds of nests than in others. The phragmocyttarous nests of *Polybia* and some other genera have more thorough internal partitioning (e.g., Fig. 15.1f; Wenzel, this volume: Fig. 14.48–14.58) than calyptodomous vespine nests (Fig. 15.1e; Wenzel, this volume: Figs. 14.59–14.62), so that a pheromone released at the entrance should take longer to reach the upper combs in the former type of nest. But this may be unimportant if wasps on the upper combs are mostly too young to be effective defenders.

Wenzel (this volume) has pointed out that in phragmocyttarous nests the lowest chamber is often without cells and may even be narrowed to such an extent that it appears unsuited for brood rearing. If this is the mature condition, then such a chamber would seem most likely to serve as a holding area for guard wasps, the most appropriate individuals to respond to alarm pheromone release. It is curious that in the many vespine nests that I have dissected I have never noticed any comparable elaboration of the area just inside the entrance hole.

Although we still know little more about the physical properties of carton and nests than did Henri de Saussure (as quoted above), they are plainly a very good substrate for producing vibrations, unlike mud, silk, or wax. In the course of their normal activities, females of any vigorous *Polistes* colony, for example, can be seen to shake the nest and occasionally to scrape or rub it audibly. Many types of such vibrations would seem well suited for communication among nestmates.

By playing back recordings of returning foragers of a species of stingless bee, Esch (1967) showed that workers at the nest respond to the particular sounds that returning foragers make. Inferences of responses by social wasps to airborne vibrations remain equivocal, in my view. Some polistines react strongly to human whistling (Overal 1985), but it is plausible that this induces vibrations in the nest material, which the wasps then feel. The response of *Vespa orientalis* workers to recordings of larval hunger signals (Ishay and Schwartz 1973) would seem comparable to those noted above for stingless bees, and I know of no direct objection to the evidence. However, the use of (poorly localizable) airborne sound to solicit food makes so little biological sense that I reluctant to accept it.

On the other hand, the communication functions of several types of substrate-borne vibrations is now well established for social wasps. The two best studied classes of such signals are the lateral vibrations, or tail wagging, of *Polistes* females (Esch 1971, Gamboa and Dew 1981, Down-

ing and Jeanne 1985, West-Eberhard 1986) and the hunger signals of vespine larvae (Ishay and Landau 1972, Ishay and Schwartz 1973, Es'kov 1977, Ishay 1977a).

Tail wagging (also known as abdominal wagging; see Reeve, this volume) may rattle the nest-comb and may be distinctly audible to a human observer. Because, within foundress groups, most tail wagging is done by the dominant queen (West-Eberhard 1969, 1986; Hermann and Dirks 1975; Gamboa et al. 1978; Strassmann 1981a; Hughes et al. 1987), some authors have inferred a dominance function for the behavior. I find this inference unconvincing. Tail wagging is also known from lone foundresses (Hermann et al. 1975, Gamboa et al. 1978), and foundresses of at least some species continue tail wagging after subordinate foundresses have disappeared (Starr, unpubl.). As several authors (e.g., Pardi 1942a) have noted, tail wagging is closely associated with the inspection of cells and food exchange with larvae, and my own experience with *Polistes annularis* and *P. exclamans* is that it very rarely occurs outside of this context. Present evidence points to a general function as an alerting signal to larvae, much like the antennal drumming of various species (Evans and West-Eberhard 1970, Pratte and Jeanne 1984), rather than as a means of communication between adults. This hypothesis is consistent with data showing that *P. annularis* tail wagging is a more usual part of cell inspection after the first larvae have hatched (Strassmann 1981a) and with the prediction that dominant foundresses inspect much more than others. Jeanne's (1972) observations of a very similar behavior in *Mischocyttarus drewseni* also agree with this interpretation.

This is not to suggest that tail wagging must have only one function or the same function(s) for all species. I merely contend that no strong evidence has yet been presented for any other. Tail wagging evidently transmits a clear signal to everyone on the nest, and it would be odd if it were utilized for only one kind of message. Still less is there reason to think that similar movements reported from vespines (Ishay 1977a, Ross 1982a) must have the same function(s). (For another view of tail wagging, see Reeve, this volume.)

