Distribution of Resources Collected Among Individuals From Colonies of *Mischocyttarus drewseni* (Hymenoptera, Vespidae)

by

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ABSTRACT

The aim of this study was to analyze the distribution pattern of the food collected among groups of individuals in *Mischocyttarus drewseni* colonies. This behavior is one of the first actions exhibited by the foragers when they arrive in the colonies. Regarding nectar and prey collection, 95.90% of the collected nectar was given to larvae, whereas 3.57% to dominant individuals and 95.94% of the collected prey were given to the larvae, 2.54% to the dominant members, while the remainder of both was given to the workers. Despite not being significant, it was possible to observe a difference in food distribution among larvae, with larger larvae receiving more food than others. When the forager returns to the nest with pulp, it adds this material to cells in 64.29% of the times. Males showed agitated behavior with the arrival of the foragers, and sometimes took the foraged material from them.

INTRODUCTION

Mischocyttarus de Saussure (1853) is the largest group of social wasps, consisting of 245 species, distributed in nine subgenera, being mainly Neotropical (Richards 1978; Carpenter & Marques 2001; Silveira 2008). These wasps are considered primitive eusocial species, with independent foundation and without morphological caste differentiation. The dominant and subordinate females may assume any role, according to their colony's need, due to the small number of individuals and the fact they are all potentially reproductive (Litte 1981; Jeanne 1986; Murakami 2007).

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Although these wasps have high behavioral plasticity, the dominance hierarchy creates a social dynamic based on the nutritional cost and benefits from the behaviors performed. The dominant members avoid activities with high energy cost, such as foraging, by creating a nutritional reserve that improves their reproductive capacity in the colony; thus, increasing their dominance over other females (Markiewicz & O'Donnell 2001).

Therefore, the foraging activity, which consists of leaving the nest to collect resources for the maintenance of the colony, is a crucial aspect to elucidate issues related to the evolution of sociality (Smith 2005), since the main behavioral interactions conducted by social wasps are related to the capture and division of materials collected among the members of the colony (Rocha & Giannotti 2007).

The distribution of the resources collected among individuals from the colony is one of the first behavioral acts exhibited by foragers after the arrival in the field. This behavior is the main goal of the foraging process, and often the trophallaxis among adults is held immediately after the arrival of foragers, even before entering the nest (Rocha & Giannotti 2007; Sugden & Mcallen 1994; Cruz *et al.* 2006).

Despite its importance, studies related to foraging activity in species of the genus *Mischocyttarus* are scarce and have only been conducted for *M. drewseni* (Jeanne 1972), *M. labiatus* (Litte 1981), *M. flavitarsis* (Cornelius 1993), *M. mastigophorus* (O'Donnell 1998), *M. cerberus styx* (Silva & Noda 2000) and *M. consimilis* (Montagna *et al.* 2009).

The objective of this study was to analyze the distribution of resources collected by foragers of *Mischocyttarus drewseni* de Saussure, 1857 in the following aspects: (1) the distribution of food among larvae (small, medium and large), (2) what proportion of the food is divided between the immature and adult females (dominant and subordinate), (3) if the forager shares wood pulp collected with other individuals in the colony and what proportion of pulp is shared among dominant and subordinate indivduals, and (4) in what proportion males receive the resources that arrive in the colony.

MATERIAL AND METHODS

The field work was carried out at the Unesp – Universidade Estadual Paulista, Rio Claro, São Paulo State, Southeastern Brazil (22°24'36"S; 47°33'36"W and an average altitude of 612 meters), in a population of *M. drewseni*. Data were obtained from 21 colonies in the pre-and post-emergence stages for 189 hours of observation.

At the onset of the experiment, the colonies were found, identified and mapped to verify the number of cells, immature (eggs, larvae and pupae) and adults, and find out the colony stage of development. Next, in order to identify the behavioral roles of each individual (dominant, subordinate and male) in the colony and their foraging habits, the wasps were collected, marked and then returned to the nest. The mark was made on the mesosoma with a ceramic paint pen.

