Chapter 7
The Biology of Swarm-Founding Epiponine Wasp, *Polybia paulista*

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Abstract The tribe Epiponini belongs to the swarm-founding polistine wasps and has achieved a remarkable ecological success in Neotropical regions. 20 out of 26 genera of the subfamily Polistinae are Epiponini, suggesting that these wasps have undergone an evolutionary radiation. Social wasps are quite common in Brazil, wherein 304 species in 22 genera are found. In particular, the species *Polybia paulista* is a common wasp, being found in the states of São Paulo, Goiás, Mato Grosso, Paraná, and Minas Gerais. Although several earlier studies in 1980s investigated mortality and development of colonies in this species, studies in the last two decades intensively have addressed various aspects of biology in this species, especially by morphological, genetical, population, and chemical approaches. In this chapter, I will review the biology of *P. paulista* inclusively by gathering studies for the last four decades.

Keywords Neotropical regions · polygyny · Epiponini · swarm-founding · *Polybia*

The subfamily Polistinae (26 genera and 958 species; Pickett and Carpenter 2010) comprises species with diverse social organization and can be divided into two groups according to colony foundation modalities, i.e., the independent founders and swarm founders. Colonies of independent-founding species are initiated by one or several inseminated queens, independently of any workers. Dominance behavior and reproductive skew among founding queens have been reported for species belonging to all five genera (*Polistes*, *Mischocyttarus*, *Belonogaster*, *Parapolybia*, and several species of *Ropalidia*) (Gadagkar 1991, 1996). Generally, reproductive dominance is based on direct physical attacks by the queens (Pardi 1946), while egg-laying queens of *R. marginata* rarely dominate or interact aggressively with other co-founding queens (Gadagkar 2001).

In the swarm-founding species, a colony is initiated by a swarm consisting of a large number of workers accompanied by a smaller number of queens (Jeanne

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1991). Swarm-founding Polistinae (the other species of *Ropalidia*, *Polybioides*, and the tribe Epiponini) widely occur in tropical regions, although the ranges of several species exceed the limits of the tropics (Jeanne 1991). Particularly, all 20 genera of the tribe Epiponini are very common in Neotropical regions (Jeanne 1991, 2003). Aggressive interactions between queens are rare, and the clear reproductive specialization in queens exists. Moreover, there is no evidence that queens attack, harass, or otherwise physically intimidate workers into action (Herman et al. 2000, but see Kelstrup et al. 2014a).

In the swarm-founding epiponines, several lines of studies have been done during the last few decades (Jeanne 2003). The first one is morphological caste difference. A striking feature is that caste dimorphism among epiponines is not as great, even in species with a great number of adults. In *Agelaia vicina*, whose colonies can exceed 10^6 adults (Sakagami 1996), queens are only 5% larger than workers (Sakagami 1996; Baio et al. 1998). In *Parachartergus smithii*, *Protopolybia exigua*, *Pseudopolybia vespiceps*, and recently *Synoeca septentrionalis*, there is no evidence of morphological differences among castes (Mateus et al. 1997; Shima et al. 1998; Santos et al. 2018). In contrast, queens are significantly smaller than workers in *Polybia dimidiata* (Shima et al. 1996). From these evidences, Jeanne (2003) concluded that the degree of morphological differences correlates with colony size very weakly in the swarm-founding wasps, particularly Epiponini.

The second is colony genetic structure related to the maintenance of polygyny. A colony alternates between polygyny and oligogyny, eventually monogyny, in the course of its life cycle (West-Eberhard 1978). New queens are only produced when the number of old queens is reduced to one or very few, and consequently new queens are highly related, often as full sisters. The process, called cyclical oligogyny, has the effect of elevating genetic relatedness between daughter offspring of the new queens. All analyzed species showed lower effective number of queens contributed to queens than to worker production, suggesting that the Epiponini exhibits cyclical oligogyny (see Table 7.1). On the contrary, division of labor among workers includes a genetic component in *Polybia aequatorialis*, suggesting that colony-level selection on variation in division of labor is a possible factor favoring

Table 7.1 Comparison of the effective number of queens that produced queens and workers in epiponine wasps

	Effective no. of queens that produced		
Species	Queens	Workers	References
Parachartergus colobopterus	1.2	1.2–4.3	Strassmann et al. (1991, 1998)
Polybia emaciata	1.5	3.6	Strassmann et al. (1992)
Polybia occidentalis	1.4	1.4–4.8	Queller et al. (1993a), Strassmann et al. (1998)
Protopolybia exigua	0.9	0.9–1.9	Gastreich et al. (1993), Strassmann et al. (1998)
Brachygastra mellifica	1.2	20	Hastings et al. (1998)
Polybia paulista	1.2	21	Kudô et al. (2005a, b)

the evolutionary maintenance of high genotypic variability (though low relatedness) (O'Donnell 1996).

