Sociobiology 64(1):105-110 (March, 2017) DOI: 10.13102/sociobiology.v64i1.1142

Sociobiology
An international journal on social insects

RESEARCH ARTICLE - WASPS

Opportunistic Strategies for Capture and Storage of Prey of Two Species of Social Wasps of the Genus *Polybia* Lepeletier (Vespidae: Polistinae: Epiponini)

KB Michelutti[1], ERP Soares[1,], F Prezoto[2], WF Antonialli-Junior[1]

1 - Laboratório de Ecologia Comportamental (LABECO), Universidade Estadual de Mato Grosso do Sul, Dourados, Mato Grosso do Sul, Brazil

2 - Laboratório de Ecologia Comportamental e Bioacústica (LABEC), Universidade Federal de Juiz de Fora, Minas Gerais, Brazil

Article History

Edited by
Marcel G. Hermes, UFPR, Brazil
Received 07 June 2016
Initial Acceptance 24 October 2016
Final Acceptance 14 December 2016
Publication date 29 May 2017

Keywords
Foraging, Nectar Storage, Prey, Swarming Wasps.

Corresponding author
Kamylla Balbuena Michelutti
Programa de Pós Graduação em Recursos Naturais
Laboratório de Ecologia Comportamental (LABECO)
Universidade Estadual de Mato Grosso do Sul
CEP: 79804-970, Dourados-MS, Brasil
E-Mail: kamylla_michelutti@yahoo.com.br

Abstract

Foraging activity in social wasps is a complex behavior that involves the ability to locate and transport the necessary resources for the colony. This activity is opportunistic and generalist, sometimes adapting to the availability of resources when colonies are exposed to critical environmental conditions. This study aimed at evaluating the opportunistic behavior of two species of *Polybia* wasps for prey capture and storage in the form of flights of winged individuals. Five colonies of *Polybia occidentalis* (Olivier) and two colonies of *Polybia paulista* (L.) were analyzed. Six of them contained stored winged individuals of termites, and one contained winged specimens of ants. The results indicated that these two species practice an opportunistic foraging strategy and they are able to store large quantities of protein resources in their colonies.

Introduction

Foraging activity is considered one of the most important and complex behaviors exhibited by social wasps (Lima & Prezoto, 2003), and it is dependent on the ability of the insects to interact with the environment, as well as the availability of essential resources to support the colony (Gomes et al., 2007). Most species of predatory social insects obtain the necessary protein resources for the development of the colony by capturing other insects, especially immature beetles, termites, and lepidopterans (Rabb & Lawson, 1957). Social wasps collect nectar and pollen in flowers, and prey on other arthropods, especially lepidopteran caterpillars (Prezoto et al., 2007).

The essential skills required to capture the prey during foraging activity include the ability to recognize the target, capture and transport it. These attributes in social wasps have been investigated in several studies, cited in the review of Richter (2000). Foraging activities present significant risks to the workers, due to the high energy costs and the greater exposure to predators that ultimately affects longevity (O'Donnell & Jeanne, 1995). Workers of *Mischocyttarus mastigophorus* (Richards) are responsible for the execution of riskier or more stressful tasks, at higher rates, compared to the dominant insects (O'Donnell, 1998). Hence, when social wasps find an abundant resource they predominantly forage on this food source (Santos et al., 2007).

An abundant resource is available when termite and ant colonies release their winged forms, and there is documented evidence of social wasp foragers attacking termites during the flight of the winged individuals (Mill, 1983). This foraging activity in social insects involves the recruitment of nest mates to an area where a higher concentration of workers is required, optimizing the acquisition of resources for the

ISSN: 0361-6525

colony by increasing the number of foragers exploiting a particular resource (Wilson, 1971).

Social wasps employ a solitary opportunistic foraging strategy (Jeanne et al., 1995), in which foragers often return to forage in a fruitful location (Richter, 2000). In order to optimize this form of foraging, signals can be exchanged between nest mates to facilitate the collection of resources to the colony (Taylor et al., 2011). This behavior has been reported in colonies of *Polybia occidentalis* (Olivier) (Hrncir et al., 2007; Schueller et al., 2010). Therefore it is evident that social wasps exhibit opportunistic generalist behavior, and that they can forage according to their previous experiences (Richter, 2000).

