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ECOLOGY, BEHAVIOR AND BIONOMICS

Reproductive Status of Females in the Eusocial Wasp *Polistes ferreri* Saussure (Hymenoptera: Vespidae)

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Abstract

In the subfamily Polistinae, caste dimorphism is not pronounced and differences among females are primarily physiological and behavioral. We investigated factors that indicate the reproductive status in females of *Polistes ferreri* Saussure. We analyzed females from nine colonies and evaluated morphometric parameters, ovarian development, occurrence of insemination, relative age, and cuticular chemical profile. The colony females showed three kinds of ovarian development: type A, filamentous ovarioles; type B, ovarioles containing partially developed oocytes; and type C, long and well-developed ovarioles containing two or more mature oocytes. The stepwise discriminant analysis of the cuticular chemical profile showed that it was possible to distinguish the three groups of females: workers 1, workers 2, and queens. However, the stepwise discriminant analysis of the morphological differences did not show significant differences among these groups. The queens were among the older females in the colony and were always inseminated, while the age of the workers varied according to the stage of colony development.

Introduction

The order Hymenoptera is one of the most diverse groups of insects, with approximately 130,000 species, including bees, wasps, and ants. Wasps of the family Vespidae are extremely important for understanding the origin and evolution of social behavior in insects (Markiewicz & O'Donnell 2001) because the group includes a range of solitary and eusocial species (Evans & West-Eberhard 1970, Wilson 1971, Carpenter 1991). In this family, caste distinction is an essential evolutionary feature, since the presence of large differences between castes indicates a higher degree of sociability (Jeanne 2003).

The patterns of caste development among the families of social wasps vary widely. In the subfamily Stenogastrinae, for example, queens are similar in size to the workers and show only physiological and behavioral differences (Pardi & Piccioli 1981, Turillazzi 1991). In the Vespinae, the queen is larger than the workers, i.e., the caste differences are typically pronounced (Spradbery 1991). Members of the subfamily Polistinae show an intermediate condition between the other two subfamilies (Carpenter 1982), and its species range from those with morphologically similar castes to others with very distinct castes (Richards 1978, O'Donnel 1998).

Although caste differences in Polistinae are less evident than those in Vespinae (Spradbery 1973), the morphological and behavioral characteristics can be quite different among species (Jeanne 1980, Jeanne *et al* 1995). This distinction between castes can be determined in two ways. In the pre-imaginal stage, the caste is determined before the individual emerges and usually morphological differences are present. Pre-imaginal caste determination occurs in more-derived species (Hunt 1991, O'Donnel 1998). The other, post-imaginal, occurs in less-derived species, in which the caste is determined at least in part when the wasp is an adult. Generally in these species, morphological differences are small or absent (Gadagkar 1991).

Several studies have examined caste distinctions in Polistinae. For the tribe Polistini, studies have involved behavioral aspects, ovarian development, morphology and cuticular hydrocarbon profile of *Polistes* females (Strassmann *et al* 1984, Solis & Strassmann 1990, Dani 1994, Giannotti & Machado 1999, Gobbi *et al* 2006, Tannure-Nascimento *et al* 2008, Torres *et al* 2009). Studies analyzing the determination, differentiation, and characterization of castes in Mischocyttarini were also performed (Noda *et al* 2001, Torres *et al* 2012, Murakami *et al* 2009, 2013). All these studies involved behavioral analyses. In the tribe Ropalidiini, the best known species is *Ropalidia marginata* (Fabricius), for which studies range from behavioral aspects of caste and chemical communication to determination and caste differentiation (Gadagkar & Joshi 1983, Gadagkar *et al* 1991, Premnath *et al* 1996, Gadagkar 2001, Mitra *et al* 2011, Mitra & Gadagkar 2012). Other studies that investigated the division of labor in this tribe were performed with *Ropalidia rufoplagiata* (Cameron) (Sinha *et al* 1993) and *Ropalidia romandi* (Le Guillou) (Fukuda *et al* 2003).

The ability of colony individuals to recognize each other is an important factor in establishing and maintaining reproductive dominance. Communication by means of chemical compounds is the most widely used recognition mechanism in colonies of social wasps, as well as in other social insects (Matthews & Matthews 2010, Bagnères & Blomquist 2010). The compounds involved in this type of communication and identified as acting in intra- and interspecific recognition are the cuticular hydrocarbons (CHCs), which have received increased attention in recent decades (Monnin 2006, Bagnères & Blomquist 2010).