The third is organization of tasks by workers, which has been summarized in reviews by Jeanne (1991, 2003). Jeanne (2003) pointed out that "full task partitioning of all material-handling tasks in the swarm founders is what enabled clear-cut age polymorphism to evolve in the epiponines." *Polybia occidentalis* has been best studied in this respect. In this species, the handling of all four materials (pulp, water, prey, and nectar) is fully partitioned into two tasks, collection and utilization. In addition, three team tasks can be identified in colonies, i.e., nest construction, nest cooling, and swarm emigration.

The last one is chemical communication among nestmates. According to a review by Jeanne (2003), there is evidence for existence for three chemical signals in the Epiponini, i.e., alarm pheromones contained in the venom, emigration trail pheromones, and queen pheromones (Landolt et al. 1998). Recently, in addition, a few studies have analyzed the correlation between cuticular hydrocarbons (CHCs) and fertility in epiponine wasps. Kelstrup et al. (2014a) showed in *Polybia micans* that queens and workers exhibit remarkable differences in their CHC profiles, with two compounds (3-methyl-pentacosane and *n*-pentacosane) being far more abundant in queens. These compounds increase in female during ovarian development and with high levels of juvenile hormone. CHC profiles of queens and workers are also distinct in *Synoeca surinama* (Kelstrup et al. 2014b) and *S. septentrionalis* (Santos et al. 2018). Furthermore, a recent study also showed that the CHC compositions of fifth instar larvae in *Polybia paulista* are significantly different among colonies, which may function as a nestmate larval discrimination (Kudô et al. 2017; see this chapter).

This chapter reviews the biology of an epiponine wasp, *Polybia paulista* (Fig. 7.1). *P. paulista* is one of the common swarm-founding wasps in Brazil, being found in the states of São Paulo, Goiás, Mato Grosso, Paraná, and Minas Gerais, also present in Paraguay and Argentina (Richards 1978). In the early 1980s, some Brazilian researchers have published ecological studies on mortality and development of colonies in *P. paulista* (Machado 1980, 1984; Simões and Mechi 1983). Since then, however, any studies had not been made in *P. paulista* until Itô et al. (1997) described the initial development of colonies. After the Itô's study, biologi-

Fig. 7.1 A mature nest of (left) and workers around the entrance of the nest (right)

cal information in *P. paulista* has been accumulated in various aspects in the last two decades, i.e., morphological caste differences, nest materials, colony genetic structure, parasitism, nestmate recognition, and individual and colony mortality. Thus, it must be important to introduce the biology of *P. paulista* by gathering those studies for the last four decades. I hope this review will help many people who are interested in social wasps understand the evolution and maintenance of highly eusociality in wasps.

7.1 Colony Cycle

It is perhaps difficult to describe the colony cycle of *P. paulista* correctly, because swarming can occur in several contexts and, when a swarm is collected in the field, it is impossible to determine the context that gave rise to it (see also Jeanne 1991). Colony initiation occurs at any months during the year, but is observed intensively in rainy, nest-growing months (November to April, hereafter "summer") in Ribeirão Preto (Machado 1984; Simões and Mechi 1983; Kudô et al. 2003). Swarms build several stacked combs in quick succession. Particularly, the first three combs and the envelope covering those combs are quickly completed within only few days (commonly, 3–4 days) after colony initiation. After colony initiation, while many individuals are actively engaged in nest construction, a large number of individuals remain tightly clustered adjacent to the incipient nest (Fig. 7.2a). Wasps that sit around the nests are very aggressive, especially just after colony initiation, and the cluster size gradually decreases with colony development. Individuals that are outside of the clusters orient the head toward the opposite direction from their nests (Fig. 7.2a). The cluster disappears within 10 days after colony initiation, as the wasps move inside the nest or to the envelope. Days spent until the disappearance of the cluster tended to be shorter in summer colonies than in winter colonies (May to October) (Kudô et al. 2003).

Successive nest construction is stopped within a month from colony initiation. Days for the initial nest development in summer colonies (12.6 days) tended to be shorter than those in winter colonies (24.5 days) (Kudô et al. 2003). The authors examined colony composition at pause of nest development in a summer colony; the nest consisted of five combs and had ca. 3400 cells, 577 eggs, and 320 first and/or second instar larvae. Presence of second instar larvae suggests that nest development was paused after few days from larval emergence.

After the nest is built by the founding swarm, there is no addition of cells to the nest for weeks or even months. Jeanne (1991) mentioned that when nest expansion does occur in swarm-founding wasps, it is typically a discrete event, lasting only several days. In a winter colony of *P. paulista*, I observed construction of new cells and the envelope covering the comb that was just 3 weeks after the pause of initial nest development (Kudô et al. 2003).

