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The Disappearance of Eggs and Larvae from the Nests of the *Mischocyttarus* (Monogynoecus) *montei* Zikán (Hymenoptera: Vespidae), Especially in Autumn and Winter: Can it Mean an Adaptive Cannibalism to Ensure the Survival of Colonies?

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Abstract

The aim of this study was to verify the disappearance of eggs and larvae from the nests of the *Mischocyttarus* (*Monogynoecus*) *montei,* especially in autumn and winter, and at the same time, to discuss about the cannibalism as the main reason for survival of the colonies during the unfavorable climatic conditions. Forty one colonies were studied during the seasons of the year, period from March in 1999 to September 2000. A total of 314 disappearances of immature individuals was counted, corresponding to 95 eggs (27,1 %) and 229 larvae (72,9 %). The results showed that the disappearance of eggs and larvae were significantly higher during the autumn and winter In addition, the disappearance rate of larvae increases with the falling of rainfall and of temperature, in autumn and winter. There were no relation between the disappearance of eggs and any climatic factors. From the total number of disappearances, small larvae disappeared from the cells at a higher frequency (55,9%, n = 128) than medium (18,3%, n = 42) and large (25,8%, n = 49) size larvae. It is probably that these immatures (eggs and larvae) were cannibalized due to scarcity of prey and nectar under unfavorable climatic conditions, especially during the cold and dry periods of the year.

Introduction

Cannibalism is a behavioral trait which occurs in many group of animals, although the most of the reports are based on behavioral observations of laboratory (Fox, 1975). Further, according to the same author, the intraspecific predation can be a control agent for homeostasis of the population.

In a review study, Polis (1981) described the intraspecific predation in about 1300 species. For this author, the cannibalism is important for the population structure, history of life, competition for sexual partners or resources, and several behavioral aspects of these species.

In social wasps, studies have suggested that cannibalism on larvae is caused when food is scarce (Kudô & Shirai, 2012). Larval cannibalism of brood can be induced by poor nutrition of adult individuals in social wasps (Hunt, 1991). In independent-founding wasps, the ingestion of immature individuals from the same colony has been related frequently as the result of conflicts among females to ensure the individual fitness. Oliveira et al. (2012) have reported that, in *M. montei,* the occurrence of cannibalism on eggs and larvae resulted in the replacement of dominant female or in the colonial fission, after the intense conflict among females of the colony. In *M. drewseni,* cannibalism on eggs has occurred at higher frequency after the emergence of first larvae and, the females ingested their own eggs in four of five times, whereas in another occasion, one egg was ingested by other female (Jeanne, 1972). Prezoto et al. (2004) have verified that the dominant female of *M. cassununga* monopolizes the reproduction doing cannibalism on eggs of her subordinate workers. Litte (1977) reported that many eggs and larvae disappeared from the nest after the queen removal of *M. mexicanus*, moreover, about one week after the queen removal, one female started to lay her eggs and became the queen of colony. Intracolonial cannibalism of

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eggs was reported in *M. cerberus styx* by Giannotti (1999) and intercolonial cannibalism in *M. mexicanus* by Clouse (1995).

Brood cannibalism also occur in species of the genus *Polistes*, as reported by Giannotti (1994) in *P. simillimus;* Giannotti & Machado (1999) in *P. lanio lanio;* Tannure & Nascimento (1999) in *P. versicolor* and *P. ferreri*; Zara & Balestieri (2000) in *P. versicolor* and Torres et al. (2009) in *P. canadensis canadensis*. Furthermore, there are the classic studies of Deleurance (1963), Gervet (1964) and West-Eberhard (1969) which showed the occurrence of differential oophagy in the genus *Polistes*. In *Metapolybia aztecoides,* a swarm-founding wasp from Epiponini tribe, the same behavior was reported by West-Eberhard (1982).