After locating and capturing prey, workers cut them into pieces, then chew the materials and distribute them to offspring (Gomes et al., 2007). In some cases, they can store food source, such as nectar, together with parts of prey (Silveira et al., 2005). According to Ross and Hunt (1988), nectar storage can be performed in two ways: i) storage in empty cells that can generally be observed during the cold season, as it has been described in colonies of *Polybia paulista* (Von lhering) (Machado, 1984); ii) storage in cells occupied by eggs or small larvae, as observed in colonies of *Mischocyttarus drewseni* (Saussure) (Jeanne, 1972), *Polistes simillimus* (Zikán) (Prezoto & Gobbi, 2003), and *Mischocyttarus cassununga* (Von Ihering) (Guimarães et al., 2008).

The capture and storage of prey and other materials in social wasp nests is still a relatively unexplored subject, with only a few reported studies (Machado, 1977; Mill, 1983; Gobbi et al., 1984; Prezoto et al., 2005; Taylor et al., 2011), so the aim of this study is to describe an opportunistic strategy of prey capture and storage in two species of social wasps of the genus *Polybia*.

Material and Methods

Seven colonies of two species of social wasps were collected and analyzed: five colonies of *P. occidentalis* and two colonies of *P. paulista.* The number of colonies and sampling sites are provided in Table 1. The colonies were collected after 19:00 to ensure that all individuals were in the nest, using the method by Machado (1984). All members of the colony were recorded following sacrifice by storage in a freezer (-20 ºC) for 24 hours.

To identify the type, quantity, and location of prey, the nests were dissected layer by layer. Evaluation of the influence of nest size on the manner and location of storage was performed by calculating the area of each layer using the formula $A=\pi*a*b$, where a and b are the semi-major and semi-minor axes of an ellipse, since the nests of this species can be regarded as being ellipsoidal.

The number of foragers was estimated for each colony, using as a defining parameter the fact that these are workers between intermediate and older ages, as proposed by Giannotti (1997). The relative ages of the workers were confirmed using the progressive pigmentation of the apodeme of the fifth gastral sternite, which according to Richards (1971) provides an indication of age progression. After confirmation of the workers age, the total number of foragers was estimated for each colony.

In two colonies of *P. occidentalis* it was only possible to identify the types of prey captured, because the nest structure was lost due to problems at the time of collection. The number of preys captured by each forager was estimated by calculating the total number of prey divided by the total number of foragers in each colony. A linear correlation test was used to evaluate if there was a relationship between the number of foragers in the colony and the number of stored prey.

Table 1. Species and collection date and location of colonies with stored termite and ant winged.

Colony	Specie	Date	Location
01*	*Polybia occidentalis*	08/11/13	Ribeirão Preto/SP
02*	*Polybia occidentalis*	16/11/13	Nova Alvorada do Sul/MS
03	*Polybia occidentalis*	26/11/13	Dourados/MS
04	*Polybia paulista*	01/01/14	Ponta Porã/MS
05	*Polybia paulista*	04/02/14	Dourados/MS
06	*Polybia occidentalis*	07/02/14	Dourados/MS
07	*Polybia occidentalis*	09/03/14	Ponta Porã/MS

*Colony in which it was not possible to quantify the stored material.

Results and Discussion

Stored winged termites were found in four colonies of *P. occidentalis* and two colonies of *P. paulista*, while winged ants were only found in one colony of *P. occidentalis* (Table 1). This showed that these wasps employed an opportunistic strategy, taking advantage of the moments when colonies of termites and ants released winged individuals, in accordance with Mill (1983), who documented social wasps preying on winged social insects in flight.

Winged termites of the subfamily Apicotermitinae were found in all the colonies, with five termite species in colonies 1 and 5, four species in colony 6, two species in colony 2, three species in colony 3, and one species in colony 4. A species of Nasutitermitinae was found in colony 3. Winged ants were only found in colony 7 and could not be identified because only males were found.