Noll and Zucchi (2000) defined three consecutive phases in the colony cycle of *P. paulista*: (1) pre-emergence of workers, (2) emergence of workers, and (3) male production. According to the definition, no adult offspring had been produced in the

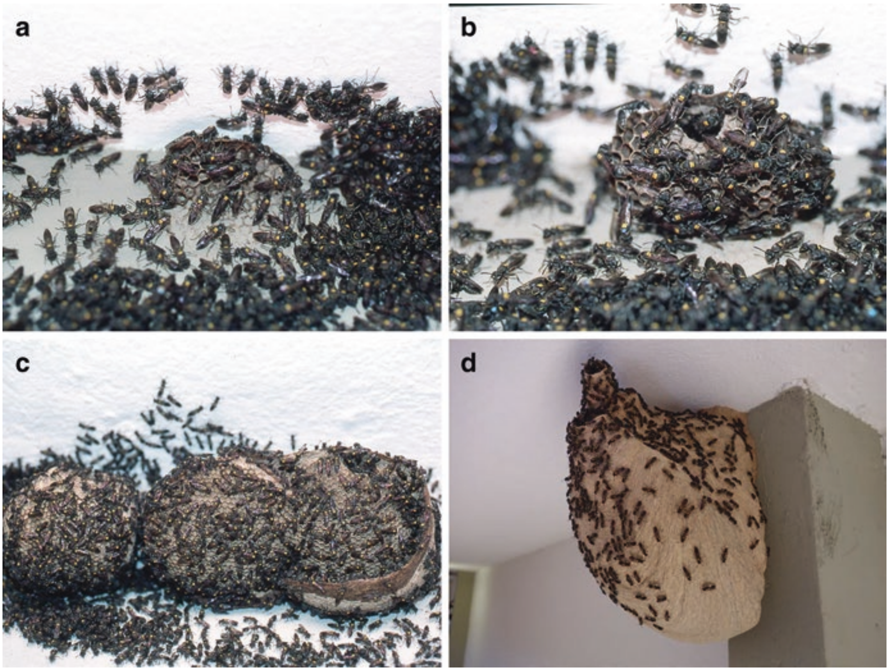

Fig. 7.2 Initial comb construction and workers outside of the clusters orienting the head toward the opposite direction from the nest (**a**), construction of new cells (second comb) on the envelope (**b**); precocious completion of first several combs (**c**); and reinforcement of primary comb(s) (upper part of the nest) (**d**)

pre-emergence phase. After producing several generations of workers, the colony has adequate number of workers and finally starts to produce males. In *P. paulista*, I observed several "reproductive swarming" (division of the colony into two or more groups) that occurred after the presence of many males on the nest envelope. This may support the definition by Noll and Zucchi (2000). However, Forsyth (1978) claims that male production of *P. occidentalis*, a consubgeneric species of *P. paulista*, is not directly correlated with colony size or stage of development of the colony but occurs in colonies that have old queens. On the other hand, Jeanne (1991) suggested that colonies of *P. occidentalis* in Costa Rica appear to occupy two nests successively during a single colony cycle, i.e., the colony produces one cohort of workers in the first nest, emigrates to found a new nest, produces several cycles of worker brood, and then reproduces.

7.2 Colony Size and Its Related Aspects

Colony size (number of adult females) in swarm-founding polistines varies tremendously among species and genera (see Fig. 6.4 depicted by Jeanne (1991)). Colony size was less than 100 individuals in *Marimbonda* spp. (Jeanne 1991), while it was estimated over million individuals in a colony of *Agelaia vicina* (Zucchi et al. 1995). In this regard, notable ranges are recognized in the genus *Polybia*, whose colony size spans at least 2.5 order of magnitude: less than 100 individuals in some species while several thousands of individuals in other species. Noll and Zucchi (2000) reported colony size in 2 *P. paulista* nests: 4747 workers in a worker emergence colony and 13,229 workers in a male-producing colony. Kudô et al. (2005a, b) estimated that the mean number of adult females in 14 summer colonies was 3457 ± 666 individuals (±SE). Colony population in *P. paulista* is likely to relate to the following two factors, i.e., (1) nesting season and (2) the phases of colony cycle. In order to know the worker demography and its seasonal change, I carried out mark-recapture experiments for four *P. paulista* colonies from the middle of summer (January) to the middle of winter (August) in 2001 at the campus of the Universidade de São Paulo, Ribeirão Preto (Kudô et al. 2011a, b). The study showed that the colonies experienced substantial reductions in worker number from summer to winter (Fig. 7.3).