Studies about the influence of climatic factors and availability food on the disappearance of brood from the nest of *Mischocyttarus* species are still non-existent. However, some studies in *Polistes* species revealed that young larvae of *P. dominulus* were preferentially cannibalized in limited conditions of food, ensuring a fast production of workers in initial development of colony (Mead et al., 1994).

More recently, the relationship between availability of food and larval cannibalism of the foundress of *P. chinensis antenalis* was studied by Kudô and Shirai (2012), in laboratorial conditions. According to this study a higher frequency of cannibalism occurred under limited conditions of food, i.e., young larvae were cannibalized at higher frequency during limited conditions of prey whereas old larvae were cannibalized at higher frequency during limited conditions of honey.

Mischocyttarus is the only genus of the tribe Mischocyttarini (Carpenter, 1993) and represents a large group in the subfamily Polistinae of social wasp, with 245 species described in 9 subgenera (Silveira, 2008) distributed almost exclusively in South America (Richards, 1978). The genus *Mischocyttarus, Polistes* and most part of the genus *Ropalidia* found nests by haplometrosis (only one female) or by pleometrosis (a group of females) (Jeanne, 1972; Richards, 1971, 1978). Colonies are usually characterized by absence of age polietism (Jeanne, 1980), the social hierarchy is established through behaviors of dominance and subordination (Richards, 1971, 1978; Jeanne, 1972; Noda et al., 2001; Prezoto et al., 2004; Murakami & Shima, 2006, 2010; Costa-Filho et al., 2011; Oliveira et al., 2012), there are no morphological differentiation between female castes (Murakami et al., 2009) and all adult individuals show a plasticity on the social role in the colony (Richards, 1971; Jeanne, 1972; Cowan, 1991; Murakami & Shima, 2006, 2010; Costa-Filho et al., 2011; Murakami et al., 2013).

In *M. montei* there are only studies about some social behavior aspects which were realized by Richards (1978) and by Oliveira et al. (2012). The present study was aimed at investigating the disappearance of eggs and larvae from cells of the nest of *M. montei*, especially during the autumn and winter, discussing this disappearance as an adaptive strategy for colony development during the unfavorable climatic conditions.

Materials and Methods

Forty one colonies were mapped during the pre- and post-emergence phase, from twice to four times per week, since 10th March 1999 until 06th February 2000, at Campus of the São Paulo State University, Rio Claro/SP, Brazil (22°24’36”S, 47°33’36”W) with an average elevation of 612 meters.

The disappearance of eggs and larvae was considered when a cell, previously with an egg or a larva, was found empty or the position of the egg had changed during the mapping of the nest. The frequencies of eggs and larvae removal were inferred when previously filled cells with eggs and larvae were empty and /or when the positions of the eggs in cells were changed. Larvae were classified as large, medium or small size, according to Murakami and Shima (2006).

The data collection was made after the establishment of social hierarchy in the colonies, i.e., when there was no conflict among females and, thus, discarding the hypothesis of the disappearance of immature individuals caused by differential cannibalism to ensure the individual fitness of the dominant female in the colony. This point was important because it is very common the occurrence of a differential oophagy or larviphagy by the queen or dominant female in independent-founding wasps. In our study, there was not observed an occurrence of a hierarchical conflict related to differential oophagy or larviphagy because there was no aggression or any aggressive behavior that would indicate the existence of a hierarchical dispute in the colony until the end of the behavioral observations. According to Oliveira et al. (2012), colonies of *M. montei* are usually founded by an association of females in the pre-emergence and it may contribute to the success of association during pre-emergence, once it tends to reduce conflicts during initial phases of colonial development. On the other hand, the occurrence of conflicts tends to be more intense, usually involving more physical contacts during the post-emergence phase.