Cuticular hydrocarbons are constituents of the lipid layer that composes the insect cuticle and acts to prevent desiccation (Lockey 1988) and to form a barrier against microorganisms (Provost *et al* 2008). CHCs also act as contact pheromones, allowing identification of conspecifics; this attribute helps to maintain the colony hierarchy and identify the physiological status (Monnin 2006, Provost *et al* 2008), functioning as a specific chemical signature of the individual.

Several studies have demonstrated the importance of CHCs for the recognition of the role individuals have in the colony (Dapporto *et al* 2004), recognition of nestmates (Layton *et al* 1994, Tannure-Nascimento *et al* 2007, Antonialli-Junior *et al* 2007), reproductive status (Sledge *et al* 2001, Monnin 2006), and fertility (Izzo *et al* 2010). Such studies have highlighted the role of the cuticle chemical composition in establishing and maintaining the colony hierarchy (Dapporto *et al* 2005, Cotoneschi *et al* 2009).

According to Monnin (2006) there is a strong correlation between the reproductive status and the CHC profile in social insects, which is important for the establishment and recognition of reproductive dominance in colonies of species with independent foundation, as in many Polistinae. In these species, it was formerly believed that the queen maintains her reproductive status only by behaving aggressively towards other females. However, in recent decades, many studies have demonstrated the importance and role of CHCs in communication among members of the colony and in maintaining the status of the queen (Bonavita-Cougourdan *et al* 1991, Peeters *et al* 1999, Liebig *et al* 2000, Sledge *et al* 2001, Dapporto *et al* 2005).

Polistes ferreri (Saussure) is a Neotropical eusocial wasp found in Brazil, Argentina, Uruguay, and Bolivia (Richards 1978). Studies with this species have examined foraging activity (Andrade & Prezoto 2001, De Souza *et al* 2008), the role of males in the colony (Sinzato *et al* 2003), dominance relationships in the colony (Tannure & Nascimento 1999, De Souza *et al* 2010), the colony cycle aspects, strategy for colony founding, and the use of comb cells (Sinzato *et al* 2011). Few studies have analyzed the reproductive status and CHC profile, especially in Neotropical species of the social wasps.

Among the techniques used to measure the CHC profile in social insects, gas chromatography-mass spectrometry (GC-MS) is most often used (Dietermann *et al* 1992). GC-MS is reliable and provides a sensitive quantitative analysis; however, it requires several steps of sample preparation and a lengthy process to quantify each hydrocarbon present in the sample. Recently, Fourier transform infrared photoacoustic spectroscopy (FTIR-PAS) has been used; this technique is able to identify different types of compounds to study the distinctions among castes, sexes, and species of ants (Antonialli-Junior *et al* 2007, 2008) and acquisition of the chemical profile in polistine parasitic wasps (Neves *et al* 2012, 2013).

This study applied a new analytical method to the chemical profiling of social wasps by adding morphological and physiological analyses to test the hypothesis that the ovary development leads to a difference in the chemical profile of *P. ferreri* females.

Material and Methods

Nine colonies of *P. ferreri* were collected in Mundo Novo, MS (23°56′23″S, 54°17′25″W) from April 2011 through March 2012, and 90 females were evaluated. Three colonies were in the pre-emergence stage, five in post-emergence (pre-male), and one in post-emergence (post-male), according to the classification proposed by Jeanne (1972).

After the colonies were collected, the gaster of each female was placed in an individual Eppendorf vial containing absolute ethyl alcohol (PA 99.8%) for checking the ovary development stage, insemination, and relative age. The rest of the body was preserved by freezing and later used for morphometric analysis and CHC profiling. Thus, the status of each female was determined by means of several combined parameters.

Ovaries were classified according to the stage of ovariole development stage based on Baio *et al* (2003a) in workers,

Table 1 Peaks analyzed for separation of the groups of *Polistes ferreri* females based on the cuticular chemical profile. Wave number, coefficients of the two canonical roots, functional group, and vibrations mode of the peaks in the infrared absorption spectra of the thorax of females for analysis of the effect of ovarian development in *P. ferreri*.