The audible movements of vespine larvae bumping their heads and scraping their mandibles against cell walls unambiguously function in food solicitation from adults (Ishay and Landau 1972, Ishay and Schwartz 1973, Es'kov 1977, Ishay 1977a). These "hunger signals" are thus in apparent functional symmetry with some vibratory signals of adults, such that one conveys a demand for food and the other an offering.

Vibrations in carton would seem extremely well suited for transmitting alarm, and in a few swarm-founding polistines there is evidence for such a role (Chadab 1979b, West-Eberhard 1982b). I therefore find it odd that similar organized tapping, scraping, or buzzing reactions have

not been reported from disturbed vespine colonies. West-Eberhard (1969) noted that *Polistes* females may scrape the comb in the course of taking off in a flight attack and suggested that this may serve in alarm communication. However, my observations of several *Polistes* species failed to show that either their threats or attack flight serve to alarm nestmates (Starr 1990).

Unlike chemical signals, vibratory communication cannot very well be indifferent to nest structure. At least in vespine nests, vibrations propagate well within a comb but hardly at all from one comb to another or to the envelope (Ishay 1977a). This property would seem to increase their value by ensuring against the production of noisy, hard-to-localize signals. There is no indication, though, that the nest is in any way elaborated to facilitate vibrational communication. At present the best hypothesis seems to be that such communication has evolved to utilize existing nest features.

We can take this point a step further by saying that no feature of any social wasp nest is yet suggested to have been shaped by the colony's communication needs, comparable to the top platform of an *Apis florea* comb, for example (Lindauer 1971). But let me emphasize that nests seem not to have been examined with this question in mind. Why, for example, do the nests of *Synoecca* species have such a sturdy, regularly ridged envelope (Fig. 15.1g)? I know of no evidence that it amplifies or regulates alarm vibrations (Overall 1982), nor has it been shown that the ridges are needed for structural support.

## CONFLICTS OF GENETIC INTEREST

I have considered above how nest features can influence the colony's struggles against outsiders. Many of these struggles are at least potentially mirrored in the uneasy tolerance among colony-mates with conflicting genetic interests.

A female wasp's most fundamental route to classical fitness (a measure of success in rearing her own offspring) is to monopolize egg laying in the colony. It is well known that co-foundresses of some species undergo an intense struggle over this prize early in the colony cycle (reviewed by Jeanne 1980a, Fletcher and Ross 1985, Röseler, this volume). In addition, a queen may be in conflict with unfertilized workers over the laying of male eggs (Bourke 1988).

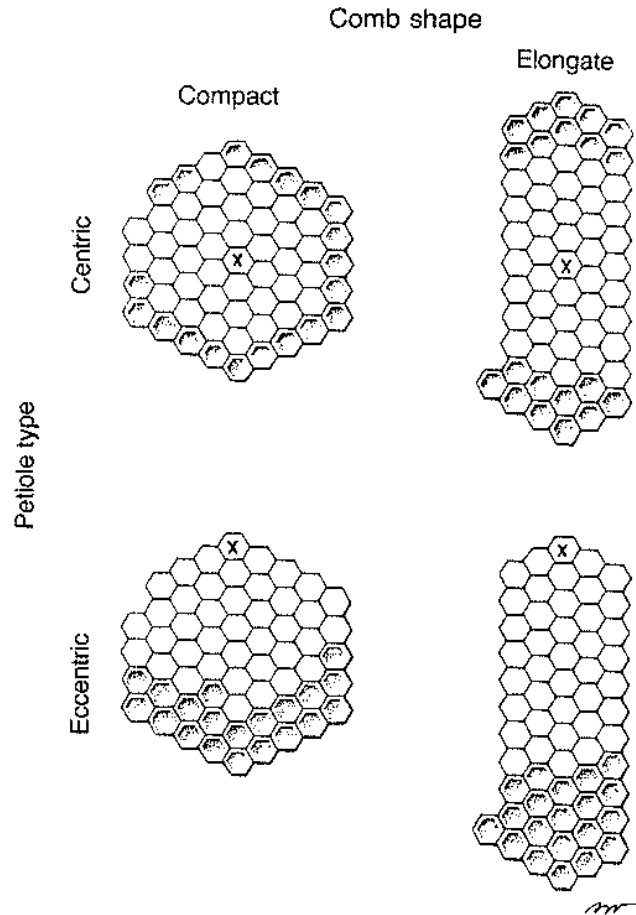
The partitioning of the brood-rearing space into cells is unavoidably central to this struggle. In the first place, it strictly limits the number of brood reared at one time. If a queen can keep all cells occupied by her own brood, a nestmate has nowhere to reproduce. Second, the cellular comb keeps the brood stationary, which must give the dominant queen



