Dominance and Subordination Interactions Among Nestmates in Pre and Post-Emergence Phases of the Basal Eusocial Wasp *Mischocyttarus (Monogynoecus) montei* (Hymenoptera, Vespidae)

by

[1]Oliveira, VC, [1]Desuó, IC, [1]Murakami, ASN & [2]Shima, SN

ABSTRACT

In basal eusocial wasps the social organization is based on a dominance hierarchy which is maintained through agonistic interactions. The dominant wasp is usually the most aggressive individual and assumes the reproductive function of the colony. These wasps lack morphological caste differences and the physiological conditions and behavioral repertoire define the role of each female in the nest. However, the position in the rank and its function in the colony are not definitive and tradeoffs in the social rank, at least in some species, are common. In this study 8 colonies of *Mischocyttarus (M.) montei* in pre and post-emergence phases of colonial development were observed in field conditions in order to study the interactions of dominance and subordination among nestmates, thus allowing a better understanding of the establishment of the dominance hierarchy and consequently the social regulation of this species. Our results showed that all colonies in pre-emergence were founded by an association of females which had established the hierarchy previously in their natal nest. Such pattern may contribute to the success of association during pre-emergence, once it tends to reduce conflicts among cohorts during initial phases of colonial development, increasing the chances of colonial success. During post-emergence, the conflicts tend to be more intense, usually involving more physical contacts and in this phase, tradeoffs in the social rank are more frequent. During post-emergence, the number of females increases, more cells are available to lay eggs and the reproductive condition of the main egg-layer is probably reduced, aggravating the competition for reproductive dominance of the colony.

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1. Programa de Pós-graduação, Departamento de Zoologia, Instituto de Biociências, UNESP, Av. 24-A, 1515, CEP:13506-900, Rio Claro, SP, Brazil. E-mail: ivan.desuo@yahoo.com.br.
2. Departamento de Zoologia, Instituto de Biociências, UNESP, Av. 24-A, 1515, CEP:13506-900, Rio Claro, SP, Brazil.

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INTRODUCTION

In basal eusocial wasps, the social dominance represents the ability of a female to monopolize the reproductive control of the colony (West-Eberhard 1969; Wilson 1971; Jeanne 1972). Moreover, the maintenance of the reproductive control increases individual fitness, as the dominant wasp produces most of the colony brood. However, it also involves costs, since the main egg-layer tries to avoid other females from laying eggs. In this group of wasps, the social roles of the nestmates are determined through aggressive interactions, leading to the establishment of a linear dominance/subordination hierarchy (Pardi 1942; Gadagkar 1991). The most aggressive female is usually coined as "the dominant wasp" and assumes the role of the main egg-layer, whereas the most subordinate individuals became typically foragers. In these wasps, the dominance hierarchy is not so static and tradeoffs in the dominance rank are commonly observed, especially in some species of *Polistes* (Reeve 1991). Their nests are founded solitarily or by an association of few cohorts (pleometrosis), and the choice between nestling alone or in an association is direct related to environmental and biological restrictions, mainly the availability of nestling sites, survivorship insurance and nest usurpation (Reeve 1991). The basal eusocial Polistinae wasps are characterized by a lack of morphological caste differences resulting in flexibility in the social roles of adults; however, physiological conditions and behavioral repertoire differ among adults (Gadagkar 1991; Murakami & Shima 2009, 2010). Age, at least in some species of basal eusocial wasps, is important to determine dominance hierarchy and the most dominant female tends to be the oldest individual of the colony (Murakami & Shima 2009 2010 – *Mischocyttarus cassununga*; Giannotti & Machado 1994 – *Polistes lanio*; Huges & Strassmann 1988 – *Polistes instabilis*; Strassmann & Meyer 1983 – *Polistes exclamans*).

The degree of aggressiveness is quite variable among basal eusocial wasps and depends on the phase of the colonial development (Gadagkar 1991; Reeve 1991; Röseler 1991). In *Polistes* the interactions are usually more intense, involving injuries among opponents (West-Eberhard 1969; Spradbery 1973; Yamane 1985; Röseler 1991; Tindo & Dejean 2000). This is especially true in the initial phases of colonial development in nests founded by association of other cohorts. In *M. drewseni* the rate of dominance encounters was low (Jeanne 1972) when compared with *Polistes gallicus* (Pardi 1948). In *Ropalidia* species the dominance and subordination interactions seems to be generally less violent than those of *Polistes* (Gadagkar & Joshi 1982; Itô 1983, 1985). On the other hand, agonistic interactions in *Mischocyttarus* are moderate and may not even involve physical contact.