Peak	Wave number (cm^{-1})	Canonical root 1	Canonical root 2	Functional group	Vibration mode
(1)	667[a]	1.002	0.472	Out of plane	Bending
(2)	895[a]	1.843	0.154	Out-of-plane C–H (benzene)	Bending
(3)	953[a]	−1.250	1.183	Out-of-plane C–H (benzene)	Bending
(4)	1030[a]	−2.597	−1.436	In-plane C–H (benzene)	Bending
(5)	1076[a]	1.660	2.183	In-plane C–H (benzene)	Bending
(6)	1115	–	–	In-plane C–H (benzene)	Bending
(7)	1157[a]	−0.771	−3.649	In-plane C–H (benzene)	Bending
(8)	1238[a]	0.328	3.259	–C–N	Stretching
(9)	1377	–	–	$C–CH_3$	Symmetric bending
(10)	1450	–	–	CCH_3	Symmetric bending
(11)	1524	–	–	–N–H	Bending
(12)	1651	–	–	–C=O	Stretching
(13)	2634[a]	−1.240	1.083	C–N and $C–CH_3$	Asymmetric bending scissors
(14)	2877	–	–	–C–H (CH_3)	Asymmetric stretching
(15)	2962[a]	1.257	−4.449	–C–H (CH_3)	Asymmetric stretching
(16)	3082[a]	−1.760	1.727	–N–H	Overtone bending
(17)	3290[a]	0.359	2.010	–N–H	Stretching

[a] Meaningful peaks for separating the groups of females.

females with filamentous or partially developed ovarioles; and queens, females with fully developed ovarioles. The insemination status was checked by staining the spermatheca in a 1:1 solution of acid fuchsin (1%) for observation of sperm cells under a light microscope.

Nine morphometric measurements were made on each female, modified from Shima *et al* (1994) and Noll *et al* (1997): *head*: width (HW), minimum interorbital distances (IDx); *mesosome*: width, length, and height of mesoscutum (MSW, MSL, and MSH, respectively); *metasome*: basal and apical heights of tergite 2 (T_2BH and T_2AH), length of tergite 2 (T_2L); and *wing*: partial length of the forewing (WL).

The relative age was determined according to the pigmentation of the transverse apodeme, as follows: LY (light yellow), LB (light brown), DB (dark brown), and BA (black). According to Richards (1971) and West-Eberhard (1973), this color sequence indicates a progression in the age of individuals.

For cuticular chemical profile analysis, the thorax of each female was analyzed by FTIR-PAS after drying for 48 h in a vacuum oven to minimize the water content following

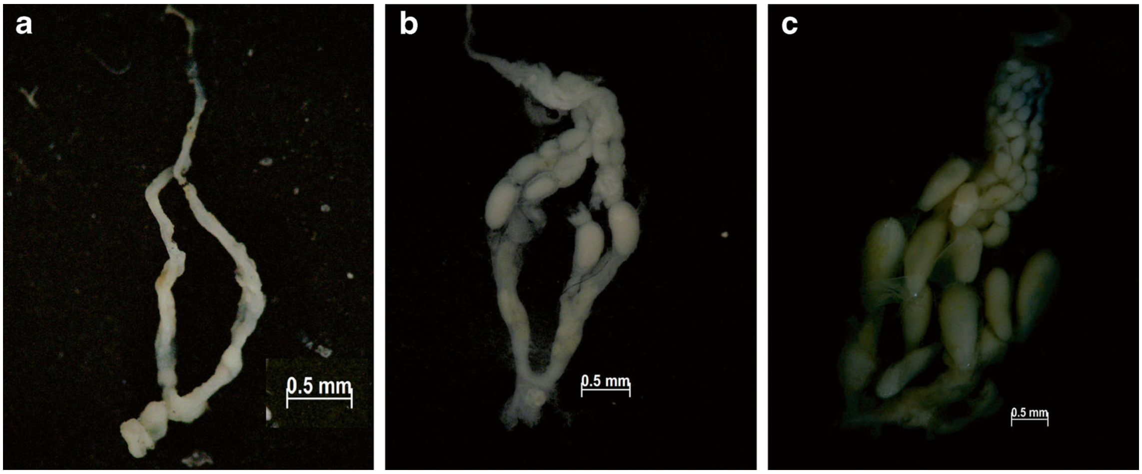

Fig 1 Three types of ovary development found in females of *Polistes ferreri*. **a** Filamentous ovarioles without visible developed oocytes. **b** Ovarioles containing partially developed oocytes. **c** Well-developed, longer ovarioles containing two or more mature oocytes.