From 41 studied colonies, the parasitoidism was detected in 7 cases, i.e., only 1 egg, 6 larvae and 9 pupae were parasited. Thus, due to the occurrence at low frequency, the hypothesis that the disappearance of brood was influenced by parasitoidism rate was discarded. The higher frequencies of disappearance of immature individuals were detected during the autumn and winter, thus it is impossible to suppose that the disappearance of eggs and larvae occurred due to removal caused by parasitoidism or some disease. Furthermore, all colonies had continued its natural development even under unfavorable climatic conditions (especially during the cold and dry periods).

The climatic factors as temperature, relative humidity and rainfall index were obtained from CEAPLA (Centro de Análise e Planejamento Ambiental) located at Campus of São Paulo State University, Rio Claro/SP, where the present study was realized.

Chi-square test for a Contingency table ($P < 0,05$) was applied to verify the relationship between disappearance rates of brood and the months (seasons) of the years, whereas

Spearman correlation test ($P < 0,05$) were applied to measure the relationship between disappearance rates of brood and the climatic factors (Zar, 1999).

Results

The frequencies of disappearance of eggs and larvae from the nests during the four seasons (in months) of the year according to temperature, relative humidity and rainfall index is showed at Table 1 and Figure 1. The total of disappearance of eggs and larvae was 85 (27,1 %) and 229 (72,9 %), respectively (Table 1). The highest frequency occurred during the winter (a total of 31 eggs and 103 larvae), in June and July, when the average temperatures 18,3^o and 18,0^o, respectively. The second highest frequency of disappearance was observed during the autumn (27 eggs = 37,0 % and 73 larvae = 63,1 %), more specifically in April. In Spring, the total frequency of disappearance was 46, being 19 eggs and 27 larvae. The disappearance at lowest frequency occurred during the summer when a total of 8 eggs and 26 larvae removed from the cells (Table 1 and Figure 1). Chi-square test for Contingency table showed that the frequency of disappeared larvae significantly differed ($P < 0,05$) according to the month of the year (seasons) ($x^2_{larva}= 443,15$; G.L.$_{larva}= 3$; $C_{larva}= 0,81$).

The analysis of Spearman showed a significant and strong negative correlation ($P < 0,05$) between the frequency of disappearance of larvae and average temperature ($r = -0,6165$), as well as between this frequency and rainfall index ($r = -0,7133$). The Spearman coefficient (r) between the disappearance of larvae and relative humidity was -0,1189, indicating a weak correlation without a significance (Table 2). Although the Contingency