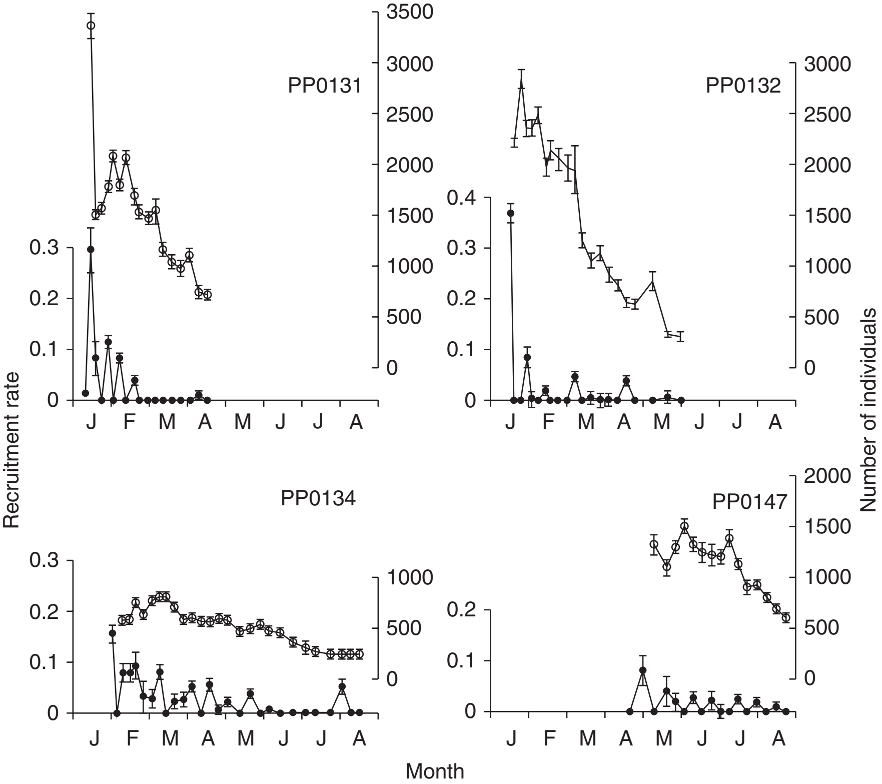

Fig. 7.3 Seasonal change in the number of workers (open circles) and recruit rate (closed circle) in four colonies (Kudô et al. 2011a)

This reduction may be related to lower foraging rates (Kudô et al. 2003; Canevazzi and Noll 2011) and a few or absence of brood in winter colonies of *P. paulista*. Actually, 60–70% colonies do not rear broods in the city during winter, and few nests contain nectar deposits (Kudô unpublished data). On the contrary, there is no study to compare the difference in colony population among the phases of colony cycle. However, as colony size just prior to "reproductive swarm" is large adequately, it is likely that there is a relation between colony size and the phase of colony cycle.

7.3 Nests

7.3.1 Sites

P. paulista nests are naturally built under broad leaves such as palm trees. The nests are sometimes built on the small twigs (a few centimeters) of trees, but such nests are easily destroyed by strong wind and heavy rain. Rather than natural substances for nest building, *P. paulista* prefer to build their nests under man-made structures. These circumstances together with broad leaves provide rain-sheltered conditions, which are beneficial not only in protecting nests from direct rain but also reducing the amount of oral secretion for nest maintenance (Simões and Mechi 1983; Kudô et al. 1998).

In addition to rain-sheltered places, swarms select a particular orientation as nest sites. Kudô and Zucchi (2009) showed that swarms selected various orientations as nest sites, but there was a particular trend that swarms in the winter period preferred to build northward-facing nests. Northward-facing nests are warmer through the gain of direct solar heat during the winter period; consequently, choosing northward-facing sites may be advantageous for swarms in terms of a shortened brood development and shortened time need to increase metabolic rates during warm-up for flight. Because architecture of *P. paulista* nests has insulation effect from ambient temperature, thermal conditions inside nests are stable even in the summer period (Hozumi et al. 2005; see later).

7.3.2 Materials

Wenzel (1991) mentioned that *Polybia* species exhibit great diversity in nest building materials: long woody fibers, plant hairs, short vegetable chips, and mud. The diversity is remarkable when compared with those of *Polistes* (long woody fibers and plant hairs), the most primitive genus in Polistinae (Wenzel 1991). SEM observations supported his description, and *P. paulista* wasps used vegetable chips, which are a dominant material, plant hairs, and mud and/or inorganic particles as nest building materials (Fig. 7.4a, b; Kudô et al. 2001). I have seen that *P. paulista* workers collected nest materials from decayed woods, which support that the workers collected short vegetable chips.

