

# THE SOCIAL BIOLOGY OF WASPS

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## *Belonogaster, Mischocyttarus, Parapolybia, and Independent- founding Ropalidia*

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Animals that live in colonies of individuals of more than one generation, cooperate in brood care, and relegate reproduction to one or a small number of colony members are said to represent that pinnacle of social evolution, eusociality (Michener 1969, Wilson 1971). Except for the naked mole-rat, which lives in underground tunnels in Africa (Jarvis 1981), eusociality has been achieved only by ants and termites and by some bees and wasps. With the exception of one or a few species of sphecids (Matthews 1968a, this volume), all eusocial wasps belong to the family Vespidae. This family has traditionally been divided into three subfamilies, namely Stenogastrinae, Polistinae, and Vespinae (Richards 1962, 1978a,b). Carpenter's (1982) recent classification recognizes three additional subfamilies within the family Vespidae—namely, Eumeninae, Masarinae, and Euparagiinae—but eusociality is restricted to the three previously mentioned subfamilies.

Stenogastrines have sometimes been thought to be rather different from the polistines and vespines (Spradbery 1975), and their phylogenetic position within the Vespidae has been debated (Vecht 1977a), although Carpenter's (1982) cladogram indicates that the Stenogastrinae form the sister group to Polistinae + Vespinae (see Carpenter, this volume). Stenogastrines are regarded as primitively eusocial (see Cowan, this volume: Table 2.1, for definitions of levels of sociality) or, perhaps in some instances, as presocial (Turillazzi, this volume). Vespines represent a uniformly highly eusocial group (Matsuura, Greene, this volume).

That leaves the Polistinae, a rather large group consisting of 29 gen-

era and about 800 species. Richards (1962) subdivides the Polistinae into three tribes: Ropalidiini (consisting only of the genus *Ropalidia*), Polistini (consisting of *Polistes* and "*Sulcopolistes*"), and Polybiini (consisting of about 26 genera). However, there are problems with this classification (see Distribution and Systematics). In any case, further subdivision of the Polistinae based on phylogenetic considerations may be less rewarding to students of social evolution than subdivision based on behavior and nest architecture. An elegant example of the latter has been provided by Jeanne (1980a) who distinguishes two subgroups, the *independent-founding* and the *swarm-founding* Polistinae (see also Jeanne, this volume: Chap. 6).

Independent-founding Polistinae live in relatively small colonies (rarely more than 100 adult wasps) and construct small, simple, unenveloped combs that are normally suspended by a narrow pedicel. Queens initiate new colonies either singly or in small groups, but without the aid of workers (that is, independently). Swarm-founding Polistinae live in more populous colonies (often with 1,000 or more adults) and have correspondingly large nests that sometimes have several tiers of combs covered by an envelope. New colonies are always initiated by queens in the company of workers (that is, by swarms). This classification on the basis of behavioral and architectural features is supported by concomitant morphological specializations.

Queens of the independent-founding Polistinae, with their small colonies, do not normally use a pheromonal means of control over their nestmates; overt physical dominance is the rule. Queens in swarm-founding groups, however, must find it quite impossible to subjugate large numbers of nestmates by physical dominance and have, perhaps for this reason, evolved a pheromonal means of control. Independent-founding species have a special problem with ants. Direct physical resistance to marauding ants is difficult enough with small numbers of adult wasps, but when the nest and its brood have to be left completely unguarded while a single foundress is away foraging it is impossible. Not surprisingly, independent-founding species have evolved a chemical defense against ants. Independent-founding species have a well-developed gland (named van der Vecht's gland) on the sixth (terminal) gastral sternum from which an ant-repellent substance is secreted. The gland is associated with a tuft of hairs that presumably serves as an applicator brush (Jeanne et al. 1983). Swarm-founding species never leave their nests unattended and usually have a substantial adult population to physically rid the nest of scouting ants. Also, they typically build enveloped nests with only one or a small number of entrance holes. Most swarm-founding species studied appear not to have the specialized ant repellent-producing van der Vecht's gland. Instead, at least some of them have a well-developed Richard's gland

on the fifth gastral sternum that is often used to lay an odor trail to guide the members of a swarm to their new nesting site (Jeanne 1981a, Jeanne et al. 1983; see also Downing, this volume).

Swarm founding is characteristic of 24 polistine genera, as well as some species of *Ropalidia*. Independent founding is seen in five genera: *Belonogaster*, *Mischocyttarus*, *Parapolybia*, *Polistes*, and some *Ropalidia*. It is easy to argue that the independent-founding polistines provide perfect model systems for studies of social behavior. Small colonies make it possible to mark and study every adult wasp, and the open combs hide nothing from the observer. The nests of many species are quite abundant and often are built in remarkably accessible places. A relatively primitive level of eusociality, characterized by a lack of morphological caste differentiation, an essentially behavioral mechanism of queen control, and considerable flexibility in social roles of the adult wasps make the independent-founding polistines especially attractive subjects. Indeed, they have received increasing attention since the 1970s and have contributed more than any other group of social wasps to the formulation and testing of ideas concerning the forces that mold the evolution of group living and sterile worker castes.

The genus *Polistes*, unrivaled in its wide distribution and in the attention it has received, is the subject of the previous chapter (Reeve, this volume). The present chapter deals with the remaining four genera of independent-founding Polistinae. Some earlier information regarding these wasps may be obtained from several general reviews (Richards 1971, Spradbery 1973a, Iwata 1976, Akre 1982).

## DISTRIBUTION AND SYSTEMATICS

*Belonogaster*, *Parapolybia*, and *Ropalidia* are restricted to the Old World, whereas *Mischocyttarus* is found exclusively in the New World (Vecht 1965, 1967) (Fig. 5.1). All four genera are best represented in the tropics, although at least a few species of each extend into neighboring temperate latitudes. *Belonogaster*, comprising 79 species, is widely distributed in Africa south of the Sahara, with scattered populations in northern Africa, Arabia, and India. The latest comprehensive taxonomic revision of the genus is that of Richards (1982; see also Hensen and Blommers 1987). Since Roubaud's (1916) classic study of *B. juncea*, the biology of only one species, *B. grisea*, has been studied in detail (Marino Piccioli and Pardi 1970, 1978; Pardi 1977; Pardi and Marino Piccioli 1970, 1981). More recently, several modern studies have been initiated on *B. juncea* and *B. petiolata* (Richards 1969, Keeping and Crewe 1983, Kojima and Keeping 1985, Keeping et al. 1986).

*Mischocyttarus* is one of the largest genera of social vespids. In spite



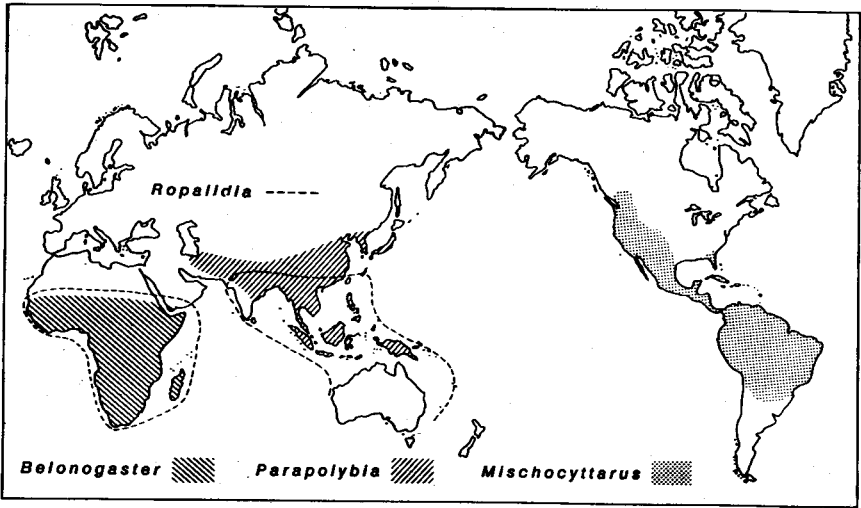


Fig. 5.1. Distributions of *Belonogaster*, *Mischocyttarus*, *Parapolybia*, and *Ropalidia*. (Redrawn from Vecht 1967, courtesy of the author and Koninklijke Nederlandse Akademie van Wetenschappen.)

of its taxonomic diversity (206 species), it is essentially restricted to tropical South America, although two species extend into the southern and western portions of North America. The most authoritative account of the systematics of this genus is that of Richards (1978a). A few species have been studied in considerable detail. Notable among these are *M. drewseni* in Brazil (Jeanne 1972), *M. labiatus* in Colombia (Litte 1981), *M. flavitarsis* in Arizona (Litte 1979), and *M. mexicanus* in Florida (Litte 1977) and in Georgia (Hermann and Chao 1984a). Preliminary information has been published on *M. angulatus* and *M. basimacula* in Panama (Itô 1984b).

*Parapolybia* is a refreshingly small genus with only five species distributed from Iran in the west, to Japan, the Philippines, and New Guinea in the east (Vecht 1966). Only three of the five species are known to any extent. Yamane (1980, 1984, 1985) has provided a detailed account of *P. varia* in Taiwan along with fragmentary information on *P. nodosa*, while *P. indica* in Japan has been studied by Sugiura et al. (1983a,b) and Sekijima et al. (1980).

*Ropalidia*, another large genus, with about 136 known species, occurs in tropical Africa, southern Asia, Australia, and Okinawa. The Indo-Australian species have been revised by Vecht (1941, 1962), the Australian and New Guinea species by Richards (1978b), the Philippine species by Kojima (1984a), the Nepalese species by Yamane and Yamane (1979), and the Indian species by Das and Gupta (1989). Although Vecht (1962) recognized three subgenera, it is now common to recognize six (Richards 1978b). Of these, the subgenera *Anthreneida*, *Icariola*

*Polistratus*, and *Ropalidia* can be characterized as independent-founding, although at least a few species in the subgenus *Icariola* appear to be swarm founders (R. Jeanne, unpubl.). *Ropalidia marginata* (Gadgil and Mahabal 1974; Gadagkar 1980; Belavadi and Govindan 1981; Gadagkar et al. 1982a,b; Gadagkar and Joshi 1982a, 1983), *R. cyathiformis* (Gadagkar and Joshi 1982a,b, 1984, 1985), *R. variegata* (Yamane 1986), *R. fasciata* (Itô 1983, 1985b, 1986b; Itô et al. 1985; Kojima 1983a,b,c, 1984b,c; Suzuki and Murai 1980), and *R. cincta* (Darchen 1976a) are the only independent-founding species studied in any detail, and all of these belong to the subgenus *Icariola*.

The phylogeny of social wasps is now being vigorously investigated (Carpenter 1982, 1987a,b, 1988a, this volume; Rasnitsyn 1988), particularly with regard to the relationships within the diverse subfamily Polistinae. The main problem with Richards's (1978a) subdivision of Polistinae into tribes is that the four Old World polistine genera (including the swarm-founding *Polybioides*) appear to have affinities that unite them as a natural group, so that Richards's inclusion of the Old World genera *Parapolybia*, *Polybioides*, and *Belonogaster* with the New World swarm-founding genera in the tribe "Polybiini" is inappropriate. A fascinating behavioral trait linking the Old World polistine genera is their meconium extraction behavior. Usually in social wasps, the larval meconium (fecal pellet) is left at the bottom of the brood cell, but *Belonogaster*, *Polybioides*, *Parapolybia*, and *Ropalidia* have evolved an elaborate behavior of chewing a small hole at the bottom of the cells and removing the meconium (Marino Piccioli 1968; Marino Piccioli and Pardi 1970, Kojima 1983c, Gadagkar, unpubl.). Although differences in the details of this behavior and the means by which the holes are closed are evident, all four Old World genera have windows at the bottoms of cells from which adults have emerged, while such features have not been seen in any of the remaining 25 genera of polistines. This fact alone strongly suggests a monophyletic origin for the four Old World genera (Jeanne 1980a), as Carpenter's cladistic analysis (this volume) confirms.

