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RESEARCH ARTICLE

Colony cycle, foundation strategy and nesting biology of a Neotropical paper wasp

Ciclo colonial, estrategia de la fundación y biología de anidación de una avispa de papel neotropical

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ABSTRACT

Polistes ferreri Saussure, 1853 is a Neotropical paper wasp often found in anthropic environments. However, there is little information available on biological, ecological and behavioral interactions of this species under these environmental conditions. This study investigated the colony cycle, foundation strategy and nesting biology of this species. From March of 2000 to February of 2004, several colonies were studied in the municipal district of Juiz de Fora, in southeastern Brazil. The colony cycle events of *P. ferreri* are concentrated in specific periods of the year. The colonies are established principally by association of females, the latter is the foundation strategy that confers the greatest success. Nidification on manmade substrates seems common for the species. The peduncle of the nest is increased in width to support the weight of colony members. Likewise, cells are increased in height, in accordance with the size of the layers of meconium, allowing accommodation of the immature. It is suggested that, at least for post-emergent colonies of *P. ferreri*, the cost of nest construction is not a factor limiting the development of the colonies. Finally, the results also support the idea that the reuse of cells is an advantageous strategy because it saves costs related to the construction of new cells.

Key words: colony productivity, colony success, foundation pattern, *Polistes ferreri*.

RESUMEN

Polistes ferreri Saussure, 1853 es una avispa de papel neotropical encontrada a menudo en ambientes antrópicos. Sin embargo, hay poca información disponible sobre las interacciones biológicas, ecológicas y de comportamiento de esta especie en estas condiciones ambientales. Este estudio investigó el ciclo de la colonia, la estrategia de fundación y la biología de anidación de esta especie. Desde marzo de 2000 a febrero de 2004, varias colonias fueron estudiadas en el municipio de Juiz de Fora, en el sureste de Brasil. Los eventos del ciclo de la colonia de *P. ferreri* se concentran en determinados períodos del año. Las colonias se establecen, principalmente, por asociación de hembras, siendo esta la estrategia que se traduce en un mayor éxito. La nidificación en sustratos artificiales parece común para la especie. El pedúnculo del nido va aumentando en ancho para soportar el peso de los miembros de la colonia. Del mismo modo, las celdas aumentan en altura, de acuerdo con el tamaño de las capas de meconio, lo que permite el alojamiento de los inmaduros. Se sugiere que, al menos para las colonias de postemergentes de *P. ferreri*, el costo de la construcción del nido no es un factor que limita el desarrollo de las colonias. Por último, los resultados también apoyan la idea de que la reutilización de las celdas es una estrategia ventajosa porque reduce los costos relacionados con la construcción de nuevas celdas.

Palabras clave: éxito colonia, fundación, *Polistes ferreri*, productividad de la colonia.

INTRODUCTION

Among the eusocial wasps (Hymenoptera, Vespidae, Polistinae), *Polistes* Latreille, 1802 has been distinguished as the genus most studied. They are cosmopolitan insects with more than

200 described species (West-Eberhard 2006). Its colonies rarely exceed 100 individuals, who live in a nest without envelope, making behavioral observations easy. Its relatively primitive social organization, shown up by the small cast differentiation and by the high potential

for reproductive conflicts between individuals (Reeve 1991), allows investigations on social evolution to be carried out. It is known that the initial stages of eusociality in arthropods could have taken place in tropical habitats (O'Donnell & Joyce 2001, Del-Claro & Tizo-Pedroso 2009). In this way, investigations on the biology of primitively social tropical wasps can help in the understanding of the evolutionary origin and maintenance of eusociality.

Comparing species of *Polistes* from several climatic zones, it is possible to verify differences as to occurrence of the colony cycle phases. In temperate regions, such events are synchronized by the climatic seasons, with foundations and desertions taking place in specific periods of the year (Yamane 1996). Differently from what takes place in temperate regions, in the tropical regions the colonies can be initiated in any season (Giannotti 1997, Prezoto 2001) and there is a tendency for desertions and clusterings to take place principally in the cold season (Gonzalez et al. 2002, Gobbi et al. 2006, Torres et al. 2009).