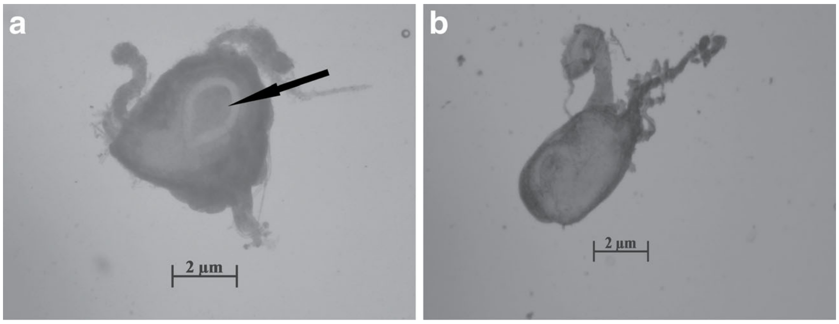

Fig 2 Spermatheca of females of *Polistes ferreri.* **a** Inseminated, with the *arrow* indicating the sperm package. **b** Not inseminated.

Antonialli-Junior *et al* (2007, 2008) and Neves *et al* (2012). The FTIR-PAS technique measures the radiation absorbed by the sample. The radiation absorbed by the sample (thorax) in the mid-infrared spectral region, including wavelengths from 400–4000 cm^{-1}, was used. Thus, it was possible to identify and distinguish molecular radicals and chemical bonds in the samples.

For statistical analyses, values corresponding to 17 peaks of absorbance in each absorption spectrum were used, which represent the compounds of the cuticle, mainly CHCs. These peaks were defined by Antonialli-Junior *et al* (2007) and are listed in Table 1 with their respective wave number, functional group, and vibrancy mode.

The discrimination among defined groups of females was based on the degree of ovarian development, morphometric data, and the cuticular chemical profile. These differences were evaluated by stepwise discriminant analyses and revealed the group of variables that best explains the evaluated groups in case of a difference, which is indicated by Wilks' lambda, a measure of the difference, if any, between the groups (Quinn & Keough 2002). For all analyses, the variable was considered significant when the level reached was <0.05, and calculations were performed in Systat 11 software.

Results

After the evaluation of the ovary development (Fig 1) and the insemination status (Fig 2), the females were categorized into three groups: workers 1: females with filamentous ovarioles without visible development of oocytes (type A), which could be inseminated or not; workers 2: females containing partially developed ovarioles (type B), inseminated or not; and queens: females with fully developed ovarioles containing two or more mature oocytes (type C) and that were always inseminated.

Type A ovaries were found in 21.1% of females, type B in 68.9%, and type C in 10% (Table 2). In 77.8% of the colonies, only one inseminated female was present (Fig 2 and Table 2), except colonies 3 and 4, which had four and two inseminated females, respectively, with ovarian development type A or B. However, in each of these colonies, only one female was the queen, with type C ovary and inseminated (Fig 1c and Table 2). In all colonies analyzed, regardless of stage, most females had partially developed ovarioles (type B).

From the spectra analyzed by FTIR-PAS, a mean curve (Fig 3 and Table 1) was constructed for each group of females (workers 1, workers 2, and queens). The curves showed 11 peaks that were meaningful for separation of the groups,

Table 2 Number of females with different types of ovary development present in the colonies of *Polistes ferreri* in different colony stages.

Colony	Colonial stage	Total number of females	Number of females inseminated	Types of ovary development		
				A	B	C
1	Post-emergence (pre-male)	19	1	7	11	1
2	Post-emergence (pre-male)	12	1	5	6	1
3	Post-emergence (pre-male)	17	4	0	16	1
4	Post-emergence (pre-male)	8	2	3	4	1
5	Post-emergence (post-male)	14	1	0	13	1
6	Pre-emergence	7	1	0	6	1
7	Pre-emergence	5	1	1	3	1
8	Pre-emergence	2	1	0	1	1
9	Post-emergence (pre-male)	6	1	3	2	1