## NEST ARCHITECTURE

Social wasps show considerable variation in nest architecture (Jeanne 1975a, Vecht 1977b, Wenzel, this volume), but the independent-founding polistines all build simple stelocytarus (suspended by a pedicel), gymnodomous (unenvolved) combs, so that there is relatively little variation in nest architecture within the group (Fig. 5.2). A single comb is the rule, and this may be either oriented in a vertical plane (held by a horizontal pedicel) or oriented in a horizontal plane with the cells and brood facing downward (held by a vertical pedicel). The comb is usu-

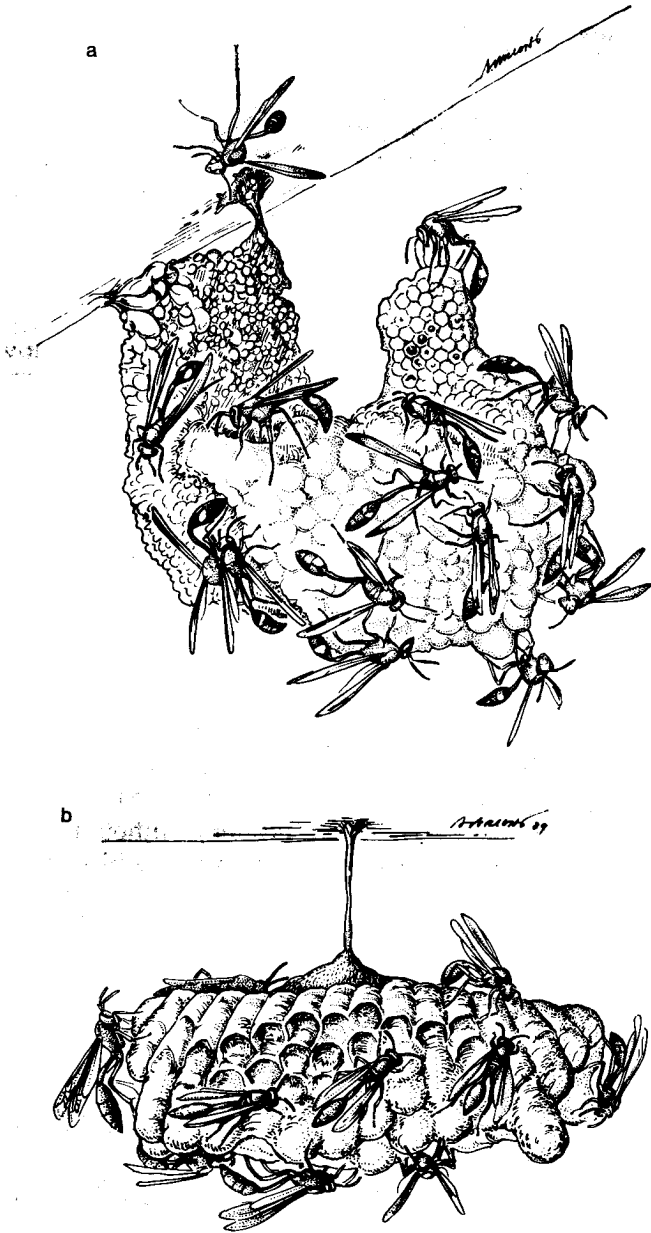
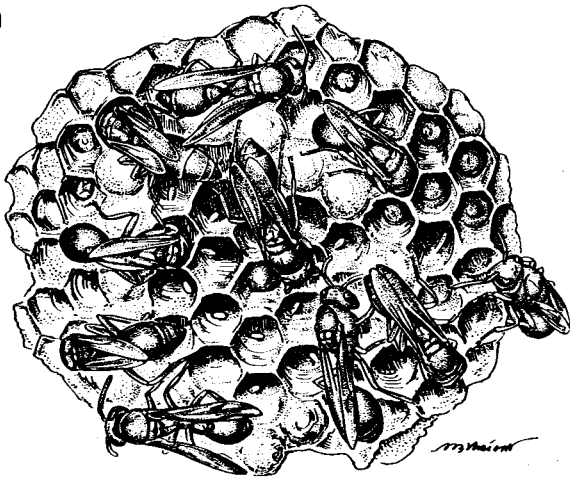


Fig. 5.2. Mature nest of (a) *Belonogaster grisea* (based on a photograph in Marino Piccioli and Pardi 1970, courtesy of L. Pardi and *Monitore Zoologico Italiano*), (b) *Mischocyttarus drewseni* (based on a photograph in Jeanne 1972, courtesy of the author and Museum of Comparative Zoology, Harvard University), (c) *Parapolybia varia* (based on a photograph in Yamane 1984, courtesy of the author and VEB Gustav Fischer Verlag), and (d) *Ropalidia marginata* (based on an original photograph). All views are from the side except (d), in which the comb face is viewed from the front. This comb is perpendicular to the ground and attached to the substrate by a horizontal pedicel that is not visible.

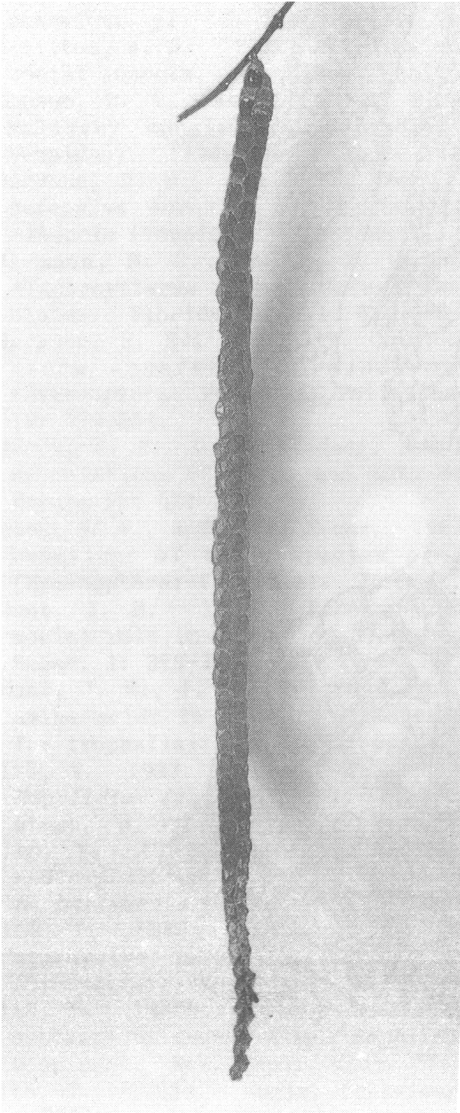
c



d



ally circular or oval, although it may be irregular or may have sharp corners to suit the substrate on which it is constructed. Some species invariably build long combs with two columns of cells (e.g., *R. variegata*: Davis 1966a,b, Yamane 1986, Gadagkar, unpubl.; *R. revolutionalis*: Hook and Evans 1982, Itô 1987a; *M. punctatus*: Richards 1978a) (Fig. 5.3).



**Fig. 5.3.** A typical long nest of *Ropalidia variegata* with two columns of cells.

The suspending of the comb by a long and narrow pedicel coated with an ant repellent is clearly a major defense of these wasps against predation by ants (Jeanne 1970a), although this form of defense appears to be compromised in many nests of *Ropalidia* where the pedicel is short and many secondary pedicels are constructed (see Enemies and Colony Defense). Furthermore, such a means of chemical defense remains to be demonstrated in *Parapolybia*.

Sometimes several combs are built close to one another and function as a single colony (Gadagkar and Joshi 1982b, Kojima 1984b, Herre et al. 1986, Itô 1986b) (Fig. 5.4). The advantages of this are not entirely

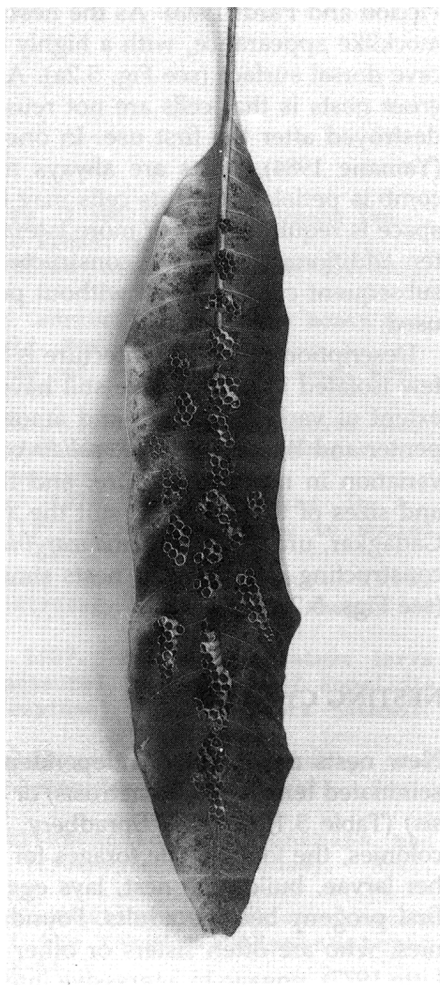


Fig. 5.4. Multiple combs of a *Ropalidia* nest from India.

clear, although this strategy might conceivably minimize damage from certain predators or parasites (see Jeanne 1979a). At least some instances of multiple-comb construction are for a rather different reason. When renesting after the original nest is destroyed, females working on a new nest start construction of several combs, thereby providing opportunities for many females to simultaneously perform the task of nest construction (S. Chandran and Gadagkar, unpubl.; see also Kojima 1984b).

*Belonogaster grisea* and *P. varia* show the greatest degree of deviation from the nest architecture typical of the independent-founding polistines. Nests of *B. grisea* are single-combed and are always suspended by means of a single eccentric pedicel attached to the first cell (Marino Piccioli and Pardi 1978). As the nest grows, it takes on a unique hammocklike appearance, with a highly convex ventral surface and a concave dorsal surface (see Fig. 5.2a). Another atypical characteristic of *B. grisea* nests is that cells are not reused but are often wholly or partly destroyed after the first use. In one population of *P. varia* in Taiwan (Yamane 1984), nests are always multicombed (Fig. 5.2c). The first comb is petiolate, and its cells may be reused. As more brood-rearing space is required, two or more lateral lobes are added, and later up to ten additional combs are constructed close to the original one. These subsequent combs are all without pedicels, and their cells are not reused.

Description of nest architecture is by necessity based on studies of a few isolated species, so we still have little appreciation of the relative extent of variation within and among species (see, for example, Carpenter and Wenzel 1988). *Ropalidia* colonies in India show considerable variation in nest architecture, and the wasps clearly vary the shapes and sizes of their nests to suit the available nesting site (Davis 1966a; Gadagkar, unpubl.). *Ropalidia marginata* is capable of at least sometimes constructing multicombed nests similar to those of *P. varia* in Taiwan (see Figs. 5.2c, 5.5).

## NESTING CYCLE

New nests are initiated independently (without workers) by one inseminated female (haplometrosis) or a small group of them (pleometrosis) (Table 5.1; see also Spradbery, this volume). In single-foundress colonies, the lone female forages for building material and for food for her larvae, builds the nest, lays eggs, and defends the nest until her first progeny become adults. Foundresses in multiple-foundress colonies, who are often sisters or other close relatives (e.g., Jeanne 1972, Litte 1977), engage in aggressive interactions that lead to the establish-

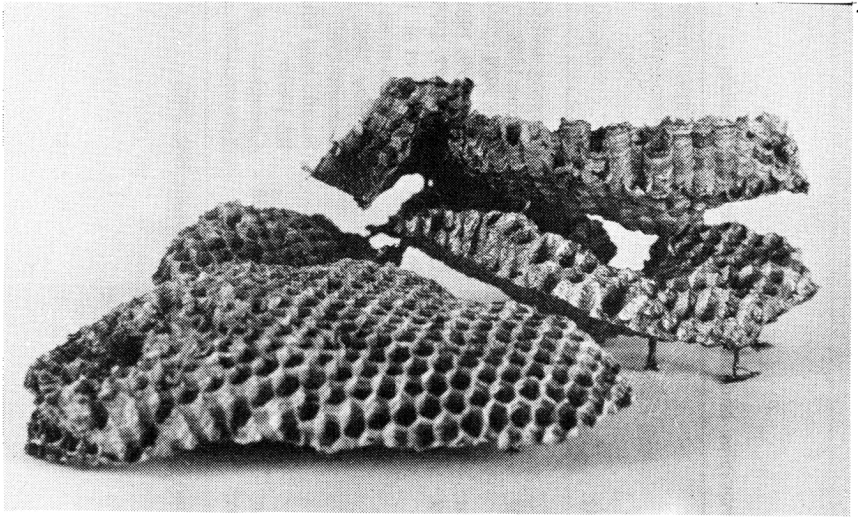


Fig. 5.5. An unusual multilobed nest of *Ropalidia marginata* from Bangalore, India. At the time of collection only one of the combs was occupied.

ment of a dominance hierarchy. One foundress at the top of this hierarchy often monopolizes all egg laying and does little else except occasionally forage for building material. Foraging for food and other duties of nest and brood maintenance are performed by one or more of the subordinate foundresses.