Another outstanding difference is observed comparing the process of colony foundation in temperate and tropical regions. In the former, the colonies are frequently begun by a single female, while in the latter, an association between founders is more common (Reeve 1991). Prezoto (2001) verified the occurrence of a paradox in the strategies of reproduction in colonies of the eusocial Neotropical wasp *Polistes simillimus* Zikan, 1951: in spite of most of the foundations having been begun by a single female (atypical standard for species of tropical regions), an association between founders was responsible for the greatest number of successful colonies. These results raise questions still not explained about how a strategy that confers less reproductive success (solitary foundation) can be more frequent (at least at the colony level) in the population than a more efficient alternative strategy (associative foundation).

During the foundation of the colonies, females of *Polistes* spp. select substrates that include twigs, leaves, dense shrubs and grass, hollow trees and elevated natural cavities and manmade structures (Wenzel 1996). Several studies have verified the nidification preference of these wasps for manmade substrates (Fowler 1983, Marques & Carvalho 1993, Lima et

al. 2000, Prezoto 2001). However, such a preference is not universal for the genus, since Clapperton & Lo (2000) observed species of *Polistes* nesting more frequently on plants, when compared with manmade substrates. Additional studies with other species of *Polistes* could explain whether nidification on manmade substrates is common for the genus or represents an exception.

In general, the basic form of the nest is simple and well known (Wenzel 1996). The pedicel is usually reinforced with additional pulp and pure salivary secretion for added support (Giannotti 1997, Prezoto 2001). If the peduncle is increased to support the weight of the colony, there must be a correlation between the size of the peduncle and the number of cells in the nest. Besides this, cells may be reused (Gobbi et al. 2009), probably as a strategy that minimizes costs of the construction of new cells.

Inagawa et al. (2001) verified that the volume of the cells in nests of *P. snelleni* de Saussure, 1862 was greater in hotter locations, if compared to colder towns in Japan, reflecting an adaptation for the accommodation of the progeny. It seems reasonable that nests of social wasps are modified for the accommodation of the progeny. Nevertheless, more empirical evidence is necessary. A prediction of this hypothesis would be an correlation between the height of the cells (from the base up to the upper limit of the opening) and the height of the layers of meconium, maintaining a relatively constant internal accommodation space.

The neotropical eusocial wasp *Polistes ferrerii* Saussure, 1853 is found in Brazil, Argentina, Uruguay and Bolivia (Richards 1978). The few studies available in the literature focus on foraging activity (Andrade & Prezoto 2001, De Souza et al. 2008) and the dominance relations between colony members (Tannure & Nascimento 1999, De Souza et al. 2010).

In this study, we attempt to answer the following questions about *P. ferrerii*: How are the phases of colony cycle distributed along the year? How females start new colonies? What substrates they use for nesting? Can architectural characteristics of the nests support the hypothesis of colony sustenance and accommodation of the progeny? Can costs of nest construction limit the development of the colony? Why females reuse cells?

METHODS

Area and period of study

Studies were conducted between March of 2000 and February of 2004, on the campus of the Federal University of Juiz de Fora, (21°46' S, 43°21' W, altitude 800 m), in the city of Juiz de Fora, Minas Gerais state, in southeastern Brazil. The area includes approximately 134.68 ha with areas of vegetation and construction.

Colony cycle

The occurrence of the different phases of the colony cycle of *P. ferrerri* was registered by means of census carried out monthly between May of 2002 and April of 2003. The terminology proposed by Jeanne (1972) was adopted, classifying the phases of development as: pre-emergence (= foundation), post-emergence, aggregation and abandoned. To check if the events of the colony cycle take place in a uniform way throughout the year, the Rayleigh test was used (Z), for circular distribution (Zar 1996). The value Z is reckoned by the formula $Z = nr^2$, where n is the number of observations and r is the length of the mean vector referring to distribution of the data. A long mean vector (that results in a high value of Z) means greater concentration of the data around the average and, thus, a lower tendency for the data to be uniformly distributed. In this case, the null hypothesis is that the events of the biological cycle in *P. ferrerri* take place in a uniform way throughout the months of the year. The distribution of frequencies of the colony cycle events was plotted in linear-circular plots, for monthly intervals, with 12 months of the year corresponding to 360° of the circumference.