Regarding the size of the larvae, the terminology described by Giannotti & Trevisoli (1993) was adapted for this study:

SL - Small larvae (L1 and L2 in Giannotti & Trevisoli, 1993): the ventral lobes of the first abdominal segment are not evident;

ML - Medium larvae (L3 and L4 in Giannotti & Trevisoli, 1993): ventral lobes of the first abdominal segment are small;

LL - Large larvae (L5 in Giannotti & Trevisoli, 1993): ventral lobes of the first abdominal segment are fully developed.

The identification of the collected material was made by observing the behavior of individuals in the colony (Silva & Noda 2000), as follows:

Nectar foraging: was considered to be when the wasp arrived at the nest with liquid food stored in its crop and performed adult-adult or adult-larva trophallaxis.

Prey foraging: was noted when the wasp arrived with a solid mass held in its mouthparts. In this case, the wasp might chew the food itself or share it with another wasp, and then offer this macerated protein to the larvae.

Pulp foraging: the collection of construction material was characterized by the arrival at the nest with a solid dark mass. This material was chewed and incorporated into the cells of the nest.

Water foraging: was noted when the liquid was deposited directly on the walls of the nest cells, without contact with another wasp.

Unfruitful foraging: collections were considered unfruitful, when the wasp returned without any apparent material, not performing trophallaxis or depositing any substance in the nest.

After the foragers' arrival, the distribution of the collected material between the individuals of the nest was observed and more than one distribution type was recorded if it occurred in a single collection. During nectar or prey distribution among larvae, the frequency of each larva (small, medium or large) receiving such food was quantified. The sum of all data collected from the colonies and the results were compiled by dividing the number of receipts for each size of larvae by the total number of larvae of the same size. This method enabled comparisons between colonies with different amounts and sizes of larvae, as follows:

Average distribution to SL = times that each SL received food/total number of SL.

Average distribution to ML = times that each ML received food/total number of ML.

Average distribution to LL = times that each LL received food/ total number of LL.

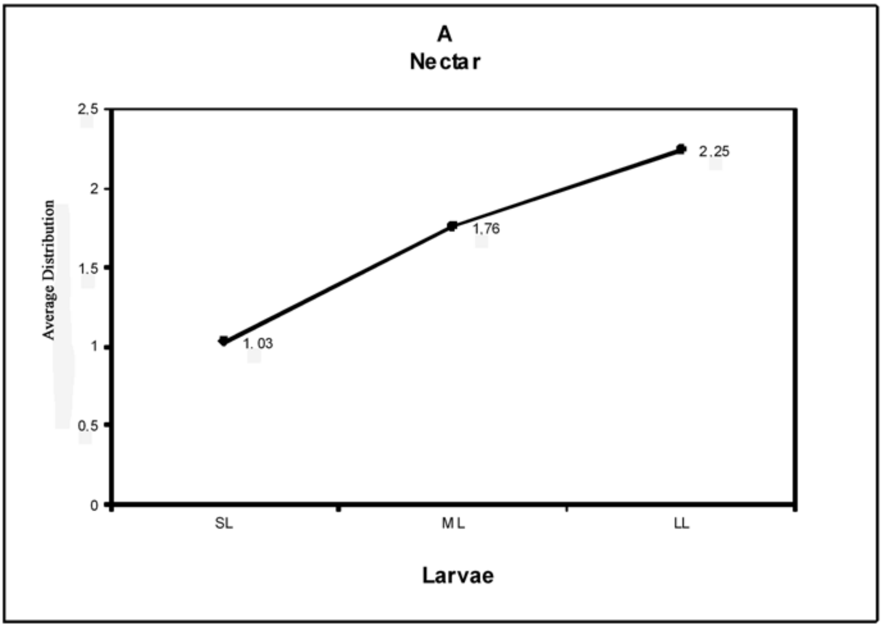
The Kruskal-Wallis test ($p \leq 0.05$) was used to verify the significance of these differences, if samples represented only casual variations, and whether the distribution of nectar and prey is different for each size of larva.

In order to quantify the food distribution between larvae, dominant females and subordinate females, it was checked how much each group received for each of the journeys made by the forager. Next, an average per hour of observation and the proportion of each group of individuals receiving food was calculated. When the forager returned to the nest with wood pulp, it was observed whether it was directly added to cells or shared with other adults, and the average time the forager stayed with the material and shared with dominant and subordinates was calculated. The food sharing between females and males was also quantified by calculating the relative frequency of times that males received nectar or prey.