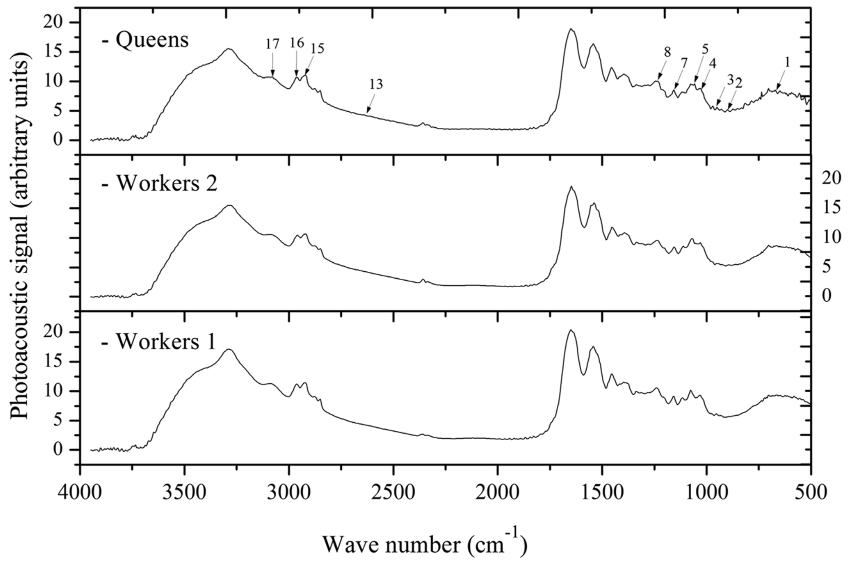

Fig 3 Mean curve for each group of absorption spectra in the mid-infrared of the thorax from females of *Polistes ferreri* grouped according to ovarian development status, indicating the significant peaks for separation of the groups.

corresponding to the functional groups of compounds formed by CHCs and chitin, which were indicated by stepwise discriminant analysis (Wilks' lambda=0.045, F=11.722, p<0.001). The chemical profiles showed a clear separation among the three groups of females (Fig 4). The first canonical root explained 78% of the results and the second 22%.

In relation to morphometric parameters, stepwise discriminant analysis (Wilks' lambda=0.757, F=4.086, p<0.001) indicated no significant differences among these three groups of females. Although the p value was low, the Wilks' lambda value was high; there was a high degree of overlap among the groups of females.

In the pre-emergence and post-emergence colony stages, older females, i.e., those with a darker apodeme, predominated (Fig 5). Younger females predominated in the colonies in the post-emergence (post-male) stage. The queens were always older females with a black or brown apodeme and, therefore, were always among the older females of the colony (Fig 5).

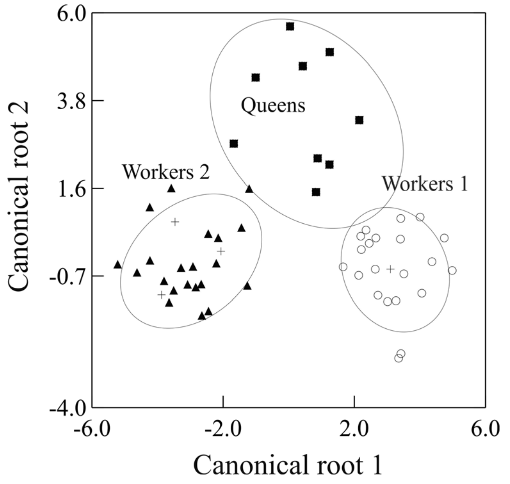

Fig 4 Dispersion diagram of the results of the stepwise discriminant analysis, showing the two canonical roots of differentiation of cuticular hydrocarbons in different groups of females of *Polistes ferreri.* All queens were inseminated; the *plus symbol* represents inseminated workers.

Discussion

We showed that *P. ferreri* colonies may contain morphologically similar females with three conditions of ovarian development, but that differ on their cuticular chemical profile.

The absence of significant morphological differences among females is a common feature of independent-foundation species (Jeanne 1986, Keeping 2000). However, differences in body size and/or physiological state can be correlated with the reproductive condition of a female (Fukuda *et al* 2003, Tannure-Nascimento *et al* 2005, Gobbi *et al* 2006, Murakami & Shima 2006). Yet, environmental changes can lead to the production of larger females that are able to survive harsher temperatures and start new colonies later, as observed in *Polistes* wasps in temperate climates (West-Eberhard 1969, Solis & Strassmann 1990, Dani 1994). The existence of little morphological differentiation among castes is also a common trait in some genera of Epiponini such as *Protopolybia*, *Parachartergus*, *Pseudopolybia*, *Polybia*, *Angiopolybia*, *Chartergellus*, and *Brachygastra* (Mateus *et al* 2004, Noll *et al* 2004).