Success of the foundation strategies

Weekly observations were carried out of 21 pre-emergent colonies, mainly in the beginning of the morning (6-8 AM) and end of the afternoon (5-6 PM). In each observation, the number of associated females and the phase of colony development were registered. This approach allowed for verification of the foundation strategies of *P. ferrerri* as well as the success of each of them. Two strategies of foundation were observed: solitary foundation, when a single founder was registered during all the pre-emergence phase, and associative foundation, when a particular colony was inhabited by more than one founder in this period. These reproductive strategies were considered successful when the colony reached the phase of post-emergence, characterized by the presence of cells with vestiges of cocoons that were broken by the emerged adults.

Nidification habits

For the study of nidification habits, the substrates used for the foundation and the height of the nests in relation to the ground were considered (n = 71). The areas of vegetation and the constructions present in the study area were verified.

Nest architecture

To test the hypothesis of colony sustenance, the number of cells was registered as well as the length and width

of the peduncle in 29 nests. The Spearman correlation test was used to check the association between these variables.

To test the hypothesis of accommodation of the progeny, the correlation between the height of the cells and of the respective layers of meconium was checked by the Spearman correlation test making use of 200 cells sampled from 29 nests. Besides this, the value obtained from the difference between the height of the cells and of the meconium layers, called the internal accommodation space, was registered.

Reuse of cells

In a total of 29 nests of *P. ferrerri* which produced at least one adult individual, the following parameters were measured: number of cells built; number of adults produced (from the counting of the meconium layers); ratio of adults produced per cell; number of unproductive cells; and the maximum number of generations produced in each cell. These parameters were used to suggest a possible explanation for the reuse of cells.

RESULTS

Colony cycle

The Rayleigh test demonstrated that each event of the colony cycle in *P. ferrerri* takes place principally in determined periods of the year. So, foundations take place principally in October, post-emergent colonies in February, aggregations in August and abandonments in February (Table 1; Fig. 1).

Foundation strategy success

The mean number of females involved in the process of foundation was (mean ± SE [amplitude]) around 2.33 ± 1.19 (1-5), 34.34 % (n = 7) of the colonies being established by a single female and 66.66 % (n = 14) established by more than one female. All the colonies established by the single female failed, being abandoned before the post-emergent phase. Among the colonies established by association of females, 86 % (n = 12) succeeded well.

Nidification habits

Colonies of *P. ferrerri* were found on different nidification substrates, including manmade substrates (83 %, n = 59), vegetation (14 %, n = 10), stones (1.5 %, n = 1) and a termite nest (1.5 %, n = 1). These colonies were around 3.78 ± 2.18 (0.27-7.00) meters from the ground.

Nest architecture

On average, the stalks presented 6.18 ± 1.09 (4.4-8.50) mm of height and 3.00 ± 1.40 (0.6-4.5) mm of width. Nests of *P. ferreri* reached up to 256 cells. A correlation was observed between the width of the stalk and the number of cells (Spearman's correlation test: $r_s = 0.667$, $P < 0.001$), but not for the length of the stalk and number of cells (Spearman's correlation test: $r_s = 0.118$, $P = 0.583$).

The size of the cells varied as a function of the number of meconium layers (Table 2). In this way, the greater the height of the meconium layers, the greater the height of the cell (Spearman's correlation test: $r_s = 1$, $P < 0.001$), maintaining a relatively constant internal

accommodation space of 20.33 ± 0.24 (20.33-20.80) mm.

Reuse of cells

The mean number of cells built per nest was 105.79 ± 67.48 (8-256). The mean productivity of the nests was 65.96 ± 58.36 (1-195) adults/nests, reflecting a ratio of 0.52 ± 0.22 (0.06-1.13) adults/cell. Besides this, the percentage of unproductive cells per nest was on average 54.28 ± 17.88 (24.40-93.75) %.

As to the reuse of cells, 68.96 % of the nests analyzed produced two generations in the same cell and 34.48 % of them produced three individuals in the same cell.

TABLE 1

Estimated values for the circular distributions of the colony cycle events of *P. ferreri*, in the municipality of Juiz de Fora, Minas Gerais.

Valores estimados para la distribución circular de eventos cíclicos de *P. ferreri*, en el municipio de Juiz de Fora, Minas Gerais.