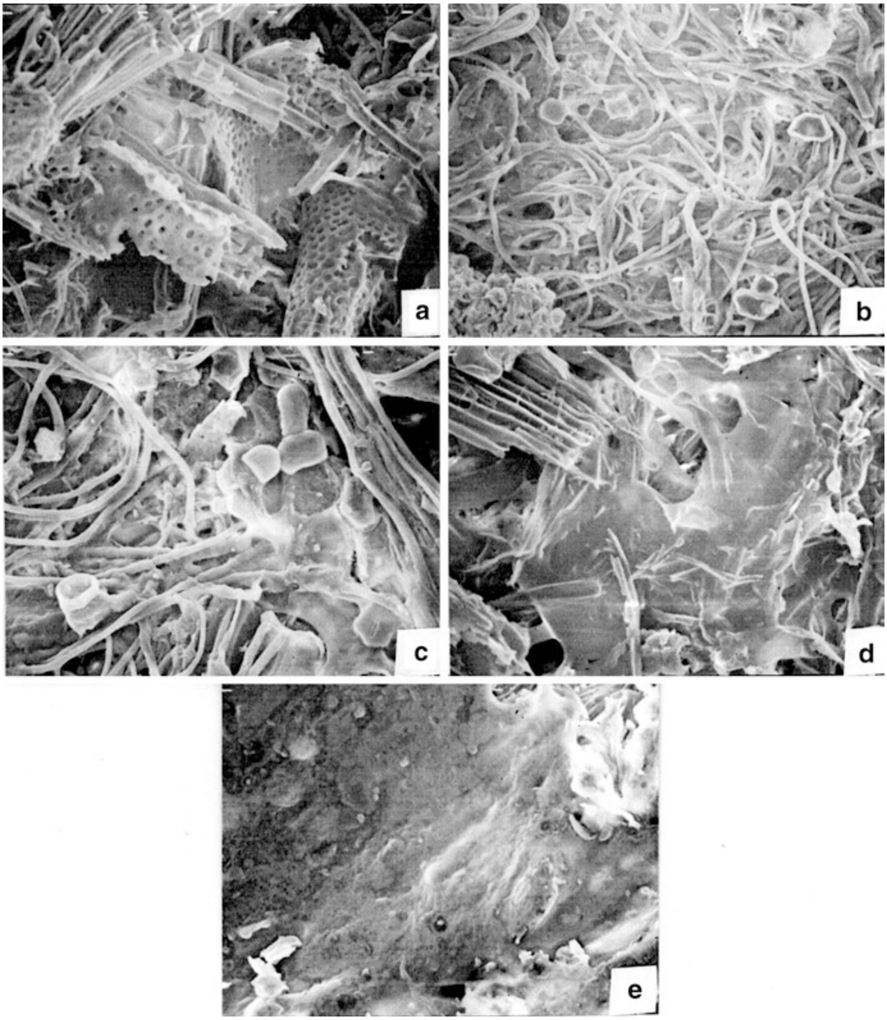

Fig. 7.4 Scanning electron micrographs of the outer surface of the upper part of the envelope (**a**), the cell walls (**b**, **c**), the outer surface of the upper part of the envelope cysts in the nest (**d**), the nest entrance on the envelope (**e**). See minute vegetable chips in **a**, plant hairs in **b**, mud and/or inorganic particles in **b**, oral secretion binding nest materials in **c** and **d**, and oral secretion covering the nest surface in **e** (Kudô et al. 2001)

Polistine wasps use oral secretion, of which a major proportion consists of proteinaceous elements, to glue nest materials (Fig. 7.4c, d). This salivary secretion is also used to physically maintain their nests (Fig. 7.4e). Kudô et al. (2001) showed that *P. paulista* used only a small amount of oral section for the construction and maintenance of their nests, compared with nests of independent-founding wasps. It has been first mentioned by Schwarz (1931) and later measured by Jeanne (1986) that the reduced role of oral secretion in *Polybia* species may be due in part to the division of labor. That is, increasing division of labor may shift the responsibility of the secretion production to progressively fewer wasps.

7.3.3 Architecture

Nest architecture of *P. paulista* is characterized by a figure (14.48) of Wenzel (1991): (1) sessile initiation (cell walls are built directly from the substrate with no paper foundation) (Fig. 7.2a), (2) construction of the envelope covering the primary comb(s) (Fig. 7.2b), (3) construction of new cells (second comb) on the envelope (Fig. 7.2b), (4) precocious completion of first several combs (Fig. 7.2c), and (5) reinforcement of primary comb(s) (upper part of the nest) (Fig. 7.2d) (Itô 1997; Kudô et al. 2003). There is no variation in nest architecture within the species except for a case that some swarms build multiple initial combs, of which combs were fused into a single one within a few days (Fig. 7.2c) (Kudô et al. 2003). This architecture is called "a phragmocyttarous nest" (Richards and Richards 1951; Jeanne 1975).

7.3.4 Thermoregulation

Hozumi et al. (2005) measured diel changes of a field nest of *P. paulista*. They showed that nest temperature followed the ambient temperature, but during the day the nest temperatures were lower than the ambient temperature, and this relationship was reversed during the night. The authors also showed a virtual lack of thermal effects from the presence of adult wasps. From these results, insulation effect of phragmocyttarous nests (narrow compartments between combs and the presence of envelope) makes stable thermal conditions of *P. paulista* nests.

7.4 Morphological Differences of Female Wasps Within a Colony

Because swarm-founding polistine wasps are highly eusocial, morphological caste differences exist. Commonly, queens are larger than workers in these wasps, but the degree varies among species. According to Jeanne (1991), colony size and caste dimorphism in swarm-founding polistines seem to be directly related. Richards (1978) noted that caste differences in *P. paulista* are indistinct. Noll and Zucchi (2000) made morphological analyses of female wasps between the castes in this species and showed that caste differences progressively increase because larger queens appeared in more abundance in later stages of the colony cycles.