RESULTS

Food distribution among small, medium and large larvae

According to Fig. 1, the mean values show that large larvae received more nectar (Fig. 1A) (average of 2.25 times for each trip) and prey (Fig. 1B) (mean 2.13 times for each trip) than the others The medium larvae received nectar 1.76 times for each trip, and the small larvae 1.03 times; while, the small larvae received prey more often (average of 1.68 times) than the medium larvae



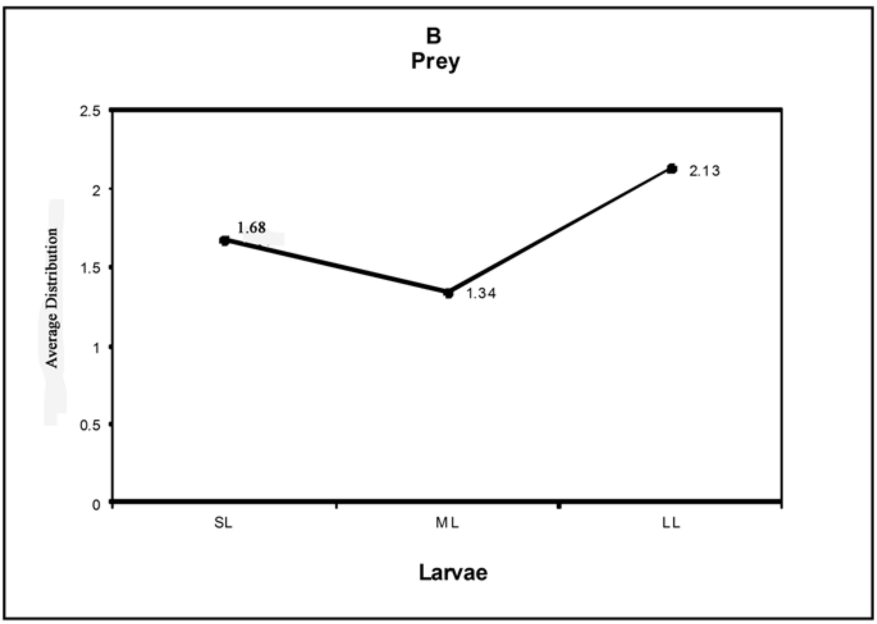


Fig. 1. Pattern of division of nectar (A) and prey (B) among small larvae (SL), medium larvae (ML) and large larvae (LL).

(average of 1.34 times). Nevertheless, statistical results (Kruskal-Wallis test) showed that these differences are not significant, nor was the distribution of nectar ($H = 3.6778$, $p = 0.1590$, $N = 195$) or for distribution of prey ($H = 5.3493$, $p = 0.0689$, $N = 83$).

Food distribution among immature (larvae) and adult females (dominant and subordinate)

As shown in Tables 1 and 2, the distribution of food between immature and adults females of the colonies was differentiated. Of the arrivals with nectar, 95.90% were distributed to larvae, 3.57% to dominant individuals and 0.54% to subordinates. On the instances where prey was brought to the colonies, 95.94% were delivered to the larvae, regardless of the size, 2.54% were given to the dominant adults and 1.42% to the subordinates The larvae received nectar 15.58 times per hour, the dominants 0.58 and subordinates 0.09. Regarding the prey collection, larvae received the macerate an average of 28.63 times per hour, the dominant adults 0.76 times and subordinates 0.42.

Wood pulp distribution among adult females (foragers, dominant and subordinate)

Out of 42 arrivals with wood pulp (Table 3), the dominant individuals received 33.33%, representing a value clearly higher than that for the subordinates, which received only 2.38% of the total, while 64.29% stayed with the foragers.

From an average of 1.79 collections of pulp per hour, 1.17 were directly deposited in the cell by the foragers, while 0.58 were delivered to the dominant adults and 0.04 to the subordinates.