	Pre-emergence	Post-emergence	Aggregation	Abandonment
Higher frequency	October	February	August	February
r	3.63	5.55	18.08	7.88
Z	11.97	11.98	11.99	11.98
P	< 0.05	< 0.05	< 0.05	< 0.05

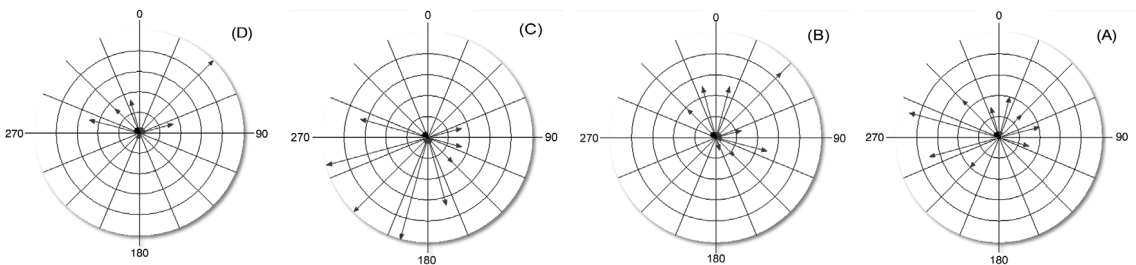


Fig. 1: Circular-linear plot of monthly frequencies (arrows) of the events of the biological cycle of *Polistes ferreri* in Juiz de Fora, Minas Gerais, southeastern Brazil. The 12 months of the year correspond to the 360° of circumference. (A) pre-emergence, (B) post-emergence, (C) aggregation, (D) abandonment.

Parcela circular-lineal de frecuencias mensuales (flechas) de los eventos del ciclo biológico de *Polistes ferreri* en Juiz de Fora, Minas Gerais, sureste de Brasil: Los 12 meses del año corresponden a 360° de la circunferencia. (A) pre-emergencia, (B) post-emergencia, (C) agregación, (D) abandono.

TABLE 2

Size of the cells and meconium layers (mm) in colonies of *Polistes ferreri* Saussure, 1853 (n = 200 cells). Mean \pm SE (amplitude).

Tamaño de las células y las capas de meconio (mm) en las colonias de *Polistes ferreri* Saussure, 1853 (n = 200 células). Media \pm EE (amplitud).

Meconium layers	Height of meconium's layers	Cells' height	N
1	2.95 \pm 0.63 (1.7-5.0)	23.28 \pm 2.91 (16.6-31.5)	111
2	4.48 \pm 1.20 (2.1-8.1)	25.28 \pm 2.98 (20.1-37.4)	75
3	6.17 \pm 1.30 (4.6-9.3)	26.84 \pm 3.48 (20.5-32.3)	14

DISCUSSION

The results suggest that each event of the colony cycle of *P. ferreri* is concentrated principally in specific months of the year, still being capable of taking place in lower proportion out of this interval (Fig. 1). The incidence of the events of the colony cycle of social wasps is influenced principally by the climatic factors that act on the colonies of a determined location (O'Donnell & Joyce 2001) and the absence of quite definite climatic seasons, common in the tropics, can reflect on the colony cycle (Young 1986). The climatic seasons in temperate regions present themselves as better defined than in the tropical regions. In the tropical regions there can be short periods during the cold season, for example, with temperatures favorable to activity of the wasps. That stimulates the occurrence of foundations in several periods of the year. Studies with other tropical species of independent foundation (Giannotti 1997, O'Donnell & Joyce 2001, Prezoto 2001, Torres et al. 2009) have been demonstrating that the events of the colony cycle do not take place in a uniform way along the year.

P. ferreri found their colonies principally by association of females. The predominance of this reproductive strategy is common for neotropical species such as *Polistes versicolor* (Olivier, 1791) and *Polistes canadensis* (Linnaeus, 1758) (Itô 1985). On the other hand, Prezoto (2001) studying colonies of the neotropical wasp *P. simillimus* verified that most of the foundations were begun by a single female. Nevertheless, the association between founders was responsible for the greatest number of well successful colonies.

This paradox raises the following question, how a strategy that confers less reproductive success (solitary foundation) can be more frequent (at least at the level of colony) in the population than a more efficient alternative strategy (associative foundation). It is possible that this apparent paradox is caused by the unit considered to establish the frequencies of each strategy, in this case, the number of foundations with one or more female. If instead of that, the total number of females who show each strategy of reproduction were considered, the results would be different. Thus, Prezoto (2001) verified that 56 % of the colonies in *P. simillimus* were established by a single female and, consequently, 44 % of the colonies were established by association of females. Thinking that each associative foundation has at least two females, at least 61 % of the females of *P. simillimus* opted for the associative foundation, while only 39 % opted for the solitary foundation. In *P. ferreri*, the predominance of the associative foundation was shown both at the colony level, and for the individual level.