Parasitism affects worker size in *P. paulista* (Kudô et al. 2004). Two kinds of parasites have been recognized in the gaster of female wasps, i.e., a strepsipteran possibly *Xenos myrapetrus* and an undescribed gregarine (Kudô et al. 2004, 2018, 2019) (Fig. 7.5). Kudô et al. (2004) compared differences in worker size between

Fig. 7.5 External view of a gaster of stylopyzed workers (**upper left**), a worker parasitized by a single strepsipteran (possibly *Xenos myrapetrus*) (**upper right**), and a worker parasitized by multiple strepsipterans (**bottom left**), and the gametocysts of an undescribed gregarine (**bottom right**). Thanks to W. Goi for the photos

uninfected workers and workers infected by strepsipterans or gregarines. Uninfected workers were larger than workers infected by strepsipterans, but smaller than workers infected by gregarines. Regarding the latter result, the authors suggested that larvae infected by gregarines, for which developmental time is extended (shown in *Polybia occidentalis*; Haward and Jeanne 2004), solicit more food from adults. The effect of parasitism on worker size was also shown in consubgeneric species, *P. occidentalis* (Kudô et al. 2011b).

7.5 Colony Genetic Structure

The evolution of eusociality in insects is understood in terms of kin selection, where workers gain inclusive fitness from rearing sexuals related to them (Hamilton 1964a, b; Hamilton 1972). In polygynous species, however, several or many queens reproduce in a colony, thus decreasing the relatedness of workers to brood. In this respect, epiponine wasps have attracted special attention, because all of the species have tens or even hundreds of queens. It has been empirically or genetically confirmed in polygynous polistines that relatedness within nestmates can be elevated by a mechanism known as cyclical monogyny, under which new queens are produced only after the number of old queens is reduced to one (West-Eberhard 1978; Hughes et al. 1993; Queller et al. 1993a; Strassmann et al. 1997, 1998; Hastings et al. 1998; Tsuchida et al. 2000) (Fig. 7.6). By using microsatellite markers, Kudô et al. (2005a, b) estimated effective queen number (the number of queens actively producing female offspring in a nest) that produced queens and workers. Queens were produced mostly by a single mother (effective number of queens = 1.2), while workers were produced by many queens (21) (Fig. 7.7). Such a lower effective number of queens contributed to queens than to worker production, suggesting that *P. paulista* also exhibits cyclical oligogyny. Regarding abundance of larger queens in later stages of the colony cycles, Noll and Zucchi (2000) suggested that queen elimination by a mechanism of cyclical oligogyny occurred in *P. paulista*. Kudô et al.

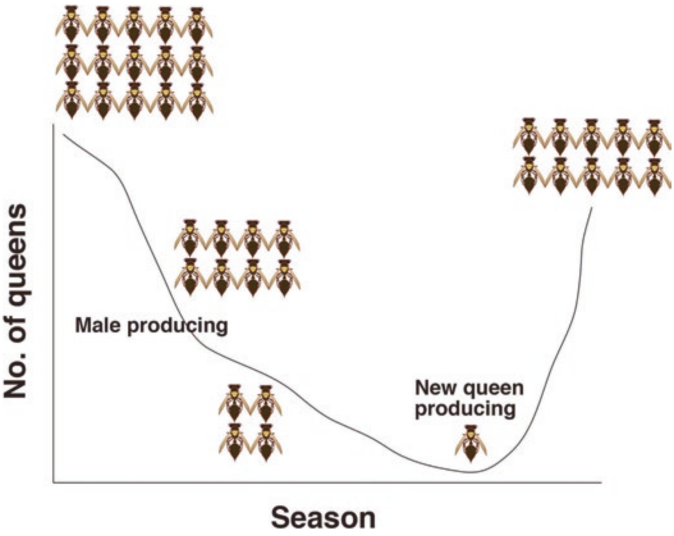

Fig. 7.6 Schematic drawing of cyclical monogyny where new queens are only produced when the number of old queens is reduced to one, while males are produced in colonies with a higher queen number. Redrawn from Tsuchida (2011)

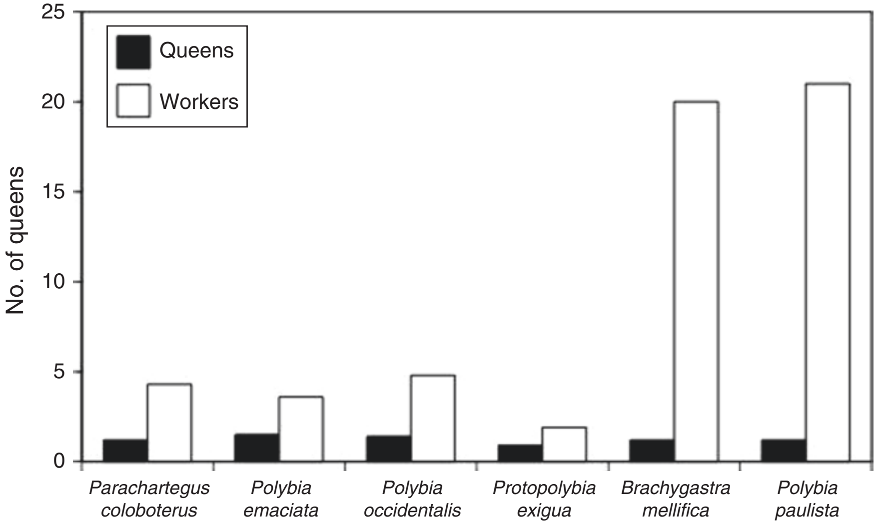

Fig. 7.7 Comparison of the effective number of queens that produced queens and workers in Epiponine wasps. (See Table 7.1)