In species with morphologically similar females, the castes are distinguished mainly at the behavioral level, where the dominant individuals specialize in certain tasks, while the subordinate individuals specialize in others (Jeanne 1986). Therefore, status is determined mostly during the adult stage, as indicated by Gelin *et al* (2008) in *Apoica pallens*

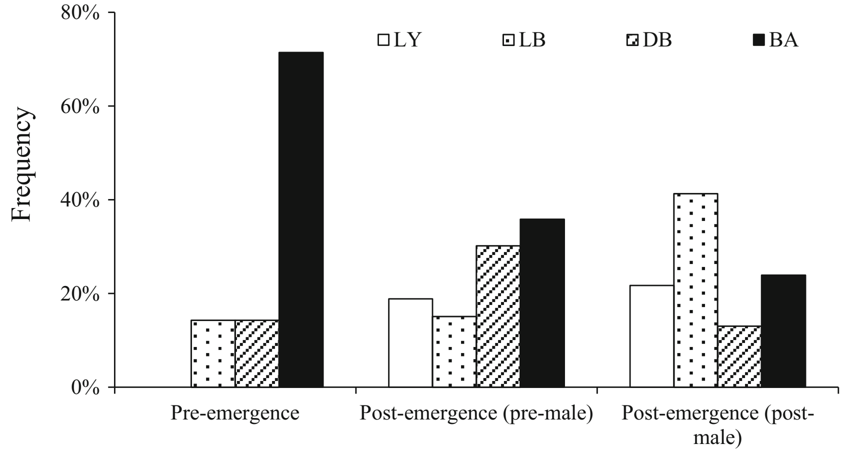

Fig 5 Frequency of the relative ages of females of *Polistes ferreri* from the nine colonies, according to the color patterns of the transverse apodeme in females from colonies of different stages. *LY*, light yellow; *LB*, light brown; *DB*, dark brown; *BA*, black.

(Lepeletier) and by O'Donnell (1998) in *Polistes* species. However, in some cases, the development of caste distinction, at least in part, may be pre-imaginal (Gadagkar *et al* 1991, Keeping 2002, Dapporto *et al* 2011, Hunt *et al* 2011).

In our study, most colonies (77.8%) had only one inseminated female. However, even in colonies with more than one inseminated female, only one had type C ovarian development, suggesting that colonies of this species contain only a single female laying eggs.

On the other hand, the other inseminated females probably would be able to replace the queen, a common feature in species of independent foundation (Murakami & Shima 2006). Thus, the difference between reproductive and nonreproductive females is flexible and complex, depending on physiological, behavioral, and ecological aspects (Murakami & Shima 2006). According to Murakami *et al* (2009), this strategy may minimize the effect of predation and parasitism, as observed in *Mischocyttarus cassununga*.

Analysis of the chemical cuticular profile indicated a variation among the three groups of females: workers 1, workers 2, and queens. This indicates that not only the physiological parameters but also the cuticle compounds are important for the recognition of the reproductive status of females. According to Monnin (2006), this relationship between reproductive status and the CHC profile is important for establishing a hierarchy in independent-foundation species. Sledge *et al* (2001) found differences among the CHC profile of alpha females, subordinates, and workers in colonies of *Polistes dominula* after the first workers in the colony emerged. These authors also reported that the removal of the alpha female leads to her replacement, and that the new female assuming this position acquires a CHC profile similar to that of the previous alpha female. Bonckaert *et al* (2012) analyzed colonies of *Vespula vulgaris* and observed that reproductive queens, spring-collected queens, virgin queens, and workers had different degrees of ovarian development, and that these corresponded to different profiles of cuticular hydrocarbons. Furthermore, females are able to recognize even subtle differences in chemical profiles (Bonavita-Cougourdan *et al* 1987, Espelie *et al* 1990, Dani *et al* 2001, Lorenzi *et al* 2004, Van Zweden & d'Ettorre 2010).

The occurrence of females with partially developed ovarioles, termed intermediate, was first reported by Richards & Richards (1951), revealing a degree of complexity in the hierarchy establishment, and thus, the role of the female in the colony. Some authors, such as Richards (1971), suggested that the role of the intermediates is to produce trophic eggs and males; however, West-Eberhard (1978) and Gastreich *et al* (1993) considered them as possible young, uninseminated queens. In any event, the degree of ovarian development coupled with the occurrence of insemination makes the position of the female in the hierarchy more evident.

According to our results (Fig 5), older females, including the queen, predominated in most colonies, as queens are among the older females of the colony (Baio *et al* 2003b, Murakami *et al* 2009, Felippotti *et al* 2010).

Therefore, in *P. ferreri*, although females do not differ morphologically, it is possible to distinguish three groups of females with significantly different cuticular chemical profiles. Most colonies had only one inseminated female; however, even in those with more than one inseminated female, only one had the degree of ovarian development typical of the queen, and these were among the older females of the colony.

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