The preys were mainly stored in the periphery of the different layers of the combs, inside and outside of empty cells, with rare exceptions in the central regions. In most cases, one prey was stored per cell, although up to three preys could be found in a single cell in the comb. In some cases, they were stored mixed with nectar, both singly and in sets with more than two individuals (Figures 1a and 1c). Preys were also found stored in the form of combined masses of winged and nectar, located in the periphery of the nest (Figure 1b). Molan (1999) reported that chemical compounds present in the nectar, such as flavonoids and aromatic acids, can inhibit microorganisms responsible for decomposition. Hence, this form of storage could reduce proliferation of pathogenic microorganisms within the colony. This would favor the opportunistic strategy, with collection of a relatively high number of preys that would not be consumed immediately, and in the long term could reduce the pressure to forage for proteins.

Most of the preys were lacking various body parts such as wings, head, legs, and antennae (Figure 1d), suggesting that preys were processed by workers, or alternatively it might have been a consequence of the process of capture and transport of the prey, as noted in *Polybia sericea* (Olivier) by Machado et al. (1988).

The total area of the nest, the number of adults, the estimated load capacity of each foraging action, and the number of stored prey are presented in Table 2. Based on these data, it can be inferred that the weight of the prey was not responsible for its selection for capture, because workers of *P. occidentalis* are supposedly able to carry up to 75% of their own weight (Hunt et al., 1987). It appears, therefore, that in this case, the main factor involved in prey selection was the opportunistic strategy. The winged were the most abundant prey at that moment, and for this reason the most captured and stored. This was supported by the load capacity (Table 2), since Hunt et al. (1987) noted that although foragers of *P. occidentalis* captured larvae of Lepidoptera in most of their travels, at certain times of the year other items were abundant and were also brought to the colony.

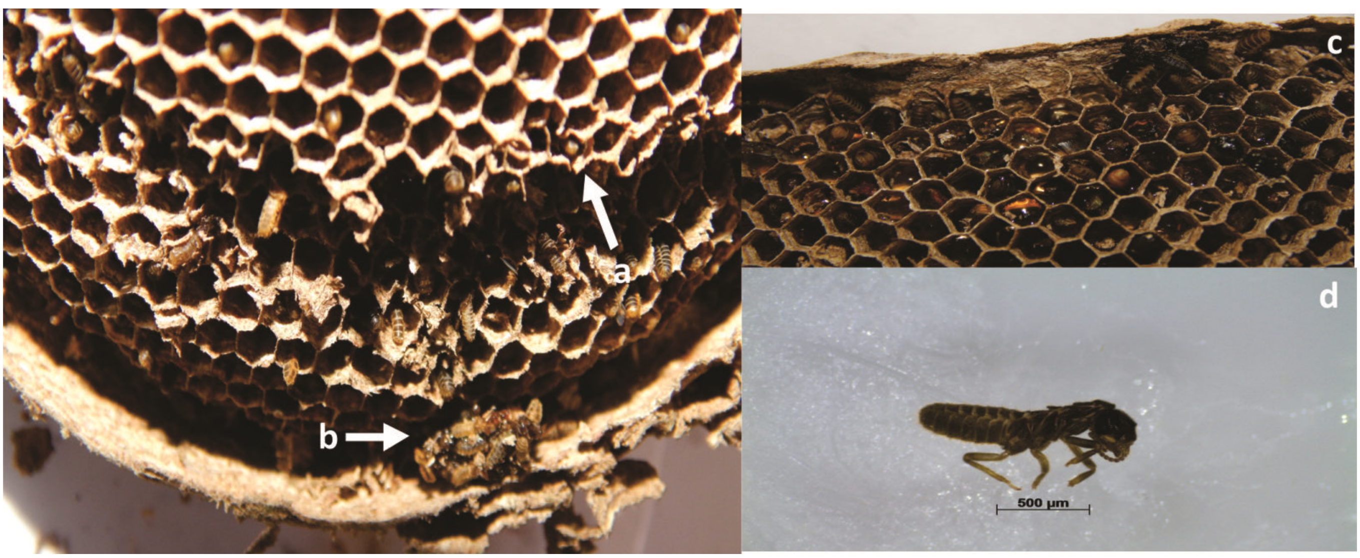

Fig 1. Termite winged stored inside cells (**a**), and in a mass mixed with nectar (**b**). Termite winged stored inside the cells with nectar (**c**), and termite winged with parts of its body extracted by foragers (**d**).