If founders association strategy confers the most reproductive success, why the solitary foundation still exists in *P. ferreri*? At this point, it is just possible make speculations. Although founders association increases colony life insurance (Tibbetts & Reeve 2003), other benefits are not equally shared among associated females, because they frequently engage in dominance subordination interactions that determine the reproductive division of labour (De Souza et al. 2010). If selective pressures are low enough to permit solitary foundation success, a subordinate female could

increase their inclusive fitness by choosing this strategy. If this is true, it is expected a tradeoff between nesting strategies.

Studies that investigate the frequencies of the different strategies of foundation in social wasps must consider the individual level, since the number of solitary and associative foundations is a consequence of the decisions taken by each individual during this phase of the cycle.

The present study demonstrated that colonies of *P. ferreri* are commonly found on manmade substrates. Lima et al. (2000), describing the nidification substrates of social wasps in the same area of study verified that 96 % of the *Polistes* nests were associated with manmade substrates. The greater frequency of nidification on manmade substrates has been reported for other species of *Polistes* (Fowler 1983, Marques & Carvalho 1993, Prezoto 2001, Oliveira et al. 2010). However, it is not universal for the genus, since Clapperton & Lo (2000) observed a higher number of *Polistes chinensis antennalis* colonies Perez, 1905 and *Polistes humilis* (Fabricius, 1781) nesting on plants, when compared with manmade substrates. Differences as to the habits of nidification can still reflect interspecies variations, unequal proportions between the substrates available for nidification or even the cost benefit relation associated with nidification on each substrate, which can vary between the areas of study.

The increase of the stalk width as a function of the number of cells in the nest of *P. ferreri* seems to constitute an adaptation so that the nest supports the weight of the colony in expansion. This hypothesis has been confirmed by other studies (Giannotti 1997, Prezoto 2001). The correlation between the size of the cell and the size of the layer of meconium, as well as the maintenance of an constant internal space in the cells in nests of *P. ferreri* suggests that cells with meconium are increased to accommodate the following generation of immature.

The occurrence of unproductive cells in nests of *P. ferreri* supports the idea that, at least for post-emergent colonies, the costs with the construction of the nest are not a factor limiting the development of the colonies of *P. ferreri*. De Souza et al. (2008), studying the foraging activity of this species, verified that the duration of the trips for collection of building materials for the nest was less than the duration of trips for collection of materials for food

(carbohydrates and prey), suggesting a greater energetic expense for forage of nutritional resources than for building materials.

An alternative hypothesis suggests that the reuse of cells is an advantageous strategy because it saves costs related to the construction of new cells. It is a prediction of this hypothesis that there must be more reuse of the cells in the species where the nest construction costs are greater. The percentage of unproductive cells was higher for colonies of *P. ferreri* (54.28 %) when compared to colonies of *P. versicolor* (44.5 %) (Oliveira et al. 2010). Proceeding from the assumption that a higher percentage of unproductive cells means less cost associated with construction of the nest, it is possible to infer that the costs with the construction are less for *P. ferreri*, when compared to *P. versicolor*. Gobbi et al. (2009) and Oliveira et al. (2010) verified that the cells in nests of *P. versicolor* can be re-used up to six times, this value being higher than that observed in colonies of *P. ferreri*. In this way, as predicted by the hypothesis, a greater reuse of the cells takes place in *P. versicolor*, in comparison to *P. ferreri*, since the costs of the nest construction are greater for the first in comparison with the second species.

It can be concluded that the events of the colony cycle of *P. ferreri* are concentrated principally in determined periods of the year. The colonies are established principally by association of females, this being the strategy of reproduction that provides greater success. The nidification on manmade substrates seems common for the species. The stalk of the nest is increased in width to support the weight of the members of the colony. Likewise, cells are increased in height, in accordance with the size of the layers of meconium, allowing the accommodation of the immature. It is suggested that, at least for post-emergent colonies of *P. ferreri*, the nest construction costs are not a factor limiting the development of the colonies. Finally, the results also support the idea that the reuse of cells is an advantageous strategy because it saves costs related to the construction of new cells.

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