(2005a, b) also tested another likely factor that can increase relatedness within nestmates under polygyny, i.e., comb partitioning by queens in *P. paulista*. If queens concentrate their egg laying on one or a subset of the available combs, then workers may be able to rear closer relatives by focusing their work on the comb where they emerged. In *P. occidentalis*, pupae within combs are significantly more closely related to each other than they are to pupae in other combs (Queller et al. 1993b). However, comb partitioning by queens was not supported in *P. paulista*.

In addition to female wasps, genetic relatedness among males was estimated in *P. paulista*. Kudô et al. (2013) reported that relatedness within males averaged 0.431 ± 0.050, which did not differ significantly from 0.5 (a possibility that a single mother contributes to male production). However, there were several alleles at least in one locus, suggesting that more than one queen produced males in each colony, as the cyclical monogyny predicts.

7.6 Nestmate Recognition

Nestmate recognition is well developed in many social insect species. However, social insect recognition systems can be dynamic and modulated in response to context-specific cues. In ants, for example, nestmate recognition can vary with colony-specific factors, such as colony size (Stuart 1991), stage (Balas and Adams 1996), and queen number (Starks et al. 1998; Vander Meer and Alonso 2002), in addition to environmental factors, such as proximity to other colonies (Heinze et al. 1996), experience with the intruding colony (Sanada-Morimura et al. 2003), and the time of year (D'Ettorre et al. 2004; Brandt et al. 2005). In social wasps, the effect of queen number on nestmate recognition has been investigated in an epiponine wasp, *Parachartergus colobopterus*, for the first time (Gastreich et al. 1990). Gastreich et al. (1990) conducted both laboratory and field recognition bioassays of this species and found no evidence that females had the ability to discriminate nestmates from non-nestmates. The authors proposed that if recognition cues are genetic, nestmate discrimination would be harder to achieve when relatedness is low. In *P. paulista*, Kudô et al. (2007) conducted a field study to examine whether workers discriminate between nestmate and alien workers. Most workers were accepted from their own colony, while all of alien workers were aggressively chased, bitten, stung, and ultimately rejected by recipients. Therefore, it was concluded that *P. paulista* workers are able to discriminate nestmates from non-nestmates.

Kudô and Zucchi (2008) examined whether *P. paulista* workers exhibit seasonality on tolerance of alien workers. There are growing evidences that social insect colonies change the acceptance rate of alien-conspecific individuals over the seasons, possibly due to the reduced costs of defense from intraspecific and social parasitism (honeybee, Bell et al. 1974, Downs and Ratnieks 2000; ants, Brunner et al. 2002, D'Ettorre et al. 2004, Brandt et al. 2005; wasp, Gamboa et al. 1991). However, the results by Kudô and Zucchi (2008) did not support it; *P. paulista* colonies did not accept any workers from alien colonies during winter as well as summer (Fig. 7.8).

In *P. paulista*, it has been examined whether young wasps acquire the colony-specific odor shortly after their emergence. Nestmates are characterized by a distinct chemical label (colony odor), which is determined by the interaction of genetic and environmental cues (Downs and Ratnieks 1999). Early in adult life, each colony member must learn these chemical labels and act to determine the colonial membership of other individuals encountered (Gamboa et al. 1986). Kudô and Zucchi

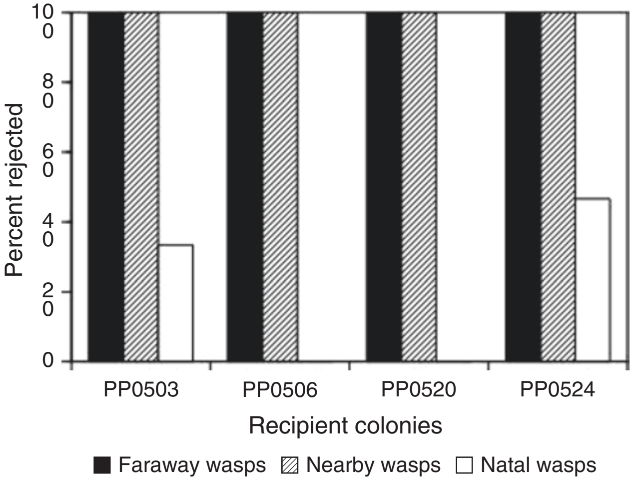

Fig. 7.8 Percentages of faraway wasps, nearby wasps, and natal wasps (control) rejected from four recipient colonies (Kudô and Zucchi 2008)