Immediately after nest initiation there is usually a rapid increase in the number of cells, all of which are filled with eggs. Foraging is mostly for building material during this so-called *egg substage*. When the eggs begin to hatch, the foundress(es) start feeding the larvae. Mature larvae spin a cap on their cells and undergo metamorphosis. The period from the hatching of the first egg to the spinning of the first cocoon is referred to as the *larval substage*, and the period from the spinning of the first cocoon to the emergence of the first adult is called the *pupal substage*. The entire period from nest initiation to the emergence of the first adult offspring is called the *preemergence phase* (*founding phase* of Reeve, this volume).

Subordinate foundresses usually begin to die or to disappear from the nest at about the time of the emergence of adult progeny. This first batch of offspring, nearly always females, become workers and take on the duties of foraging, nest building, feeding larvae, and other tasks involved in nest maintenance and defense. This is called the *worker production substage* (*worker phase* of Reeve, this volume) or, sometimes, the *ergonomic substage* (Oster and Wilson 1978). At this point, new cells are usually added to the nest. Later, males and nonworker females



**Table 5.1.** Single- and multiple-foundress colonies of *Belonogaster*, *Mischocyttarus*, *Parapolybia*, and independent-founding *Ropalidia*

Species	Single-	Multiple-	Max. no. of foundresses	Time of nest founding	Locality	Reference
	foundress colonies	foundress colonies				
	No.(%)	No.(%)				
<i>Belonogaster petiolata</i>	38(47)	43(53)	16	?	Transvaal, South Africa	Keeping and Crewe 1987
<i>Mischocyttarus drewseni</i>	20(69)	9(31)	8	Throughout the year	Lower Amazon, Brazil	Jeanne 1972
<i>M. flavitarsis</i>	131(97.8)	3(2.2)	2	March-June	Arizona, USA	Litte 1979
<i>M. labiatus</i>	14(77.8)	4(22.2)	9	Throughout the year	Colombia	Litte 1979, 1981
<i>M. mexicanus</i>	114(66.7)	57(33.3)	20	Throughout the year	Southern Florida, USA	Litte 1977, 1979
<i>Parapolybia indica</i>	49(100)	0	1	May	Southwestern Japan	Sugiura et al. 1983b
<i>P. indica</i>	108(100)	0	1	May	Southern Japan	Sekijima et al. 1980
<i>P. varia</i>	2(100) <sup>a</sup>	0 <sup>a</sup>	1	March-May	Central Taiwan	Yamane 1980, 1985
<i>P. varia</i>	1(7)	13(93)	22	December-February	Southern Taiwan	Yamane 1985
<i>Ropalidia fasciata</i>	331(75)	109(25)	13	February-April	Okinawa, Japan	Suzuki and Murai 1980
<i>R. fasciata</i>	27(46.6)	31(53.4)	22	February-April	Okinawa, Japan	Itô 1985b
<i>R. marginata</i>	8(29.6)	19(70.4)	20	Throughout the year	Pune and Bangalore, India	Gadagkar et al. 1982a
<i>R. variegata jacobsoni</i>	37(63.8)	21(36.2)	4	Throughout the year?	Sumatra	Yamane 1986

<sup>a</sup>Although only two nests were studied in detail, anecdotal evidence suggests that single-foundress colonies may be the rule (Yamane 1980, 1985).

(reproductives or gynes) are produced. In some species, this *male and nonworker production substage* (*reproductive phase* of Reeve, this volume) is well separated from the worker production substage. After the reproductives emerge, there is a considerable amount of brood destruction during the so-called *declining substage*, after which the colony usually is abandoned. The time from the emergence of the first worker to nest abandonment is called the *postemergence phase*.

The preemergence phase and the postemergence phase together constitute what might be called a colony cycle. If the nest is abandoned at the end of one such cycle, the colony cycle and the nesting cycle become equivalent; species that show this pattern may be called *determinate nesting cycle species* (after Jeanne, this volume: Chap. 6). The nesting cycles in a population of such a species are sometimes markedly seasonal and fairly synchronous (see Table 5.1). In other cases, nests are initiated asynchronously at all times of the year, but the nesting cycle is still determinate because every nest goes through the six substages of a colony cycle, after which the nest is abandoned. Finally, several colony cycles may be repeated on the same nest because the nest is not necessarily abandoned at the end of each declining substage. Species that show this pattern may be called *indeterminate nesting cycle species* (after Jeanne, this volume: Chap. 6).

### Seasonal Nesting Cycle

Most species occurring at temperate and subtropical latitudes show a markedly seasonal nesting cycle. Examples include *B. juncea* and *B. petiolata* in southern Africa (Keeping and Crewe 1983), *M. flavitarsis* in Arizona (Litte 1979), *M. mexicanus* in Georgia (Hermann and Chao 1984b), *P. indica* in Japan (Sugiura et al. 1983b), *P. varia* in Taiwan (Yamane 1980), and *R. fasciata* in Okinawa (Suzuki and Murai 1980, Itô 1983, Itô et al. 1985). Nests are typically initiated by inseminated, overwintered females early in the spring (see Fig. 5.6). Females that emerge early in the colony cycle become workers, at least partly because there are no males at this time of the year with whom they can mate. However, males of *R. fasciata* are produced at all stages of the colony cycle, and females of this species emerging from the first brood can mate and found their own nests (Itô and Yamane 1985). Colonies that show a seasonal cycle begin to decline in the fall; wasps that emerge in late summer remain on the nest for a while as nonworking individuals but later leave the nest and mate. The males die and the females hibernate, either on their natal nest (e.g., *R. fasciata*: Itô et al. 1985) or away from the nest in crevices of rocks or under the bark of trees.

The proximate causes of colony decline during the fall are not clear. The accumulation of nonworking males and females at this time may

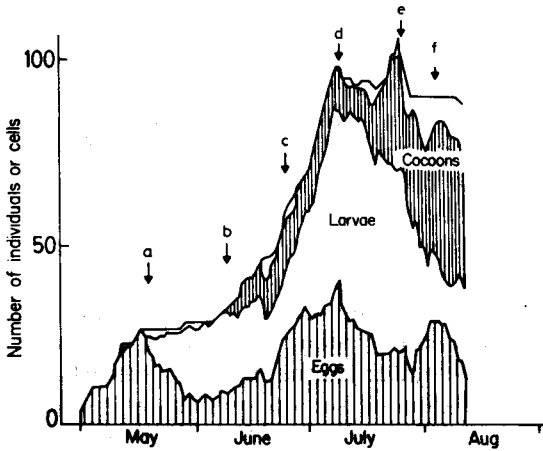


Fig. 5.6. Features of the colony cycle of *Parapolybia indica* in Japan illustrating the seasonal nesting cycle. a, first hatching of larva; b, first appearance of capped cell; c, first emergence of adult; d, death of critical number of workers; e, first male emergence; f, death of foundress. The uppermost line indicates total number of cells. (Redrawn from Sugiura et. al 1983b, courtesy of the authors and *Bulletin of the Faculty of Agriculture, Mie University*.)

be as important as declines in the food supply. However, seasonal changes in temperature, daylength, and humidity are likely to have a profound effect on the form and duration of the colony cycle, as evidenced by the relationship between duration of the nesting period and local climate. At the extremes, *P. indica* in Japan nests for only about three-and-a-half months, whereas *P. varia* in southern Taiwan nests throughout the year and does not hibernate (Fig. 5.7). Indeed, within species two examples are known in which populations follow seasonal cycles in one environment and aseasonal cycles in another (*M. drewseni drewseni*: Dantas de Araújo 1982; *M. mexicanus cubicola*: Hermann and Chao 1984b).

### Aseasonal Determinate Nesting Cycle

An excellent example of an aseasonal determinate cycle is provided by *M. drewseni* in Brazil (Fig. 5.8). Nests are initiated throughout the year, go through the typical cycle including the declining substage, and are always abandoned after about six months (Jeanne 1972). *Mischocyttarus mexicanus* in Florida seems to follow an identical pattern (Litte 1977). Because nests are asynchronously initiated, the population is expected to contain males throughout the year. It is thus quite common in these species for inseminated daughters to replace their mothers as queens or to usurp other colonies. Nevertheless, there seems to be a

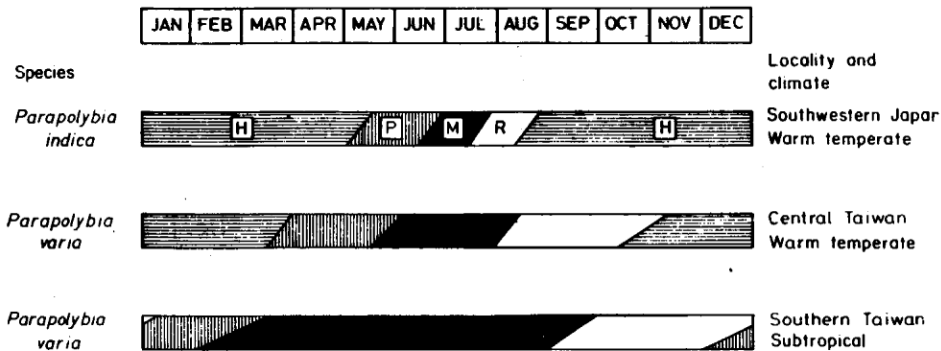


Fig. 5.7. Comparison of nesting cycles of *Parapolybia indica* in warm-temperate southwestern Japan, *P. varia* in warm temperate central Taiwan, and *P. varia* in subtropical southern Taiwan. H, hibernating phase; P, preemergence phase; M, matrifilial phase (worker production substage); R, reproductive phase (male and nonworker production substage). (Redrawn from Sugiura et al. 1983b and Yamane 1980, courtesy of the authors and *Bulletin of the Faculty of Agriculture, Mie University.*)

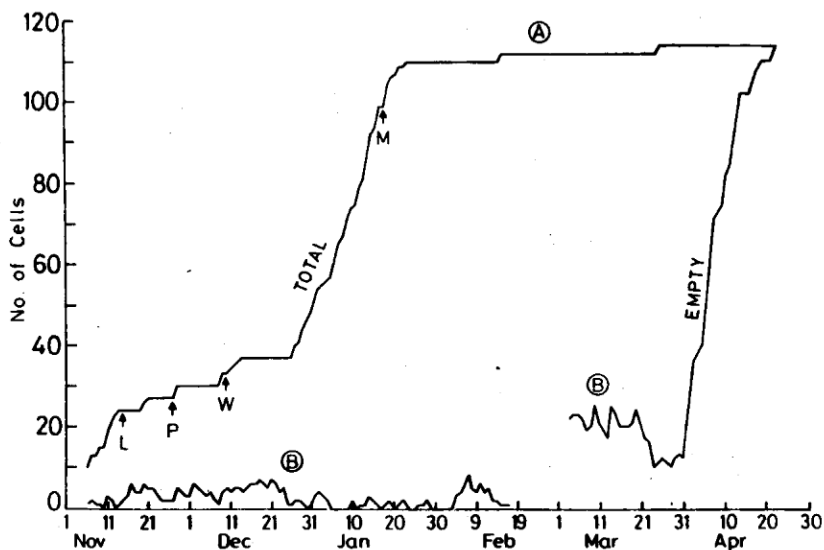


Fig. 5.8. Growth of a typical colony of *Mischocyttarus drewseni*. Colonies may be initiated at any time of the year. A, total cells; B, empty cells; L, first larva eclosed; P, first larva spun its cocoon to pupate; W, first adult worker emerged; M, first adult male emerged. (Redrawn from Jeanne 1972, courtesy of the author and Museum of Comparative Zoology, Harvard University.)

pronounced tendency to produce typical workers in early broods and nonworking females (potential reproductives) in later broods. What is the cause of this tendency, and why does the colony decline so regularly after six months of existence, independently of the season? Jeanne (1972) has argued rather convincingly that it is not environmental conditions but intrinsic factors that regulate the nesting cycle. Jeanne's hypothesis is that physical domination by the queen is necessary for a female to assume the role of worker, and as the colony grows larger more females escape such domination and become nonworkers. With a sharp increase in the ratio of nonworkers and males to workers, all go hungry, leading to brood abortion and adult dispersal.