a considerable advantage. The habit among competing foundresses of patrolling the brood-comb and destroying each others' eggs has been noted in several *Polistes* species (Pardi 1942a, Gervet 1964a, West-Eberhard 1969, Hermann and Dirks 1975, Strassmann 1981a) and in *Mischocyttarus drewseni* (Jeanne 1972) (see also Röseler, Spradbery, this volume). Queens appear only to eat newly laid eggs (Heldmann 1936a, West-Eberhard 1969), which suggests that they do not maintain a detailed map of the brood but rely on constant vigilance to detect others' eggs soon after they have been laid.

Effective vigilance probably requires a great deal of patrolling, much of which may come about in the course of other tasks. We could reasonably expect every adult on an ordinary *Polistes* or *Mischocyttarus* nest, for example, to visit every part of the nest and to contact every nestmate in the course of the day's activities. It is difficult for us to keep track of the coverage of most nests, except very small ones, but the linear arrangement of cells in nests of *Parischnogaster jacobsoni* and related species (Stenogastrinae) (Fig. 15.1d) makes it relatively easy to do so. Turillazzi and Pardi (1982) found that a *Parischnogaster nigricans* queen periodically patrols the length of her nest. Turillazzi (1985a:124) further monitored the positions of females on a *P. nigricans* nest at one-minute intervals over five hours and reported that "four distinct zones of preference are evident." However, my own reading of the same data is that the wasps' attention was spread rather evenly along the nest.

It is plain that the reproductive monopoly of many primitively eusocial wasp queens is not easily gained or kept. Sôichi Yamane (cited in West-Eberhard 1986) has suggested that the species-characteristic pattern of comb growth may influence the completeness of the queen's reproductive monopoly. Fig. 15.2 illustrates Yamane's hypothesis in slightly expanded form. If we let the shaded area of new cells be the zone of reproductive opportunity, then the figure shows that two common variables in the nest structure of independent-founding polistines—shape of the comb and the centricity of the petiole—can affect the ease with which a queen can cover this zone. (That she tries to patrol the zone of reproductive opportunity is suggested by the observation that a *P. canadensis* queen—in a population where each nest has one comb [West-Eberhard 1986]—stays mainly in the "shelf" area of new cells and drives others from it.) For either a round or an elongate comb, an eccentric petiole (e.g., Fig. 15.1b; Wenzel, this volume: Fig. 14.26) renders the zone of reproductive opportunity more compact, and hence more amenable to queen vigilance, than does a centric petiole (e.g., Fig. 15.1a; Wenzel, this volume: Fig. 14.27). The most compact zone of all is found on an elongate comb with an eccentric petiole. This illustration is intended to demonstrate one way that structural modifications of the nest can have important social effects. It is perhaps not



**Fig. 15.2.** Schematic single-comb nests of independent-founding polistines, illustrating the effects of comb shape and petiole placement on the shape of a zone of cells available to receive eggs. Each comb comprises 60 cells, with the 20 newest cells (shaded) empty or with new eggs. *x*, position of the petiole.

farfetched even to see the latter as candidates for multiplier effects (Wilson 1975), in which comb shape and petiole type affect the queen's relative reproductive hegemony, which in turn affects relatedness among workers, thence queen-worker and worker-worker conflicts of interest, the timetable of male production, length of the colony cycle, and even maximum colony size.