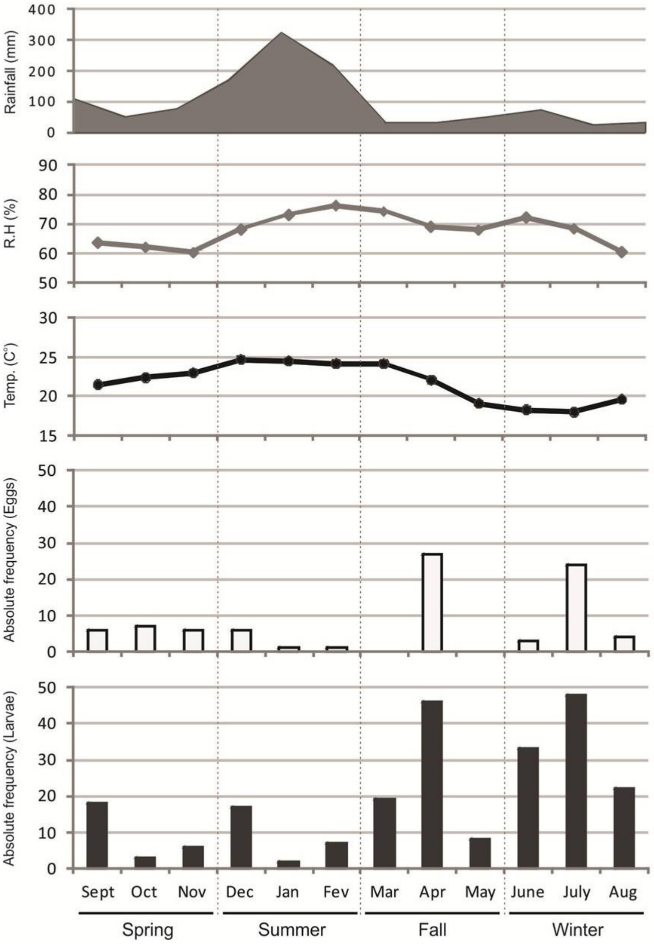

Fig 1. Graphical interface of absolute frequency (Abs) of disappearance of eggs and larvae from cells of *M. montei* nests, temperature (° C), relative humidity and rainfall rate (mm) according to the months and seasons from March 1999 to September 2000.

Table 1. Absolute frequency (Abs) and percentage (%) of eggs and larvae removed from the cells of *M. montei*'s nests according to the months and seasons, considering the average temperature (° C), relative humidity and rainfall rate (mm) from March 1999 to September 2000.

Season	Month	Eggs removal		Larvae removal		Temperature	Relative Humidity	Rainfall
		Abs	**%**	**Abs**	**%**			
	Mar	0	0	19	100	24,2	74,2	33,2
Fall	**Apr**	27	37	46	63,1	22,1	69,1	32,1
	May	0	0	8	100	19,1	67,9	50,7
	Total	27	27	73	73	21,80	70,40	38,67
	Jun	3	8,3	33	91,7	18,3	72,2	73,3
Winter	**Jul**	24	33,3	48	66,7	18	68,3	25
	Aug	4	15,4	22	84,6	19,6	60,4	32
	Total	31	23,1	103	76,9	18,63	66,97	43,43
	Sep	6	25	18	75	21,5	63,6	109,4
Spring	**Oct**	7	70	3	30	22,4	62	50,8
	Nov	6	50	6	50	23	60,2	77,6
	Total	19	41,6	27	58,4	22,30	61,93	79,27
	Dec	6	26,1	17	73,9	24,7	68	169,7
Summer	**Jan**	1	33,3	2	66,7	24,5	72,9	323,8
	Feb	1	12,5	7	87,5	24,2	76,3	219,4
	Total	8	23,5	26	76,5	24,47	72,40	237,63
Total amount		85	27,1	229	72,9			

coefficients indicated that the disappearance of eggs was significantly different (P < 0,05) according to months (seasons) of the year (x^2_{egg}= 15,53; G.L.$_{egg}$= 3; C$_{egg}$= 0,38), there were no significant correlations between the disappearance of eggs and any climatic variables (Table 2). In Table 3 it is possible to observe the absolute frequency of the disappearance of eggs and larvae according to all months of the year. The frequency of disappearance of small larvae from the cells were higher (n= 128; 55,9 %) than medium larvae (n= 42; 18,3 %) and large larvae (n= 59; 25,8 %) (Table 3).

Table 2. Spearman's correlation coefficient (r) and p-value (* p <0.05) between the absolute frequencies of eggs and larvae removed from the cells of *M. montei*'s nests in relation to average temperature (° C), relative air humidity and rainfall rate (mm) according to the four seasons (Fall, Winter, Spring and Summer).

	Eggs removal			**Larvae removal**		
	Temperature	**Relative Humidity**	**Rainfall**	**Temperature**	**Relative Humidity**	**Rainfall**
r	-0,2089	-0,4099	-0,3039	-0,6165	0,1189	-0,7133
p-value	0,5148	0,1857	0,3369	*0,0328	0,7162	*0,0121

Table 3. Absolute frequency (Abs) and percentage (%) of removed small according to size (larvae, medium and large) in *M. montei*.