### Indeterminate Nesting Cycle

*Ropalidia marginata* in peninsular India provides the only clearly documented case of an indeterminate nesting cycle among independent-founding polistines (Gadgil and Mahabal 1974, Gadagkar et al. 1982a,b, Chandrashekara et al. 1990). Nests are initiated throughout the year either haplometrotically or pleometrotically. Rates of colony failure are very high in young colonies, but successful colonies appear to go through all the stages of the typical colony cycle, including a declining substage involving brood abortion (Fig. 5.9). The main difference between the determinate nesting cycle of the *M. drewseni* type and the indeterminate nesting cycle of the *R. marginata* type is that dispersal of adults during the declining substage is not complete in the latter, so that a small number of females remain to start another colony cycle in the same nest. A given nest may be used for a series of such cycles.

Why are colony decline and abandonment not complete? One possibility is that these colonies never reach the stage where the queen is unable to dominate her daughters, either because many of the daughters leave their parental nests throughout the colony cycle or because some mechanism of queen control other than physical domination is important. If the queen, in fact, does not become incapable of dominating her daughters, then why is there a declining substage in the first place? It is conceivable that what appears to be a declining substage is really a period of intense reproductive competition and that the individual who wins in this competition may start the colony cycle anew. Alternatively, the indeterminate nesting cycle, which appears to encompass several repeats of the determinate nesting cycle, may have evolved in response to predation by *Vespa tropica*, which is especially relentless on large colonies. Colonies of *R. marginata* might find it adaptive to issue "swarms" of dispersing wasps to found new nests periodically before all is lost to *Vespa tropica*.

Future studies of such indeterminate nesting cycles are bound to

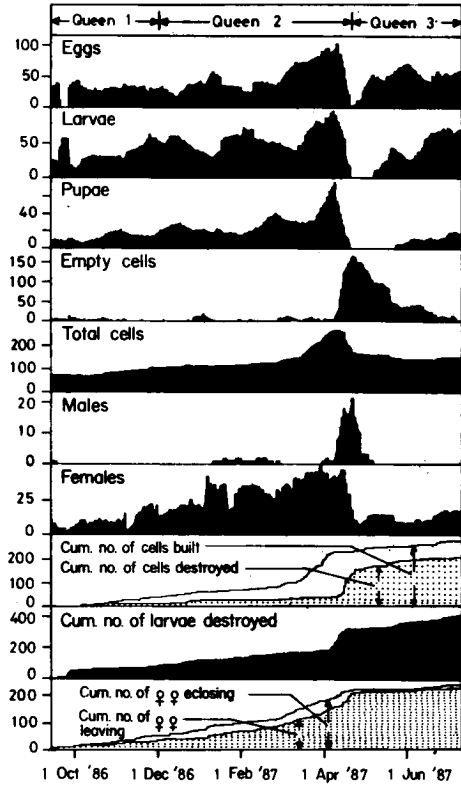


Fig. 5.9. Development of a *Ropalidia marginata* colony transplanted into a cage from which free foraging was allowed. This colony reached a maximum standing crop of 265 cells, 103 eggs, 96 larvae, 76 pupae, 21 adult males, and 47 adult female wasps. After considerable brood and cell destruction, the colony declined in late April to a standing crop of 164 cells, 4 eggs, 0 larvae, 0 pupae, 0 adult males, and 17 adult female wasps, only to continue a second colony cycle on the same comb.

provide many interesting new facts regarding the regulation of colony cycles in these wasps. Because daughters may leave their natal nests to initiate new nests more-or-less continuously, indeterminate nesting cycles may make the composition of a founding group quite heterogeneous in terms of age and social status. We know of at least one clear case in *R. cyathiformis* where a group of individuals who already had well-defined social roles on their natal nest left and initiated a new nest, largely retaining their previous roles (Gadagkar and Joshi 1984, 1985). This is not very different in principle from swarm founding. It therefore seems likely that more detailed studies of indeterminate cycles in independent-founding *Ropalidia* species will offer many surprises and may even obliterate the distinction between independent founding and swarm founding.

**ENEMIES AND COLONY DEFENSE**

Adult wasps in the genera considered here seem to have few serious enemies, but a variety of parasites and predators occasionally maraud

their nests (Appendixes 5.1 and 5.2). Birds, lizards, and bats sometimes plunder the nests, and tachinid and phorid flies, ichneumonid and torymid wasps, and pyralid moths may seriously affect productivity by parasitizing the brood. The wasps appear to have no particular defense against vertebrate predators, with the exception of *Mischocyttarus immarginatus*, which nests in association with the much more aggressive wasp *Polybia occidentalis* and thereby presumably derives some protection (Windsor 1972, Gorton 1978). It has been suggested that choice of nesting site as well as coloration of nests may help in avoiding predators (Fitzgerald 1950, Kojima 1982a, Hermann and Chao 1984a,c).

There is also no specific defense against parasites, although the alertness of the adults and their efforts to chase away parasites undoubtedly reduce the extent of parasitism. The most common response to parasitized brood is simply to ignore those cells until the parasite emerges, and then to reuse the cells. Somewhat surprisingly, the wasps seldom make any attempt to remove or destroy the affected larvae or pupae. *Mischocyttarus labiatus* is a clear exception to this rule. An attack by a phorid moth can be so devastating to a nest that the queen simply cuts the pedicel and lets the whole nest fall to the ground to be consumed by ants—brood, parasites, and all—and begins construction of a new nest in roughly the original spot (Litte 1981).

Perhaps the most serious natural enemy of *Ropalidia* in southern India (Gadagkar, unpubl.) and *Parapolybia* in Taiwan (Yamane 1980) is the hornet *Vespa tropica*, whose workers systematically search for, locate, and consume almost the entire brood of large and conspicuous prey colonies (see Matsuura, this volume). Adults of the prey species are untouched, and they usually sit around the nest completely helpless until the predator departs. They then return to the nest, inspect the cells with great agitation, and either cannibalize any remaining brood and abandon the nest, or sometimes continue to produce more brood on the same nest. Often the queen and some of the workers stay while others leave.

In the Neotropics, army ants must pose some threat to wasp colonies, although their overall impact on wasp populations is difficult to estimate. Several species of *Mischocyttarus* have presumably been under sufficient selection pressure from army ants to evolve nesting associations with "army ant-resistant" ant species. Herre et al. (1986) found that 29 out of 31 active social wasp nests, including those of ten species of *Mischocyttarus*, were built on plants occupied by *Allomerus* and *Pheidole* ants. It is clear that by such association the wasps derive significant protection from army ants, which consistently avoid such ant-bearing plants.

What is the most important enemy of these social wasps? Should this

distinction be given to the most devastating of the enemies seen in action today or to those against whom the wasps have found it necessary to evolve effective defenses? This conundrum is best illustrated by an examination of Appendixes 5.1 and 5.2, which may tell us little about those enemies that have decided the course of evolution of these wasps. The reference here is to a variety of species of ants where foraging is carried out by individual scouts who can quickly recruit additional workers upon finding a valuable source of food. The reason that the importance of such predators is not obvious is that most wasp species have evolved fairly effective defenses against them. To appreciate the overriding importance of ant predation one has only to break down such defenses: remove the adults or break the pedicel and drop the nest to the ground; it will be discovered and devoured by ants within minutes.

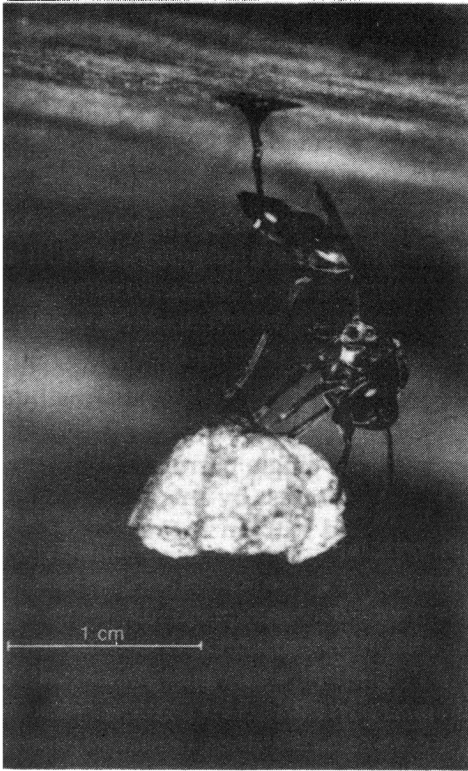
The first line of defense appears to be the single narrow pedicel suspending the comb, which restricts routes of access by ants. As a second line of defense, the pedicel is usually coated with an ant repellent produced from the van der Vecht's gland. *Mischocyttarus drewseni* is the prototype for these two forms of defense (Fig. 5.10). The nest pedicel is very narrow and long in this species, not only physically restricting access by ants but also making it easy to keep coated with ant repellent. The gland and the brush are well developed in this genus, and the efficiency of the ant repellent has been demonstrated (Jeanne 1970a).

Females of *B. grisea* (Marino Piccioli and Pardi 1970) and those of *B. petiolata* (Keeping 1990) have also been seen to rub secretions from their van der Vecht's glands onto their nest pedicels. Several recent observations (Keeping 1990) support the role of these secretions in chemical defense in this genus.

*Ropalidia* females rub their abdomens on the pedicels, the gland and brush are well developed, and the efficacy of the ant repellent has been demonstrated (Kojima 1982b, 1983a; Gadagkar, unpubl.). On the other hand, the pedicels are often so short that most ants can probably get to the nest without crossing the pedicel. Besides, secondary pedicels are often constructed at several points to strengthen the attachment of the nest to the substrate (contrast Fig. 5.11 with Fig. 5.2b), and the wasps do not appear to rub their abdomens on the secondary pedicels. All this probably diminishes the importance of the first two lines of defense in *Ropalidia*.

The third line of defense is the constant guarding of the nest by the adults, who become very agitated when ants are moving nearby. This is, of course, unavailable to a single foundress away foraging, but it appears that larger nests of *Ropalidia* depend primarily on the third line of defense. It is in recognition of the importance of the third line of



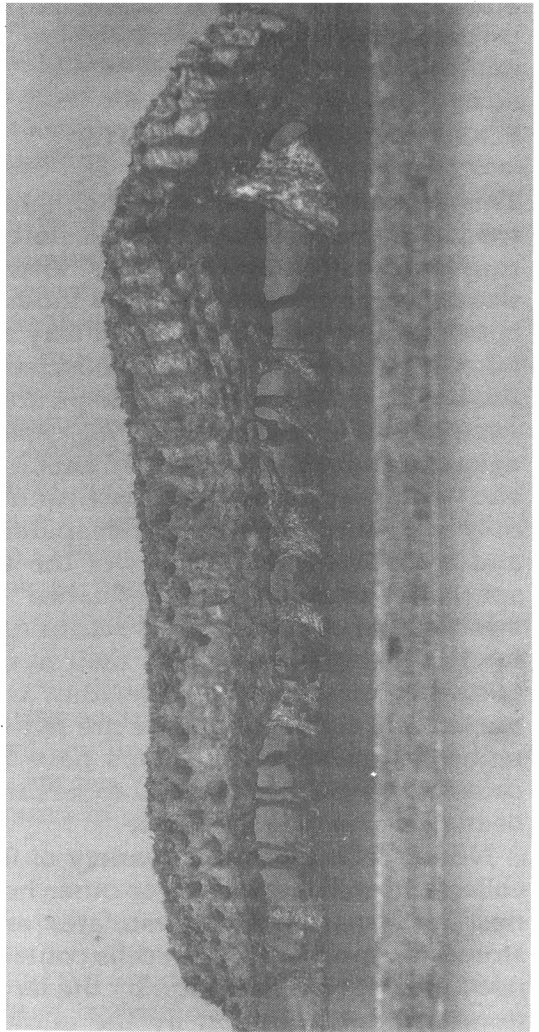


**Fig. 5.10.** Female *Mischoctytarus drewseni* applying ant-repellent secretion by rubbing the tuft of hair on the terminal gastral sternum against the nest pedicel. (From Jeanne 1972, courtesy of the author and Museum of Comparative Zoology, Harvard University.)

defense that multiple-foundress associations are often considered an antipredator adaptation (see *Origin of Social Life: A Perspective from Studying Independent-Founding Polistines*).