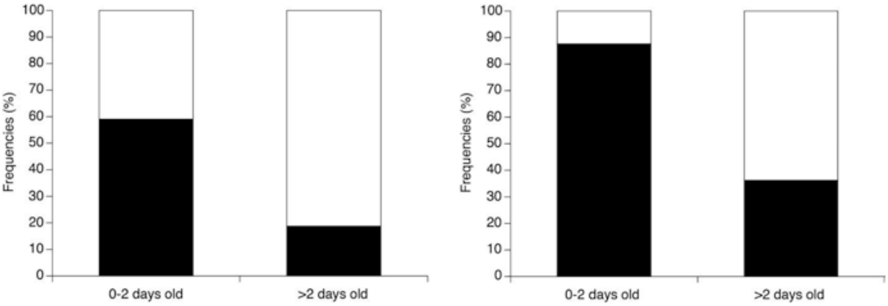

Fig. 7.9 Comparisons in frequencies of acceptance into alien recipient colonies for two age cohorts of donor males (left) and females (right) (Kudô and Zucchi 2006; Kudô and Zucchi 2008)

(2006) and Kudô et al. (2007) tested the possibility whether newly emerged individuals are accepted from alien colonies in *P. paulista*. As expected, the percent acceptance of young male and female wasps into alien colonies decreased as a function of their age (Fig. 7.9). These studies suggest that newly emerged individuals of *P. paulista* express colony-specific chemical odors shortly after emergence, as demonstrated by chemical analyses in independent-founding wasps (Paneck et al. 2001; Lorenzi et al. 2004). However, there is a result that the acceptance rate of newly emerged female wasps by alien colonies was pretty lower by male-producing colonies than worker-producing colonies (Kudô et al. 2010). Kudô et al. (2010) mentioned that the male-producing colonies abandoned soon after the field experiments, suggesting that those recipient workers rejected the introduced female wasps due to the absence of colony expansion.

Recently, whether the workers of *P. paulista* recognized their own larvae when presented outside the nest comb was investigated (Kudô et al. 2017). Behavioral tests showed that workers did not bite non-nestmate larvae more frequently than their nestmate larvae. However, they spent significantly more time licking with their nestmate larvae than with non-nestmate larvae. Kudô et al. (2017) also compared the cuticular chemical profiles of fifth instar larvae from different colonies. Analyses of the cuticular extracts of fifth instar larvae from the experimental colonies significantly allocated (100%) in their predicted groups, suggesting that discrimination of own larvae by the workers may be mediated by colony-specific, larval-borne cues. This was the first study that nestmate larval recognition could be evolved not only in independent-founding wasps (Paneck and Gamboa 2000; Cotoneschi et al. 2007) but also in colonies with many matrilines, as *P. paulista* colonies have.

7.7 Conclusions and Perspectives

P. paulista exhibits seasonal changes in colony population, which is tightly linked with foraging activities of workers. In summer between November and April, colonies produce lots of adults quickly, which is ensured by high foraging rates by workers. However, such activities may be sometimes limited because high rates of parasitism by gregarines during summer may make a part of workers idleness, as shown in *P. occidentalis*. In contrast, great proportion of colonies does not rear any brood during winter. Although it has been supported that colonies of *P. paulista* exhibit cyclical monogyny, it is unknown that changes in queen number are associated with the seasonality. Reducing to a single queen will impose some potential costs to the colony, such as the sudden loss of the remaining queens and/or loss of colony productivity. If this is the case in *P. paulista*, the reduction of queen number may not occur in the colony's growing season, i.e., summer. However, my unpublished work shows that there is no association between relatedness among workers (queen number) and seasonality.

Nestmate recognition by workers of *P. paulista* is stable throughout the year. Reeve (1989) developed the optimal acceptance threshold model to describe nestmate recognition plasticity, whereby the acceptance threshold varies according to context, to balance the fitness costs of accepting non-nestmates and rejecting nestmates. For example, in the independent-founding wasp *Polistes fuscatus*, female wasps were the most aggressive toward both nestmates and non-nestmates late in the colony cycle, possibly so as to defend nectar in the nest from conspecific intruders (Gamboa et al. 1991). In swarm-founding wasps, it has been not known that intruders enter to conspecific alien colonies to steal nectar and/or brood in the nest. It should be investigated whether CHC compositions of workers in *P. paulista* change among different seasons or colony development. Moreover, the correlation between CHCs and fertility should be needed in future works.

In the Neotropical regions, 70% of the species of social wasps (mostly Polistinae) are endemic (Noll et al. 2018). The most important threats to social wasps are the loss of their biodiversity in response to anthropogenic activities. Habitat loss due to landscape fragmentation, pesticides, and invasive species is related to reasons implicating in the species decline. Until just only 10 years ago, there had been so many diverse social wasp colonies not only in downtown area in Ribeirão Preto city but also in the campus of the Universidade de São Paulo, which is relatively conserved area. Since then, however, diversification and abundance of social wasps including *Polybia paulista* are seriously reduced. In fact, a journal *Neotropical Entomology* had a special section in 2018 ("Social insects in the Neotropics"), which informs us the importance of diversity of social insects in the Neotropics. As well as other social wasps, *Polybia paulista* should be conserved and understood in their unknown biology.

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