There was no significant correlation between the number of foragers and the number of prey stored in the colony (p=0.96, r=0.03); in other words, a colony with more foragers did not collect and store a greater number of prey. It is possible that the foraging activity could be related to the colony stage, with foragers taking fewer risks outside and performing more tasks in the nest during certain periods (Machado et al., 1988). On the other hand, in mature colonies, where there are more individuals, the demand for resources is higher and the number of workers engaged in foraging is also higher. However, the results showed that relatively small colonies could capture and store more prey than larger ones. This might be related to the requirements of the colony, or the availability of winged prey in the vicinity of the colony. Studies with Epiponini colonies have shown that seasonal differences in foraging rates are associated with the stage of colony development (Gobbi & Machado, 1985, 1986; Paula et al., 2003). A major factor that has not been evaluated in this study is the number of immature of each nest collected, since prey provide protein for the development of the offspring, so the amount of prey captured by foragers is an indirect measure of the number of immature and, consequently, the colony's demand for protein (Canevazzi & Noll, 2011). However, we believe that since this material can be stored in the colony to meet future demand, maybe the number of preys stockpiled does not represent a relation with the number of immature present in the nest at that moment.

Table 2. Nest area, number of adults, number of foragers, number of stored prey, and load capacity of each forager.

Colony	Area (cm^2)	Adults	Foragers	Prey	Number of prey by forager
03	2200.6	1291	665	20410	30.70
04	962.4	564	290	5070	17.50
05	4815.2	2825	1455	3510	2.40
06	2561.5	1503	774	700	1.00
07	350.3	205.5	106	1214	11.50

It therefore appears that colonies of these social wasps adopt an opportunistic strategy, without any direct synchronicity with the swarming periods of the termites and ants. Mill (1983) found that the most dramatic of all forms of termite predation was the opportunistic predation of winged when they left the nest for bridal or swarm flights. Indeed Taylor et al. (2011) suggested that *P. occidentalis* might display this type of opportunistic foraging strategy. Besides, it was reported by Johnson (1983) that an opportunistic strategy enabled stingless bee foragers to find and collect resources more efficiently.

Social wasps are sensitive to environmental changes and alter their behavior accordingly (O'Donnell & Jeanne, 1992). As shown in Table 1, colonies of wasps with stocked material were collected in warmer and humid times of the year, which is an ideal condition for termite colonies to release winged (Mill, 1983; Medeiros et al., 1999; Costa-Leonardo, 2002). Indeed, studies with colonies of *P. paulista* show that their foraging activity is mainly influenced by variation of temperature and relative humidity (Canevazzi & Noll, 2011). Similarly, in termites, the triggers for the release of winged on reproductive flights include, temperature, humidity, soil moisture and atmospheric pressure (Costa-Lima, 1938), as well as seasonality, meteorological and social changes, colony size, and physiological factors (Costa-Leonardo, 2002). In *P. paulista* colonies, Machado (1984) noted that the period of reproductive swarms occurred in the rainiest and hottest months, as observed in this study (Table 1), since the months in which the colonies were collected were the hottest and most humid months in the State of Mato Grosso do Sul (Zavatini, 1990).

Foraging habits of social wasps are generally diurnal (Jeanne, 1972; Rocha & Giannotti, 2007), while winged are typically released at dusk or at night (Costa-Leonardo, 2002), which could be a strategy to protect against aerial predators (Mill, 1983). This highlights the nature of the opportunism displayed by the social wasps, because the predominantly diurnal wasps needed to adjust to unusual circumstances and extend their period of activity in order to take advantage of the availability of this protein source.

Our results indicate that *P. occidentalis* and *P. paulista* both adopted an opportunistic foraging strategy. They were capable of storing large quantities of protein resources in their colonies. These wasps seem to use nectar as an inhibitor of the proliferation of microorganisms responsible for decomposition, enabling protein resources to be stored in the nests for longer periods and thereby taking advantage of the relatively short period during which a specific food resource is available in large abundance.

Acknowledgments

The authors are grateful to Dr. Danilo Oliveira for identification of the termite subfamily and the number of species. Financial support was provided by Fundação de Apoio ao Desenvolvimento do Ensino, Ciência e Tecnologia do Estado de Mato Grosso do Sul (FUNDECT); Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) provided Masters fellowships to the first and second authors; authors FP and WFAJ acknowledges research grants from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq).

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