In a 20-month study involving 113 nests, Yamane (1980) never once saw *P. varia* females rubbing the nest pedicel with their abdomens, although Kojima (1983b) reports that he saw one wasp doing it once! More important, these wasps enlarge their nest by adding several additional combs that have no pedicels. Clearly the third line of defense, namely, active defense by adults, is most important in this species too. It is probably true for all species that predation pressure from ants can be quite serious in the absence of defenses but that existing defenses are quite effective. It has therefore been rightly emphasized that predation pressure from ants has been a very important factor in the course of evolution of eusocial wasps (Vecht 1967, Jeanne 1975a), especially in the tropics (Jeanne 1979b).

A similar conundrum over the relative importance of historical versus current predation pressures concerns the function of the sting and venom. The most striking feature of wasps to anyone who comes



**Fig. 5.11.** A large comb of *Ropalidia marginata* viewed from the side. Notice the large number of pedicels and the narrow distance between the nest and the substrate.

into casual contact with them is their often formidable sting. But detailed studies show no profound role for the sting in the defensive biology of most independent-founding species. Deliberate attention to the role of the sting brings the verdict that "the venom apparatus appears to fall short as a defensive mechanism against their chief vertebrate predators" (Hermann and Chao 1984c:339; see also Starr 1985b, 1989a; Kukuk et al. 1989). Here again we must imagine that the concentrated resource that large nests with brood represent was exploited by a large number of vertebrate and invertebrate predators during the evolutionary history of the wasps, and that the sting evolved as a means of deterring these former enemies. Only a few specialized pred-

ators have been able to overcome this defense to become important present-day enemies.

## FOOD AND FEEDING HABITS

This section is intended to highlight our remarkable ignorance of the food and feeding habits of the independent-founding polistines. Barring Jeanne's (1972) study of *M. drewseni*, we have little to go by. Adult wasps forage for two classes of food: arthropods and nectar. It is a safe bet that there is no great specificity about which arthropod species are taken or where the nectar is collected from; easy availability is probably the deciding factor. These wasps are known to hunt lepidopteran larvae (Belvadi and Govindan 1981); spiders (K. Chandrashekara and Gadagkar, unpubl.); and moths, ants, spider eggs, hemipteran nymphs, and tettigoniid grasshoppers (Jeanne 1972). *Mischocyttarus* wasps not only seek out insects caught in spider webs but are actually able to land and walk along the strands of the web, presumably on account of a special adaptation of the tarsal lobes of the mid- and hind-legs (Jeanne 1972). Foragers returning to the nest with masticated solid food routinely share it with their nestmates, including males. The food is further masticated by the adult wasps, during which juices are extracted and imbibed. Larvae are fed with the solid lumps as well as by regurgitation after the lumps have been masticated. Males may also occasionally offer solid food to larvae (e.g., Pardi 1977) but have never been observed to regurgitate.

Nectar collected from a variety of flowers, and sometimes honeydew collected from mealybugs or other homopterans, is also brought to the nest and shared with nestmates and larvae. Nectar is occasionally stored in empty cells or in cells containing eggs or young larvae. This is not for direct consumption by the larvae but for later removal, distribution, and consumption by the adults. Such nectar storage is usually more frequent during times of food scarcity.

Larvae regularly produce droplets of a liquid imbibed by the adults, who often enter larval cells and solicit the secretion by mouthing the larvae. Such larval-adult trophallaxis is a rather striking feature of wasp societies but remains very poorly studied. It is clear from the studies of Hunt et al. (1982) that wasp larval secretion has enormous nutritive value for the adults, and it almost certainly is a glandular secretion rather than simply a regurgitation of food given to the larva. A recent attempt to better understand the significance of this form of trophallaxis is that of Hunt (1988, this volume), who seems to have shown that *Mischocyttarus* larvae in preemergence colonies are more likely to surrender saliva than are those in postemergence colonies. His hypoth-

esis to explain this differential behavior is that larvae in preemergence colonies face a greater risk of being cannibalized by the adults, who are themselves likely to be undernourished during this phase of the colony cycle. On the other hand, the better nourished adults in post-emergence colonies are less likely to cannibalize larvae. In other words, surrendering of saliva is hypothesized to be a kind of appeasement behavior by larvae, meant to forestall their own deaths by cannibalism.

## MATING BEHAVIOR

Most studies of presocial and primitively eusocial insects aim either to unravel the mechanism of social organization and integration or to understand the origins of cooperative behavior. Quite understandably, males, which appear peripheral to these questions, have largely been neglected. Typically, colonies first produce several worker females and later produce males and nonworking (reproductive) females. Some species, such as *M. drewseni* (Jeanne 1972) and *P. indica* (Sugiura et al. 1983b), produce males only during a relatively short period toward the end of the colony cycle. Consequently, males of species with a seasonal nesting cycle, such as *P. indica*, are present during only a small part of the year and opportunities for mating are restricted. The aseasonal and asynchronous nesting cycle of *M. drewseni*, however, ensures the presence of males in the population throughout the year.

*Ropalidia fasciata* (Itô and Yamane 1985) and *R. cyathiformis* (Gadagkar and Joshi 1984) males are produced over a fairly long period, so that even if the nesting cycle is seasonal opportunities to mate are more widespread. This has important consequences for social organization, as females reared from the first brood can potentially mate and establish their own colonies or usurp the egg-laying position of their mothers (for examples in *Polistes*, see Reeve, this volume).

The behavior of adult males is quite diverse. The males of some species, such as *P. varia* (Yamane 1980), *R. marginata*, *M. drewseni*, and *M. flavitarsis*, remain on their natal nests for a few days after they emerge but then leave to spend the remaining several days of their lives attempting to mate. Males of other species, such as *M. labiatus* (Litte 1981) and *R. cyathiformis* (Gadagkar and Joshi 1984), appear to spend their entire lives on their natal nests, leaving only for several hours every day (presumably to attempt to mate). Males have never been observed to mate on their natal nests.

*Mischoctytarus drewseni* males in Brazil patrol areas where females are likely to forage, pouncing on conspecific females as well as conspecific males and the similar-looking females of *Polybia sericea* (Jeanne and Castellón Bermúdez 1980). These males make no attempt to mark or

defend territories. Males of *M. labiatus* in Colombia similarly patrol areas that are likely to be frequented by females, but drag their abdomens and appear to apply glandular secretions to their perch sites. The function of this application seems not to be as much to mark territories and exclude other males as to attract females (Litte 1981). Males of *M. flavitarsis* in Arizona exhibit lekking behavior. They mark their perch sites and defend them against other males, sometimes using abandoned or active conspecific nests as perch sites (Litte 1979). Males of this species possess well-developed exocrine glands on their sterna, which open onto a dense brush of hairs, presumably aiding in pheromone application (see Downing, this volume). Males of other species in the genus that do not conspicuously drag their abdomens generally do not have such well-developed glands and lack the applicator brush (Post and Jeanne 1982b).

Patrolling males appear to orient visually to anything crudely resembling a conspecific female. Subsequent recognition and release of copulatory behavior is clearly mediated by chemical cues from the female's venom gland and possibly also head and thorax (Litte 1979, Keeping et al. 1986).

## SOCIAL ORGANIZATION

Any society, be it insect, avian, or mammalian, should have a set of rules that govern division of labor and access to resources if it is to function efficiently. Without doubt, insect societies deserve to be studied with a view to discover these rules, and, indeed, honey bee and ant societies have been used as model systems with great profit (Oster and Wilson 1978, Seeley 1985, Winston 1987). The study of social organization in insect societies such as those considered in this chapter has even more to offer. Because these primitively eusocial wasps are not obligately social, at least to the extent that single-foundress colonies are still possible, an appreciation of social organization is crucial for an understanding of the evolution of eusociality itself. The study of social organization is thus certain to shed light on the forces that mold the evolution of group living.

All independent-founding polistines, including *Polistes* (Reeve, this volume), have a fundamentally similar social organization. When colonies are founded singly there is, of course, no society until the first progeny emerge, but in multiple-foundress colonies social organization and division of labor are crucial issues in both the preemergence and postemergence phases. In species with seasonal nesting cycles, especially in temperate regions where hibernation is required, foundresses are always of the same generation (even-age cohorts). But with the

emergence of the first workers foundresses other than the queen begin to die or disappear, so that the postemergence phase consists primarily of a mother queen and her daughters (see Yamane 1985). Social organization during the pre- and postemergence phases may thus be expected to be different, as has been emphasized in some studies of temperate-zone species (e.g., Yamane 1985). In less-seasonal environments, where asynchronous nesting cycles occur, foundresses may not necessarily belong to the same generation; thus differences in social organization between pre- and postemergence colonies are less pronounced. For instance, no consistent differences have been noticed between pre- and postemergence phases of the indeterminate nesting cycle in *R. marginata* (Gadagkar, unpubl.). I shall therefore consider social organization in general and mention pre- and postemergence phases only when striking differences are evident.

### Dominance Hierarchies

Independent-founding polistine wasps are characterized by a lack of morphological caste differentiation and consequent flexibility in the social roles of adults. When a group of wasps nest together it is of interest to know who will become the queen and who will take on the worker role. As Pardi (1948) showed in a classic study, role differentiation is determined largely by means of aggressive interactions leading to the establishment of a dominance hierarchy (see also Gadagkar 1980, Gadagkar and Joshi 1982b, Roseler, this volume). Dominance interactions are seen in all species, but the intensity and frequency of such interactions vary widely (e.g., Marino Piccioli and Pardi 1970, Gadagkar 1980, Kojima 1984c, Itô 1985a). Severe fights may involve grappling, biting, and stinging, occasionally leading to injury and even death. More frequently, however, one sees highly ritualized mock fights.

The most common such ritualized interaction in *R. marginata* and *R. cyathiformis* consists of one animal, dominant by definition, climbing on top of another and attempting to reach out and bite its mouthparts. The animal being so treated, subordinate by definition, becomes motionless, keeping its body as compact as possible and its mouthparts inaccessible (Gadagkar 1980, Gadagkar and Joshi 1982b, 1983). *Ropalidia cincta* (Darchen 1976a) and *B. grisea* (Marino Piccioli and Pardi 1970) appear to have a very similar form of dominance interaction. There are also other less frequent forms of dominance interaction, especially in *R. cyathiformis* (Gadagkar and Joshi 1982b), such as a dominant wasp nibbling, chasing, sitting on, or holding a wing or leg of a subordinate. Dominance interactions described by Yamane (1985) for *P. varia* and by Jeanne (1972) for *M. drewseni* appear not to be radically different from

these. It seems probable that there are species-specific differences in dominance-related behaviors, but this has not yet been demonstrated.

Frequencies of dominance interactions vary greatly. Many colonies of *R. marginata* may be observed for days without evidence of aggressive interactions, while other colonies of the same species may show dozens of aggressive interactions per hour of observation. Itô (1983, 1984b, 1985a, 1986a,b) has attempted to discern some pattern in this variation, suggesting that increased levels of dominance interactions in postemergence as opposed to preemergence colonies constitute evidence of maternal manipulation, and that the inherently low levels of dominance interactions characteristic of some *Ropalidia* species may have facilitated the evolution of group living. Considering that so few quantitative data are available, the observed variation in dominance interactions of species such as *R. marginata* and *R. cyathiformis* leads one to suspect that intraspecific variation may often equal or exceed interspecific variation.

But what makes some females dominant and others subordinate? Although crucial, this question is almost entirely unanswered in this group of wasps. Body size, age, and hormone levels suggest themselves as factors that might influence an animal's probability of becoming dominant over another (Röseler, this volume), but only future work can tell us more.