Food distribution among males and females

Males were restless with the arrivals of the foragers in the colony. On occasion one to three males investigated the female who had just arrived from the field and often took the foraged material, either nectar or prey. From a total of 85 arrivals of nectar, which was divided only among adults, 47 (55.3%) were given to female adults, subordinate or dominant, and 38 (44.7%) were divided between males. Males received 11.5% of all prey that were brought to the colonies, and of seven total instances where males received the prey, three (42.8%) were partially delivered and four (57.2%) were given whole (Table 4).

Table 1. Distribution of nectar among larvae and adult females (dominant and subordinate).

	Nectar		
	Larvae	Dominant	Subordinate
Total	1075	40	6
Average/Hour	15.58	0.58	0.09
Standard deviation	12.47	0.79	0.28
Percentage	95.90%	3.57%	0.54%

Table 2. Distribution of prey among larvae and adult females (dominant and subordinate).

	Prey		
	Larvae	Dominant	Subordinate
Total	945	25	14
Average /Hour	28.63	0.76	0.42
Standard deviation	60.32	0.67	1.15
Percentage	95.94%	2.54%	1.42%

Table 3. Distribution of wood pulp among foragers (dominant and subordinate).

	Wood pulp		
	Foragers	Dominant	Subordinate
Total	27	14	1
Average/Hour	1.17	0.58	0.04
Standard deviation	1.00	1.06	0.20
Percentage	64.29%	33.33%	2.38%

Table 4. Distribution of nectar and prey among males and females of *M. drewseni*, specifying the number of occurrences (n) and the relative frequency (%).

Adults	Nectar		Prey	
	n	%	n	%
Females	47	55.3	54	88.5
Males	38	44.7	7	11.5
Total	85	100	61	100

DISCUSSION

Foragers of *M. drewseni* appear to perform an unequal distribution of food in the act of feeding the larvae, providing greater amounts of nectar and prey for larger larvae, although this difference is not statistically significant. This result is clear from Fig. 1, and corroborates with the data observed by Kudô

(1998) in colonies of *Polistes chinensis* where this difference was attributed to the fact that large larvae require more food than small larvae.

In *M. labiatus* adult prefer to feed large larvae and have a tendency to concentrate their feeding efforts on one larva at a time (Litte 1981). Larval development time depends on feeding rates in social insects (Wilson 1971). Therefore, both in colonies with lone-foundresses and colonies with multi-foundress, the older larvae are always given priority over the younger larvae and these older larvae pupate considerably earlier than the others present in the nests (Litte 1981). This conclusion has been demonstrated during the pre-emergence phases of colonies of *M. drewseni* when the mean duration of the first larvae appearance is less than that of later-appearing larvae (Jeanne 1972), suggesting that in this species, feeding efforts are also concentrated on the first emerging larvae.

Moreover, the better fed larva has more chance to be the reproductive female of the colony, so the differential distribution of food among larvae may be related to caste determination (Rossi & Hunt 1988; Hunt 1991; Gadagkar *et al.* 1988; Gadagkar *et al.* 1991).

Regarding the distribution of collected resources among individuals of the colony, it was found that most of the food is directed to larvae and distribution of supply among adults follows a hierarchy, with the dominants receiving more than the subordinates.

The high rate of larva-adult trophallaxis in this study may be related to the attraction of adults by larval salivary secretions, which may have been the reason for the evolution of social wasp species in a context of trophallaxis as mutual exchange of food (Roubaud 1916). Reproductive maturation and capacity of oviposition appear to be influenced by larval trophallaxis, mainly in those species of primitive social wasps, in which morphological differences between reproductive and worker castes do not exist (Gadagkar 1991). Thus, food offered by the foragers to the larvae does not appear to be a purely altruistic act, since the females who collected and distributed the food to immatures will also be favored.