Total frequency (n=229)					
Small larvae		**Medium larvae**		**Large larvae**	
Abs	**%**	**Abs**	**%**	**Abs**	**%**
128	55,9	42	18,3	59	25,8

Discussion and Conclusion

Studies about the intraspecific cannibalism of brood and its relationship with climatic factors are scarce. On the other hand, there are many studies about the cannibalism of eggs and larvae to ensure the individual fitness among female wasps (caused by a competition in the dominance hierarchy of the colony), especially in the independent-founding wasps (West-Eberhard, 1969, 1982; Richards, 1971, 1978; Litte, 1977; Hunt, 1992; Tannure-Nascimento & Nascimento, 1999; Oliveira et al., 2012; and others). Close (1995) reports that conspecific predation was more frequent after the usurpation of nests of *M. mexicanus,* which were founded by haplometrosis. Giannotti (1999) observed that larvae of *M. cerberus styx* were removed from cells by workers with her jaws and first pair of legs, and then, this food resource could be divided among other adult females and brood of the nest. This behaviour also was described in *Polistes lanio* by Giannotti and Machado (1999). Based on the analysis of Spearman correlation our results showed that, the adverse climatic conditions in autumn and winter (low temperature and low index of rainfall) influenced the disappearance of brood through the cannibalism. This behaviour probably occurred due to scarce resource of food (especially in winter) and difficulties for foraging (for example, as happened in cold and rainy days). According to Giannotti (1994), a high frequency of cannibalism after dispersion of aggregate was related to the absence of food resource during the foundation of colonies in the *Polistes simillimus*. Our study also shows that small larvae disappeared from the cells at higher frequency than medium and large larvae.

Once the most part of larvae was cannibalized, it is probably that the cannibalism of small larvae would be advantageous to the colony. Small larvae need a higher demand of time and forage activity to complete their development in comparison to medium and large larvae. Thus, adult wasps can feed larger larvae through the cannibalism of smaller larvae to obtain a faster production of adult individuals for colony. As observed by Kudô and Shirai (2012) in laboratorial conditions, the cannibalism occurred more frequently under prey- and honey-limited conditions. However, young larvae were cannibalized at high frequency under prey-limited conditions whereas old larvae under honey-limited colonies. The authors concluded that a limited condition of nutrition induces the larval cannibalism and/or the production of first workers in the colony. Mead et al. (1994) analyzed the frequency of cannibalism during the nest foundation of *P. dominulus* and they verified that young larvae were more frequently cannibalized under prey-limited condition when compared to colonies with availability of prey. Furthermore, in his work, it was observed that adult wasps preferentially feed old larvae in the colony. Although it was not possible to observe the behavior of females after removals of eggs and larvae of *M. montei*, this phenomenon probably occurred in the studied colonies. The following facts support the hypothesis of larval cannibalism as an adaptive strategy to overcome unfavorable climatic conditions: 1st- Our hypothesis about the cannibalism of eggs and larvae to ensure the individual fitness is not considered here because the collection of data was made without the existence of conflict among females which can do the differential cannibalism (Pardi, 1948, West-Eberhard, 1969, Jeanne, 1972, Oliveira et al., 2012); 2nd- The disappearance of eggs and larvae did not occur due to parasitoid attacks on the nests. This fact was observed in low frequencies (7 colonies from 41 studied colonies totalizing 1 egg, 6 larvae and 9 parasited pupae); 3rd- Cannibalism in the social wasps was related under induced conditions with poor nutrition of adult individuals of the colony (Hunt, 1991), when the resource is limited (Mead et al., 1994; Kudô & Shirai, 2012) and in unfavorable environment conditions; and 4th- The similarity between our results under natural conditions and the results obtained by Mead et al. (1994) and by Kudô and Shirai (2012) under manipulated conditions showed that it is possible to hypothesize the high disappearance of brood caused by scarce of food resource in adverse climatic conditions during the cold and dry period of the year. Thus, we believe that the cannibalism of small larvae, which occurred more frequently than cannibalism of medium and large larvae, represents an adaptive strategy of *M. montei* to ensure the development of the colony cycle, especially during unfavorable climatic conditions (during the autumn and winter).

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