### Role of the Egg Layer

Without exception, the most dominant female (queen) is the principal if not sole egg layer. Subordinates may lay no eggs (e.g., *R. marginata*: Gadagkar et al. 1990a; preemergence colonies of *P. varia*: Yamane 1985; *P. indica*: Sugiura et al. 1983a) or may lay some eggs, most of which are eaten by the queen (e.g., *B. grisea*: Marino Piccioli and Pardi 1970). In at least some cases, however, subordinates lay a substantial proportion of the eggs, which are not necessarily eaten (e.g., *M. mexicanus* fall nests: Litte 1977; *R. cyathiformis*: Gadagkar and Joshi 1982b).

The behavioral repertoire of the queen varies considerably from species to species. At one extreme is the queen of *R. marginata*, who does almost nothing other than lay eggs. In most colonies she rarely indulges in overt dominance interactions with her nestmates, let alone performs any other tasks, although her superior status is obvious—nestmates simply withdraw from her presence (Gadagkar and Joshi 1983). The queen of *R. cyathiformis*, on the other hand, is often the most aggressive and active individual in her colony, running about, physically attacking and challenging her nestmates, yet never leaving the

nest (Gadagkar and Joshi 1984). Even more active are *M. drewseni* queens, who chew the silk caps off vacated cells and prepare them to receive fresh eggs; initiate new cells in postemergence colonies; elongate cell walls; solicit food, building material, and nectar from returning foragers; distribute food to larvae and nestmates; and even leave the nest to forage (Jeanne 1972). *Mischocyttarus labiatus* queens have been described as "the primary but not the sole egg-layers", "the only egg-eaters", and "frequent biters and solicitors of nestmates" (Litte 1981:11). *Parapolybia varia* queens are said to have "rarely left the nest and monopolized most ovipositions by physically disturbing the subordinates' attempts to oviposit" (Yamane 1985:27). In all species studied, subordinates (workers) have the primary responsibilities for tasks other than oviposition, such as foraging, brood care, nest building, and other nest-maintenance activities.

### Behavioral Caste Differentiation

The foregoing discussion is based on an emphasis of a queen-worker dichotomy modeled after the highly eusocial insects, but this is arguably an insufficient if not misleading analogy for primitively eusocial species. Variability among workers of the latter is often large, and the range of behaviors or other traits of workers may sometimes overlap that of the queen. More significantly, in primitively eusocial insects, caste is at least partly determined in the adult stage, and workers therefore have not completely lost their capacity for direct reproduction. Challenging and replacing the queen, laying eggs in the presence of the queen, or leaving the nest to found their own nest are various ways by which workers may realize direct reproductive success. One might therefore expect workers to adopt a variety of strategies to maximize their chances of direct reproduction. Consequently, variability in worker behavior must hold important clues to the nature of reproductive competition, a fact that has rarely received the attention it deserves.

As an example, Litte (1981) distinguished three types of females in preemergence colonies of *M. labiatus* in Colombia; queens, dominant co-foundresses, and foraging co-foundresses. Dominant co-foundresses performed fewer tasks than even queens and sometimes laid eggs, while the foraging co-foundresses had poor ovarian development and did most of the foraging. Most daughters became foragers on their natal nests but were nevertheless capable of founding new nests and were therefore considered potential reproductives.

Investigations of *R. marginata* and *R. cyathiformis* in India have been explicitly concerned with the elucidation of interindividual variability and its potential for understanding social organization, reproductive



competition, and, ultimately, the evolution of eusocial behavior (Gadagkar and Joshi 1982a, 1983, 1984, 1985). Departing somewhat from typical approaches, time activity budgets have been constructed for individually identified wasps using all common activities. The behaviors documented include seemingly trivial ones, such as "sitting" or "sitting with raised antennae," behaviors that traditionally have not been the focus of much attention. Multivariate statistical techniques used to examine patterns of interindividual differences show that each colony has three distinct kinds of individuals or behavioral castes. Superimposing this cluster analysis on data for frequencies of traditionally studied behaviors has permitted the designation of these behavioral "castes" as "Sitters," "Fighters," and "Foragers" (Fig. 5.12). Sitters are those wasps that spend a relatively large proportion of their time sitting and self-grooming. Fighters spend a great deal of time sitting with raised antennae and also show high frequencies of dominance behaviors. Foragers are absent from the nest a great deal of the time and show high frequencies of bringing food and building material back to the nest.

The position of the queen among these clusters is of particular inter-

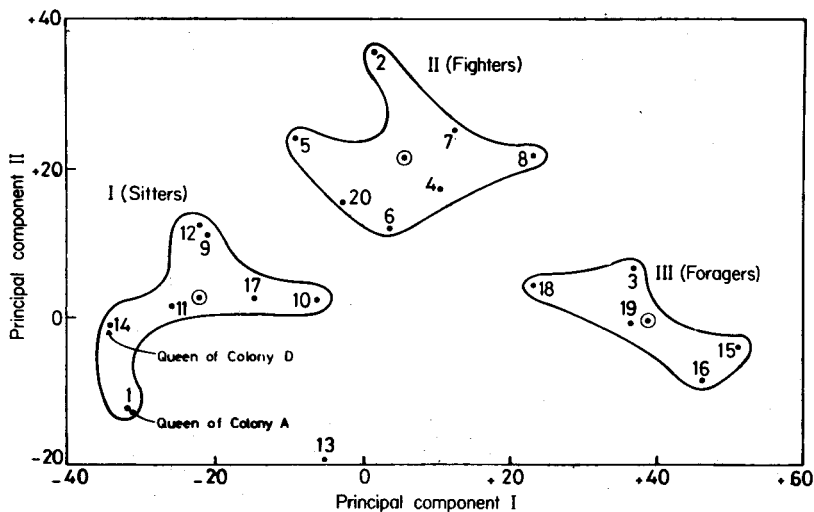


Fig. 5.12. Behavioral profiles of 20 individually identified females (numbered) from two colonies of *Ropalidia marginata* analyzed by principal components analysis. Each point represents one wasp plotted in the coordinate space of the first two principal components. The points fall into three clusters (referred to as behavioral castes) by the nearest-centroid (circled dot) criterion. (From Gadagkar and Joshi 1983, courtesy of *Animal Behaviour*.)

est in view of the fact that data on egg laying, the traditional criterion defining the queen-worker dichotomy, were not used in the cluster analysis. In 13 out of 14 *R. marginata* colonies studied, the queens were Sitters (Gadagkar and Joshi 1983, Chandrashekara and Gadagkar 1990). An obvious interpretation of this is that the queens are programmed to spend little time and energy doing anything other than laying eggs. Since there is normally only one queen per colony, the remaining Sitters who are not queens may be thought of as hopeful queens attempting to maximize their chances for future reproduction. Fighters are probably performing the function of keeping the colony active and guarding it against parasites. That Fighters may also be hopeful queens is suggested by the fact that they show the highest frequency of fighting, not with Foragers as might be expected, but among themselves. It seems likely that Foragers, who leave the nest to perform the risky tasks of gathering food and building material, have the least chance of becoming queens. Both Sitters and Fighters have significantly better developed ovaries than Foragers (Chandrashekara and Gadagkar 1990).

These hypotheses regarding the evolutionary significance of behavioral caste differentiation can be evaluated using both comparative and experimental methods. A comparative study of *R. marginata* and *R. cyathiformis*, both of which are common in peninsular India, has revealed that social organization in these two species is very similar, with an important difference being that in all *R. cyathiformis* colonies studied, queens belong to the Fighter caste. This means that the queen of *R. cyathiformis* does more than just lay eggs. In fact, in contrast to *R. marginata* queens, she is one of the most active individuals in the colony, routinely taking part in aggressive dominance interactions with her nestmates and spending much of her time sitting with raised antennae.

Why do queens of *R. marginata* and *R. cyathiformis* differ in this way? One possibility is that a queen of *R. marginata* is a Sitter because she faces relatively little reproductive competition from her nestmates, while a queen of *R. cyathiformis* is a Fighter because she faces relatively high levels of such competition. This idea is supported by several facts. First, *R. cyathiformis* colonies sometimes have multiple egg layers (Sitters and Foragers also occasionally lay eggs in this species), whereas *R. marginata* colonies usually have only a single egg layer. Second, in single-foundress colonies of *R. cyathiformis*, the queen or egg layer belongs to the Sitter caste rather than the Fighter caste. In other words, a queen of *R. cyathiformis* is also a Sitter when she faces no reproductive competition. (Notice that even solitary foundresses can be classified as Fighters because the delineation of a Fighter is done on the basis of time activity budgets of behaviors other than fighting.)

Evolutionary hypotheses concerning behavioral castes are also amen-

able to experimental testing (Gadagkar 1987). The approach here has been to examine behavioral caste differentiation in a colony, experimentally remove the queen, and study the consequent changes in social organization. Every *R. cyathiformis* colony seems to include one or two wasps who behave much like the queen (Fig. 5.13). These potential queens, who take over the role of the queen when she is removed, always belong to the Fighter caste, as does the queen in this species. Upon removal of the queen, not only does one of the other Fighters become the queen, but one of the Sitters may change her behavioral profile rather drastically to become a Fighter and, perhaps, the next potential queen. In short, every colony has a potential queen already differentiated even when the original queen is present. An interesting fact is that these potential queens are often young and aggressive individuals who seldom forage for food or do other work. This is in complete contrast to the North American paper wasp *Polistes exclamans*, where older foragers tend to become replacement queens (Strassmann and Meyer 1983).

Yet another line of work has provided additional insights into the social organization of *R. cyathiformis*. During a long-term study, a colony divided so that about half its members left to form a new colony

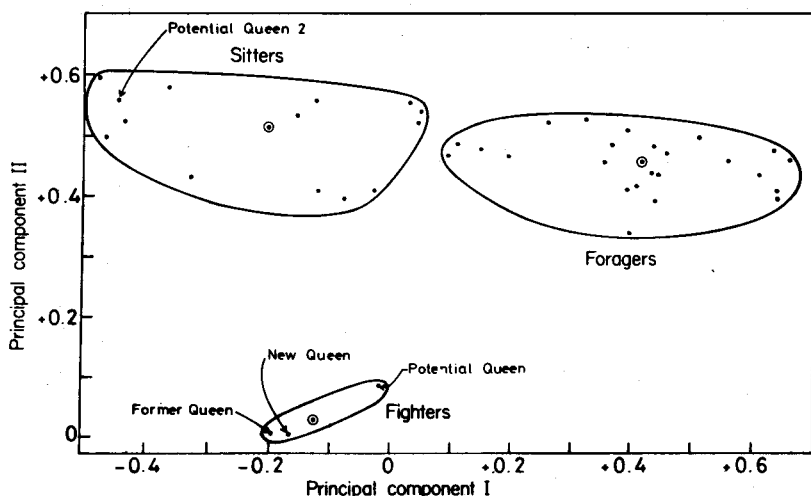


Fig. 5.13. Behavioral profiles of individually identified females in a *Ropalidia cyathiformis* colony analyzed by principal components analysis. Each point represents one wasp (either before or after the queen was removed) plotted in the coordinate space of the first two principal components. When the queen labeled *Former Queen* was removed, the wasp labeled *Potential Queen* became the replacement queen (her modified behavioral profile is labeled *New Queen*). When this new queen was in turn removed, the wasp labeled *Potential Queen 2* became the next replacement queen. (From Gadagkar 1987, courtesy of Verlag J. Peperny.)

just a few feet away from the parent colony. A behavioral analysis before and after colony fission revealed that inclusive fitnesses of the "Rebels" who left the colony, as well as of the "Loyalists" who stayed in the old colony, increased as a result of the fission (Gadagkar and Joshi 1985), probably because of the prevailing low efficiency of brood rearing before colony fission associated with high levels of aggression. The second most dominant individual before colony fission became the queen on the new colony. Here, therefore, is an instance where a wasp managed to establish herself as a queen, yet avoided the cost of challenging the original queen as well as the risk of failure that lone foundresses face. Interestingly, Loyalists and Rebels both behaved as internally coordinated groups well before the actual fission, synchronizing among themselves their times of being on or away from the nest and avoiding members of the other group (Gadagkar and Joshi 1985).