It was found that the foragers of *M. drewseni* obey a hierarchy in the distribution of resources among females that remain in the colony, and the dominant adults have advantages over the subordinates at the time of division of nectar, pulp and prey, supporting the hypothesis of Jeanne (1972). Foloni

& Giannotti (1998) quantified the number of transfers of regurgitated liquid from an adult female of *M. drewseni* to another, and noted that there is a significant difference between dominants and subordinates, so that queens spend 1.60% of their time getting food, while the workers 0.34%. Studies on *Polistes metricus* confirm this hypothesis because they claim there is a division of labor among individuals, finding that the queens stay in the nest most of the time and their journeys are of short duration (Gamboa *et al.* 1978). Noda *et al.* (2001) found that the material collected by foragers of *M. cerberus styx* delivered to another female is an act of submission and stated that the species has a well-defined hierarchy. Similarly, Costa-Filho *et al.* (2011) observed that queens of *M. cerberus styx* spends most of their time in the comb while intermediate females perform high frequencies of cell inspection and gaster rubbing; however, they also forage and the workers or foragers spend most of their time in the field collecting. Knowing that queens need food, both for survival and for development of the ovarioles, and present no foraging behavior, it becomes clear why they receive more food than subordinates (Gamboa *et al.* 1978)

The distribution of pulp was also distinguished, and probably beyond the reproductive function. The dominant individuals of the colonies observed in this work are likely responsible for building and increase of cells in the nest, since the dominant females received a higher percentage of pulp when compared with the subordinates. In *Polistes*, the dominant females initiate the construction of most cells and perform oviposition soon after (West-Eberhard 1969; Pratte 1989), as observed in colonies of *P. lanio* in the pre-emergence stage, when the only activity performed by the dominant females was collecting wood pulp to start new cells and then laying eggs (Giannotti & Machado 1999). In the same way the dominants of *M. cerberus styx* forage for pulp at a higher rate than the workers (3.1% and 0.3% respectively, Giannotti 1999), and in *Mischocyttarus mastigophorus* the wood pulp loads were never shared with nest mates, while food loads, especially insect prey, were often partitioned with other wasps (O'Donnell 1998). This behavior may explain why a large percentage of pulp is shared with females of the highest hierarchical position.

Males received food from foragers, corroborating the findings by Jeanne (1972), who also worked with *M. drewseni* and noted that these individuals requested prey as soon as foragers arrive at the nest. Often the request of the food is aggressive, as was observed in males of *M. mastigophorus*, which do not forage, but through aggressive behavior, solicit and consume part of the food brought by foragers, representing a considerable energy cost to the colony (O'Donnell 1999).

Jeanne (1972) suggested that larval feeding by males of *M. drewseni* is associated with the removal of liquid protein, since the macerate of prey becomes smaller when chewed by a male and in one case the portion was totally dropped and was not distributed among the immatures after macerating. Makino (1993), observing *Polistes jadwigae,* stated that from the total of 27 prey, that males received four which were completely discarded after chewing. According to the author these observations indicate that larval feeding by Polistinae males is minimal, because they ingest a significant portion of the food themselves during this process.

Unlike the cases noted above, males of *M. latior* display participation in the colony activities and, in contrast to other studies, males have been observed foraging nectar, prey and water (Cecílio 1999).

In general, it may be concluded that the fact that foragers of *M. drewseni* leave the nest and go out to the field in search of resources for individuals who are not their offspring is certainly an altruistic behavior, because it involves high energy cost and risk of predation. Nevertheless, considering the theory of mutualism, when adult-larva trophallaxis occurs there is reciprocity on the part of the larvae in relation to foragers, featuring reciprocal altruism, which is reflected in the preference to feed larger larvae that solicit more food and probably produce more salivary secretion. Also, the distribution of resources among adults of *M. drewseni* has an important role in determining and maintaining the dominance hierarchy of the colony. As in *M. mastigophorus*, dominant individuals foraged for food (nectar and prey) at lower rates than subordinate individuals. In contrast, dominant wasps performed most of the foraging for the wood pulp used in nest construction (O'Donnell 1998). Dominant individuals on the nest were more likely to take food from arriving foragers than subordinate individuals. Nestmates can compete for access to loads of food provided by foragers for personal consumption. Control of food materials influences individual physiology (Hunt 1991), as well as that of the developing brood (Markiewicz & O'Donnell 2001). Wasps may also compete to control the processing of building material loads. The ability to monopolize building materials allows individuals to regulate nest growth. In addition, it is possible to note that males can participate passively in the activities of the colony, just receiving the food brought by foragers, or actively, distributing food to the larvae or possibly foraging.

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