Colonies of the more highly eusocial insects become too large and complex to allow the queen to maintain reproductive hegemony by direct physical domination. A simple proof of this is seen in the many higher termites in which the queen is much too swollen with eggs to patrol the nest (e.g., Howse 1970, Wilson 1971: fig. 6-10), and in which she may even be inescapably held in a special chamber constructed by the workers. A less extreme example is found in the vespine wasps, queens of which remain mobile but are characteristically much larger than the workers. It would thus seem that the workers could exclude their queen from reproducing just by narrowing the wasp-space between combs to deny her access. The frequent assertion that in such a situation the queen exerts control by means of the subtler action of pheromones is at best an evasion of the essential question, which is not about communication but *enforcement*. It does little good for a queen to

communicate her rank if she is powerless against insubordination. She can maintain control only by manipulating the workers' interests so that they act as enforcers against each other (Ratnieks 1988, Ratnieks and Visscher 1989), and it has been suggested (Starr 1984, Ratnieks 1990) that her own mating habits may serve this end. That is, by mating with several males, rather than just one, a queen decreases average worker-worker relatedness and thus their degree of common genetic interest without affecting her own relatedness to each worker.

It seems usually to be overlooked that larvae are also in competition with each other, as provisions are limited and a better nourished larva has a better expectation of reproductive success. Again, the division of the nest into cells is important. Unlike ant, termite, and some bumble bee larvae, wasp larvae have no direct contact with each other, nor do they have ad libitum access to a common food store, so all competition among them is necessarily mediated by adults. The tactics open to them apparently comprise exactly two behaviors that elicit visits from adults: (1) hunger signals, and (2) giving up attractive fluids in response to tactile solicitation (trophallaxis: see Hunt, this volume). It has yet to be experimentally confirmed that larvae that emit hunger signals less often or that give up less-attractive fluids are visited or fed less than others, and it will likely be difficult to do so. Nonetheless, it fits the known facts and makes biological sense that they should. Can especially demanding or generous larvae then gain a disproportionate share? The striking size uniformity in social wasps and bees among same-caste broodmates suggests that they cannot. More directly, Strassmann's (1981d) suggestion that larvae in the center of a large comb may receive more food than those on the periphery has not been upheld. Strassmann and Orgren (1983) found no such inequality of distribution of food among *Polistes exclamans* larvae.

## CONCLUDING REMARKS

The relationship between nest structure and the colony organization of eusocial insects, as presently understood, is extremely loose. In halictine bees, for example, closely related species usually have very similar nests, even if they are socially very different (Michener 1974). In contrast, closely related species of stenogastrine wasps often build widely divergent nests without any apparent divergence in social behavior (Pardi and Turillazzi 1982, Ohgushi 1986, Turillazzi 1986b). We are left, then, with only the very rough correlation between number of cells, colony size, and overall social complexity. The practical consequence of this—one that has often frustrated me a great deal—is that the social information to be gotten from even an unusual or ornate nest by itself

is quite sparse. For social wasps, the metaphor of the nest as "frozen behavior" has limitations even beyond those that Noirot (1970) indicated for termites.

Michener (1974) suggested that physical constraints on nest size may have introduced social limitations in some lineages. Hansell (1987a) applied this general line of thinking to the Stenogastrinae, arguing that an inferior pulp preparation, compared with that of other social wasps, leads to structurally weak nests of sharply limited size, which in turn limits colony size and social complexity. While the known facts do not definitely dispute this thesis, I share Wenzel's (this volume) skepticism of the importance of this physical factor.

Except possibly in the Stenogastrinae—whose profuse architectural variety is most mysterious—the evolution of social wasp nests can be related fairly confidently to the primary function of providing a safe nursery for the brood. This relationship allows only a very limited role for secondary functions in shaping nest structure, in strong contrast to the situation in higher termites (examples in Table 15.1). Does any feature of any social wasp nest show loss of a (primitive) primary function and elaboration for a secondary function? A tentative example is suggested above (see *The Elements of Nest Structure*) in the empty bottom chamber in some phragmocytтарous nests. I am not aware of any other, though it should be noted that the question has not before been posed in quite this way. In particular, nest structure as the product of worker behavior gives no indication of being influenced by conflicts of interest between queens and workers or between different groups of workers. I believe it is shown that some nest features, especially cells, strongly influence secondary functions and that some other features can be suspected of doing so, but there is not yet any clear indication of feedback from secondary functions to nest structure. I find this conclusion remarkable.

### *Acknowledgments*

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