In summary, when viewed with an emphasis on queen-worker dichotomy, social organization appears to achieve efficient division of labor and colony harmony, but when viewed with an emphasis on inter-individual variability a rich mosaic of complex behavioral strategies becomes evident, suggesting ways by which individual selection might mold worker behavior (see *Origin of Social Life: A Perspective from Studying Independent-founding Polistines*). It must be stressed, however, that the foregoing discussion of social organization is based on only a few studies of a few species. Future studies of these and the large number of as-yet unstudied species (see, for example, Itô and Higashi 1987, Itô et al. 1988) are bound to revise our current ideas.

## CASTE

Primitively eusocial wasps of the kind we are dealing with provide rich model systems for studying the role of interactions between the adults in determining social organization. But are interactions between adults sufficient to tell us all there is to know about social organization? In other words, are all females at emergence potentially capable of assuming any role in the colony? This has by and large been assumed to be so (e.g., Queller and Strassmann 1989, Reeve, this volume), but since there has never been a direct test there is no firm evidence one way or the other. An important exception is the study by Richards and Richards (1951), who clearly recognized the significance of this question and demonstrated slight preimaginal caste differentiation in a number of polistine species. However, most of their material, barring a few species of *Polistes* and *Mischocyttarus*, consisted of highly eusocial swarm-founding Neotropical polistines.

As far as the independent-founding genera are concerned, there ap-

pears to have been only one direct test of the null hypothesis that "all eclosing females are potentially capable of laying eggs" (Gadagkar et al. 1988:176; see also Gadagkar et al. 1990b). This hypothesis was tested by collecting a number of nests of *R. marginata* and isolating emerging females in individual cages. Of 299 virgin female wasps from 39 nests so tested, only 150 laid eggs. The remaining 149 died without doing so in spite of living, on average, longer than the time taken by the egg layers to lay their first eggs. This result clearly suggests that there is some preimaginal biasing of caste. But what factors determine which females will become egg layers and which will become non-egg layers? Among a large number of variables studied only two were significantly correlated with the probability of a wasp becoming an egg layer. One of these variables, the number of empty cells in the parent nest, is likely to be a strong indicator of the queen's declining influence on a colony. The second correlate, the rate of food consumption by wasps in the experiment, varied considerably in spite of all animals being housed in individual cages and being provided unlimited access to food.

On the basis of these results Gadagkar et al. (1988) proposed a model for preimaginal biasing of caste in primitively eusocial insects. With a decline in the queen's influence resulting from poor health, old age, or a temporary programmed shift in her physiology and/or behavior, a set of processes would be initiated that has two consequences: (1) the accumulation of empty cells and (2) the production of a class of female offspring programmed to feed more and so to have a high probability of becoming reproductively competent. In contrast, when the queen's influence is high there are two rather different consequences: (1) the absence of empty cells and (2) the production of a class of female offspring programmed to feed relatively less. Preimaginal caste bias is undoubtedly partial, leaving considerable potential in the adult stage for environmental and other social factors to influence caste.

Indirect evidence suggests the existence of a similar caste-biasing system in *B. grisea*. Pardi and Marino Piccioli (1970, 1981) found two distinct classes of females: (1) larger "queenlike" females who were fertilized more often, were more oophagous, and were mainly nest foundresses and (2) "workerlike" females who had the opposite traits and foraged more often. These authors postulated that preimaginal trophic factors determine the two "morphophysiological" conditions.

If the queen or other adults bias the future caste of their colony's brood, one might expect the brood in a preemergence colony to be channeled toward worker development and the brood in a mature postemergence colony to be channeled toward queenlike development. If such channeling is based on differential larval nourishment, one would expect larvae in preemergence colonies to be poorly nourished

compared with larvae in mature postemergence colonies. Although no quantitative data on larval nourishment in pre- and postemergence colonies are available, there is suggestive evidence that *R. marginata* nests with relatively well-nourished larvae produce more egg layers, whereas those with relatively poorly nourished larvae produce more non-egg layers (Gadagkar et al. 1990c).

Hunt (1988) has pointed out a factor that can potentially exaggerate such differences in larval nourishment. This is the tendency of *Mischocyttarus* larvae in preemergence colonies to give up saliva to the soliciting adults more readily than larvae in postemergence colonies (see Food and Feeding Habits). The result is an exaggeration of the difference in nourishment between larvae from pre- and postemergence phases of the colony cycle, thus providing a more powerful mechanism of channeling emerging females into their respective worker and reproductive roles.

The above discussion suggests that some form of preimaginal caste biasing already occurs at the level of social evolution represented by the independent-founding polistines. While postemergence events undoubtedly influence caste, preemergence factors should be studied with greater vigor and better techniques. Whether all adult females are equally capable of assuming any role in the colony in the absence of postemergence social interactions is still an open question for most species. If the answer is negative, as it seems to be for some species, then we should be viewing these primitively eusocial insect societies from a rather different perspective and suitably modify our theories to explain altruism.

## ORIGIN OF SOCIAL LIFE: A PERSPECTIVE FROM STUDYING INDEPENDENT-FOUNDING POLISTINES

Why do social wasps live in groups? Why do some individuals accept the role of sterile worker? During colony founding, why do some individuals nest with others even if it means few or no opportunities to lay their own eggs? During the early postemergence phase of the colony cycle, why do many females stay to help their mothers produce more offspring? Primitively eusocial polistine wasps are attractive model systems in insect sociobiology because they seem to provide the opportunity to answer such questions.

In most highly eusocial insects such as honey bees, termites, and most ants, the simple answer to those questions could be that individuals who accept sterile worker roles simply have no other choice; over evolutionary time they have lost the ability to reproduce on their own. Workers in many species are capable of laying eggs, but with rare ex-

ception (e.g., Anderson 1963) they lay only haploid, male-producing eggs, and even then such worker reproduction is usually suppressed in the presence of the queen (Hamilton 1964b, 1972; Wilson 1971, Trivers and Hare 1976; Fletcher and Ross 1985; Ross 1985; Page and Erickson 1988; Ratnieks 1988; Ratnieks and Visscher 1989; Visscher 1989).

In primitively eusocial species there are several situations in which the animals almost certainly have a choice regarding the option of direct reproduction. Single- and multiple-foundress colonies coexist in *Mischocyttarus*, *Ropalidia*, and *Parapolybia* (Table 5.1); subordinate females adopt the role of the queen if the most dominant female is lost or removed (Jeanne 1972; Litte 1979, 1981; Gadagkar 1987); daughters sometimes challenge, drive away, and replace mother queens (Jeanne 1972, Yamane 1986, Gadagkar, unpubl.); and females leave their natal nests to found new colonies (Gadagkar and Joshi 1984, 1985). All these facts strongly suggest that individuals accept subordinate roles not because they are incapable of doing anything else but because social life, even if it means partial or full sterility, must sometimes be more advantageous than solitary life. Thus, the study of primitively eusocial species such as those considered in this chapter, which have real choices concerning reproductive roles, allows us to focus on the origin of social life rather than simply its maintenance.

How can social life be more advantageous than solitary life if the former means sterility? Workers in social groups may have opportunities to gain inclusive fitness by caring for their relatives' offspring if the group consists of close kin (for discussion of inclusive fitness and kin selection, see Ross and Carpenter, this volume). We may broadly generalize Hamilton's (1964 a,b) concept of inclusive fitness and say that group life is favored over solitary life if

$$\sum_{i=1}^n r_i > 1/2 m, \quad (5.1)$$

where  $n$  is the number of individuals (offspring or other relatives) reared in the group mode,  $r_i$  is the coefficient of genetic relatedness between these individuals and the sterile workers, and  $m$  is the number of offspring reared in the solitary mode. One way in which this inequality may be obtained is for the average  $r_i$  ( $\bar{r}$ ) in the group mode to be greater than 0.5, that is, for the genetic relatedness of relatives reared to be greater than that of offspring. This may be achieved with a male haploid (haplodiploid) genetic system, such as is found in Hymenoptera, in which genetic relatedness between a female and her full (= super) sisters is 0.75. Realization of this high  $\bar{r}$  requires that colonies consist of a single egg layer mated to a single male, so that

workers need not rear any half-sisters or more distantly related individuals. Furthermore, workers either must successfully skew investment in favor of their sisters or must be able to rear their own sons instead of brothers. (Brothers are related to workers by only 0.25, while sons are related to their mothers by 0.5.)

Many features of the biology of the genera considered in this chapter suggest that conditions necessary for high  $\bar{r}$  between workers and the brood they rear may not be met (see also Ross and Carpenter, this volume). In *B. petiolata* only 15% of foundress associations consist exclusively of former nestmates (Keeping and Crewe 1987), so that co-foundresses probably are not often closely related. In *M. drewseni*, *R. variegata jacobsoni*, and *R. marginata*, queen supersedure is common (Jeanne 1972, Yamane 1986, Gadagkar et al. 1990a). Polygyny, the simultaneous presence of more than one egg layer, has been reported in *M. mexicanus* fall nests (Litte 1977), *R. cyathiformis* (Gadagkar and Joshi 1982b, 1984), *R. variegata jacobsoni* (Yamane 1986), and *R. fasciata* (Itô 1986b), and nests frequently are usurped by foreign conspecifics in *M. flavitarsis* (Litte 1979). Multiple mating by the egg layer is known in at least one species (*R. marginata*: Muralidharan et al. 1986). Among these genera, average relatedness between female nestmates has been measured in *Mischocyttarus basimacula* ( $r = 0.44$ ), *M. immarginatus* ( $r = 0.77$ ) (Strassmann et al. 1989), and *R. marginata* ( $r = 0.53$ ; calculated from data in Muralidharan et al. 1986).

Polygyny or multiple mating by the queen should pose no great difficulty for attaining high levels of inclusive fitness if workers discriminate between full sisters and less-related individuals, giving preferential aid to the former (Gadagkar 1985b). However, studies of nestmate discrimination in *R. marginata* suggest that the labels and templates used in discrimination are not produced individually, but rather are acquired from a common external source, namely the natal nest or nestmates, making it unlikely that different levels of genetic relatedness can be effectively recognized among members of the same colony (Venkataraman et al. 1988). Thus, it seems likely that workers in these primitively eusocial wasps often rear complex mixtures of full sisters, half-sisters, nieces, daughters, brothers, nephews, sons, and cousins without the ability to discriminate on the basis of genetic relatedness. Because  $\bar{r}$  in such societies rarely exceeds 0.5, it has been increasingly suspected that haplodiploidy is not as important a factor in the origin of insect sociality as was earlier thought (Evans 1977a, West-Eberhard 1978a, Andersson 1984, Stubblefield and Charnov 1986, Venkataraman et al. 1988, Gadagkar 1990a,b).

Even if  $\bar{r}$  is rarely much greater than 0.5 (or even less than 0.5), the inequality in Eq. 5.1 can nonetheless be achieved if  $n$  is sufficiently greater than  $m$ . The ecology of independent-founding polistine wasps



suggests that there must be substantial benefits to group living, that is,  $n$  must often be greater than  $m$  (see also Reeve, this volume). For instance, the probability of survival of single-foundress colonies is certainly small, as the nest and its brood are extremely vulnerable to predators and parasites (e.g., Suzuki and Murai 1980). Yet the effectiveness of protection from such enemies by even one or two supernumerary adults is obvious to anyone who has watched these wasp colonies. Furthermore, multiple foundresses are more likely to be able to rebuild a damaged nest than are solitary foundresses. This latter factor favors multiple-foundress nests even when the destructive agent is itself indifferent to group size, as in the case of predation by birds or destruction by typhoons (Litte 1977, 1979, 1981; Itô 1983, 1984b, 1985a,b,c, 1986a, 1987b; Kojima 1989). A combination of high adult mortality and slow brood development in *R. marginata* has been shown to enhance the inclusive fitness of workers relative to that of solitary foundresses (Gadagkar 1990c).

Another way by which the inequality in Eq. 5.1 may be attained is if ecological conditions exist such that a parent who manipulates a fraction of her offspring into being sterile and helping to rear her remaining (fertile) offspring leaves behind more grandchildren than her wild-type counterpart (*parental manipulation hypothesis*: Alexander 1974). A significant problem with this is whether counterselection on the offspring would be successful in making them overcome parental manipulation. A related idea, which circumvents this problem, is that subfertile females produced by whatever cause (even by accidental variation in the quantity of food obtained as larvae) will find it "easier" to give up reproduction and accept a worker role (*subfertility hypothesis*: West-Eberhard 1975). That is,  $m$  will be so small that the inequality in Eq. 5.1 may be satisfied rather easily. The general ideas embodied in the parental manipulation and subfertility hypotheses have found support in theoretical (Stubblefield and Charnov 1986), modeling (Craig 1979, 1983), and empirical (Michener and Brothers 1974) studies. The evidence for preimaginal caste bias in *R. marginata* (see Caste) suggests that at the level of primitive eusociality represented by the genera discussed here, subfertility may contribute to achieving the inequality in Eq. 5.1.

The presence of permanently sterile worker castes is the most prominent and seemingly paradoxical feature of the highly eusocial insects. Attempts to explain the evolution of eusociality have sometimes obscured the rather obvious fact that many social insect species do not possess permanently sterile workers but could nevertheless be forerunners of the highly eusocial state. The evolutionary forces that promoted the origin of such primitive levels of sociality may thus have been quite

different from those discussed above. The statements that "social behavior in insects is in part mutualistic" and that "social colonies without altruism are therefore considered a probability" (Lin and Michener 1972:131) may well prove to have been prophetic. The theory of reciprocal altruism proposed by Trivers (1971), an individual-level selection theory that suggests that aid may be given today with the hope of getting a return tomorrow, has for some mysterious reason seldom been applied to social insect colonies. A related individual selection model has been discussed by West-Eberhard (1978a) and Gadagkar (1985a). Consider two wasps that come together and nest jointly. If their joint productivity (say, 21 offspring) is even slightly greater than the sum of their individual productivities (say,  $10 + 10 = 20$  offspring) in the solitary mode, and if the roles of queen and sterile worker are assigned randomly, then wasps who take the risk of joint nesting will, on average, produce 10.5 offspring and thereby do better than those who shy away from the risks of joint nesting. In this "gambling" model, benefits of group living can be infinitesimally small, and abilities of parents to manipulate their offspring or of colony members to discriminate on the basis of differential genetic relatedness are not necessary.

## A POSSIBLE ROUTE TO EUSOCIALITY

Many features of the genera discussed in this chapter lend credibility to the idea that the initial incentive for group living comes from mutualism, reciprocal altruism, and the benefits of gambling (*the gambling stage*; Fig. 5:14). This is possible without any preadaptation for parental manipulation or for recognition on the basis of genetic relatedness, although group living among kin will evolve more easily (West-Eberhard 1978a, Schwarz 1988). The only prerequisite for the evolution of incipient societies by mutualism is a sufficiently complex behavioral repertoire to permit the necessary interactions; solitary wasps seem to possess an appropriately diverse array of behaviors (Tinbergen 1932, 1935; Tinbergen and Kruyt 1938; Brockmann and Dawkins 1979; Brockmann et al. 1979).

Once group living is established, the stage is set for manipulation (*the manipulation stage*). Accidental variations in food supply leading to subfertility can be exploited, and the ability to manipulate offspring can be selected for. As manipulation becomes increasingly effective, benefits of group living become increasingly unavailable to some individuals, who begin to lose reproductive options and to get trapped into worker roles. It is precisely at this stage that the ability to recognize

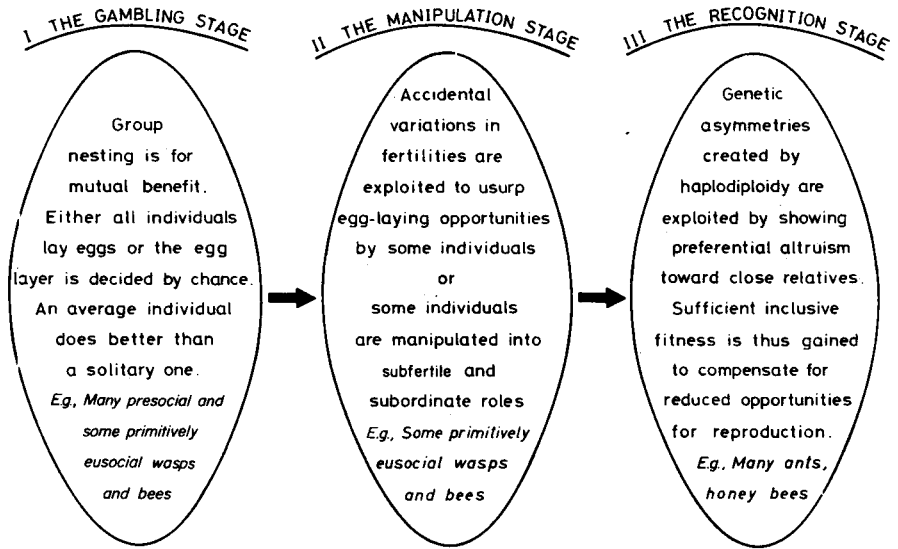


Fig. 5.14. The route to eusociality, a hypothesis concerning the evolution of the highly eusocial state from the solitary state through the gambling, manipulation, and recognition stages. The examples given for each stage are tentative, as our knowledge of the causes and consequences of group living in most social insect groups is rather sketchy.

and give preferential aid to closer relatives will begin to have selective value (*the recognition stage*). In other words, the benefits of haplodiploidy for social evolution become operative at this final stage.

This route to eusociality (Gadagkar 1990d) explains one otherwise curious fact. The ability to discriminate among the members of a colony on the basis of relatedness seems to be absent in all primitively eusocial species studied but present in the highly eusocial ants and honey bees (reviewed in Venkataraman et al. 1988). If haplodiploidy were important for the origins of insect eusociality one would expect workers in primitively eusocial species to exploit the genetic asymmetries thus created by discriminating between close and distant relatives. But if eusociality originated because of mutualistic benefits, as assumed here, and its subsequent maintenance in highly eusocial forms is due largely to haplodiploidy, the observed distribution of kinship discrimination abilities is no longer a paradox.

## CONCLUDING REMARKS

Any attempt to collate the rapidly accumulating information on polistine biology may appear aimless unless there is a well-defined structure around which this information is organized. Therefore, recogni-

tion of the existence of two behaviorally distinct groups by Jeanne (1980a), namely the "independent-founding Polistinae" and the "swarm-founding Polistinae," was perhaps the most significant recent conceptual advance in our understanding of polistine wasps. Much work since then has aimed to further consolidate such a classification. We may now have reached the stage, however, of beginning to question this classification and to start looking at exceptions to the characteristics of each group. To what extent do species of *Ropalidia* and *Parapolybia* depend on chemical defense against ants? To what extent is nest founding by several females of different ages, arriving simultaneously and sometimes having well-defined social roles in their previous colonies, really different from swarm founding? What means of communication, if any, do the independent-founding species use in choosing and reaching a new nesting site? This is not to imply that we have reached the end of the utility of Jeanne's (1980a) classification. Indeed, it is a tribute to its continuing utility that we expect significant new advances in polistine biology to be triggered by standing this classification on its head and looking for exceptions!

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**Appendix 5.1. Common Parasites of *Belonogaster*, *Mischocyttarus*, *Parapolybia*, and Independent-founding *Ropalidia***

Host species	Parasite	Locality	Stage affected	Remarks	Reference
<i>Belonogaster juncea</i>	<i>Pediobius ropalidia</i> (Eulophidae: Hymenoptera)	Ghana	Pupa	High proportion of the pupae destroyed	Richards 1969
<i>B. petiolata</i> and <i>B. juncea colonialis</i>	<i>Anacamptomyia</i> sp. (Tachinidae: Diptera) and <i>Camptotypus apicalis</i> (Ichneumonidae: Hymenoptera)	Transvaal, South Africa	Prepupa and pupa		Keeping and Crewe 1983
<i>Mischocyttarus drewseni</i>	Strepsiptera	Brazil	Adult	Only 2 out of 760 adults were affected	Jeanne 1972
<i>M. flavitarsis</i>	<i>Chalcoela iphitalis</i> (Pyralidae: Lepidoptera)	Arizona, USA	Larva and pupa	Common cause of brood mortality	Litte 1979
<i>M. flavitarsis</i>	<i>Monodontomerus</i> sp. (Torymidae: Hymenoptera)	Arizona, USA	Larva and pupa	Rare	Litte 1979
<i>M. flavitarsis</i>	Strepsiptera	Arizona, USA	Pupa and adult		Litte 1979
<i>M. labiatus</i>	<i>Megaselia</i> sp. (Phoridae: Diptera)	Colombia	Brood	Responsible for a larger proportion of nest failures than any other single factor	Litte 1981
<i>Parapolybia varia</i>	<i>Bakeronymus typicus</i> (Trigonalidae: Hymenoptera)	Taiwan	Larva		Yamane and Terayama 1983

<i>Ropalidia cyathiformis</i>	Unidentified species of Ichneumonidae (Hymenoptera)	Bangalore, India	Larva		Gadagkar, unpubl
<i>R. fasciata</i>	<i>Arthula formosana</i> (Ichneumonidae: Hymenoptera)	Okinawa, Japan	Larva	Very high percentage of cells parasitized	Itô 1983
<i>R. flavobrunnea lapiniga</i>	<i>Pseudonomadina biceps</i> (Trigonalidae: Hymenoptera)	Philippines	Brood	In addition to larvae and pupae, live adults of the parasite were found in active wasp nests	Yamane and Kojima 1982
<i>R. formosa</i>	<i>Hemipimpla pulchripennis</i> (Ichneumonidae: Hymenoptera)	Madagascar	Larva		Brooks and Wahl 1987
<i>R. marginata</i>	<i>Koralliomysia portentosa</i> (Tachinidae: Diptera)	Bangalore, India	Larva		Belavadi and Govindan 1981
<i>R. marginata</i>	Strepsiptera	Bangalore, India	Adult		Belavadi and Govindan 1981, Gadagkar, unpubl.
<i>R. marginata</i>	Unidentified species of Tachinidae (Diptera), Torymidae (Hymenoptera), Ichneumonidae (Hymenoptera)	Bangalore, India	Larva		K. Chandrashekara and Gadagkar, unpubl.

**Appendix 5.2. Common Predators of *Belonogaster*, *Mischocyttarus*, *Parapolybia*, and Independent-founding *Ropalidia***

<i>Prey species</i>	<i>Predator</i>	<i>Locality</i>	<i>Stage affected</i>	<i>Remarks</i>	<i>Reference</i>
<i>Belonogaster petiolata</i>	<i>Hoplostomus fulgineus</i> (Scarabaeidae: Coleoptera)	Transvaal, South Africa	Pupa		Keeping 1984
<i>Mischocyttarus drewseni</i>	<i>Monomorium pharaonis</i> , <i>Camponotus abdominalis</i> (Formicidae: Hymenoptera)	Brazil	Brood		Jeanne 1972
<i>M. drewseni</i>	Spiders	Brazil	Adults away from the nest		Jeanne 1972
<i>M. flavitarsis</i>	Birds	Arizona, USA	Whole nest or pieces of the nest	Inferred	Litte 1977
<i>M. flavitarsis</i>	Spiders, preying mantids	Arizona, USA	Adults away from the nest		Litte 1977
<i>M. labiatus</i>	Army ants	Colombia	Brood	Seen only once	Litte 1977
<i>M. mexicanus</i>	Ants, birds	Mexico	Whole nest or pieces of the nest	Predation by blue jays was observed, and the involvement of other birds was inferred	Litte 1977
<i>Mischocyttarus</i> spp.	Bats	Brazil	Whole nest		Jeanne 1970b
<i>Parapolybia indica</i>	<i>Vespa tropica</i> (Vespidae: Hymenoptera)	Japan	Pupa and larva	Most important enemy	Sekijima et al. 1980
<i>P. varia</i>	Ants	Taiwan	Brood		Yamane 1980
<i>P. varia</i>	<i>Vespa tropica</i> (Vespidae: Hymenoptera)	Taiwan	Pupa and larva	Most important factor regulating population levels	Yamane 1980
<i>Ropalidia marginata</i> and <i>R. cyathiformis</i>	<i>Vespa tropica</i> (Vespidae: Hymenoptera)	Southern India	Pupa and larva	Most important factor regulating population levels	Gadagkar, unpubl.

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