The genus *Mischocyttarus* is the most diverse group of wasps, with 245 species and 9 subgenus (Silveira 2008). However, it is almost restricted to the South America, with only two species occurring on the south and west sides of United States (Gadagkar 1991). Despite its great diversity, this genus is poorly studied and the mechanisms which regulate sociality are barely known. Thus, the aim of this work was to study the interactions of dominance and subordination among the nestmates of the basal eusocial wasp *Mischocyttarus (Monogynoecus) montei* in the pre and post-emergence phases of colonial development. This paper represents the first behavioral study in this species.

MATERIALS AND METHODS

Dominance interactions among nestmates were recorded under field conditions in 8 colonies of the basal eusocial wasp *Mischocyttarus (Monogynoecus) montei* (Fig. 1) in pre and post-emergence phases of colonial development. The observations were carried out at the campus of the Universidade Estadual

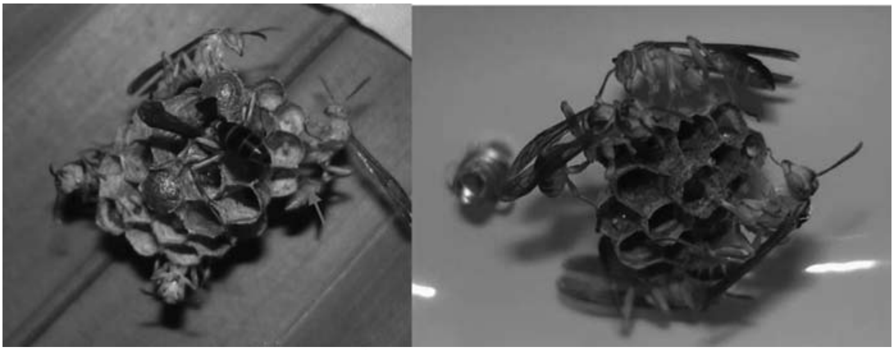

Fig.1. Two colonies of *Mischocyttarus (M.) montei*. It's possible to see that the ventral portion of gaster (arrow) is whitish which differs from *M. cerberus styx*, where it is totally black. (Photos by Guilherme Gomes)

Table1. Colonies of *Mischocyttarus (M.) montei* observed in this study.

Colony	Period of observation	Time of observation (hours)	Colony phase
I*	Jan/03 to Mar/03	16.3	Pre-emergence
II*	Mar/03 to Jun/03	12.0	Pre-emergence
III*	Mar/03 to Jun/03	12.3	Pre-emergence
IV*	Mar/03 to Jun/03	10.0	Pre-emergence
V#	Apr/02 to Feb/03	37.3	Post-emergence
VI#	Mar/02 to Mar/03	35.3	Post-emergence
VII	May/02 to Dec/02	29.6	Post-emergence
VIII	Nov/02 to Jan/03	11.6	Post-emergence

* These colonies were found from known colonies in post-emergence stage and then the dominance hierarchy was pre-established;

In these two colonies tradeoffs in the hierarchical rank were observed, data was taken after the stabilization of the new social rank.

Paulista (UNESP), in Rio Claro, São Paulo state, southeastern Brazil. Each colony was mapped weekly from March 2002 to June 2003 to establish their stages of development and observed during 164.4 hours (Table 1).

The colonial phases of development were identified and classified according to Jeanne (1972) as follows: (1) Pre-emergence (PE) – period from the colony foundation to the emergence of the first adult and (2) Post-emergence (PO) – period from the emergence of the first adult to the decline of the colony. A colony was considered to be in decline when it had more than 50% of empty cells and the presence of few nestmates.

The individuals were marked with acrylic, non-toxic, fast-drying paint to identify their position in the dominance hierarchy. Ethological data were collected based on the studies of several authors (Jeanne; 1972; Itô 1985; West-Eberhard 1986; Noda *et al.* 2001) and a brief description of the behaviors used to discriminate the hierarchical position of the females is provided as follows:

Trophallaxis: Exchange of fluids among nestmates. The dominant female usually receives a larger share of the load brought by incoming foragers (O'Donnell 1998; Prezoto *et al.* 2004);

Approach: the simple presence or approach of the dominant female, without any body contact. It may act as a signal of aggressiveness, leading the other nestmates to move away or change their position in the nest. Commonly, the subordinate females assume a submissive posture, lowering the antennas, wrinkling the legs and wings;

Attack type I: it occurs when a dominant female, initially in resting position, suddenly attacks a subordinate female in movement;

Attack type II: while moving in the nest, a dominant female detects a subordinate resting and immediately attacks her. This behavior acts as a signal for the subordinate female to start an in-nest task or to forage;

Evade: once in the presence of the main egg-layer or during an attack attempt, the subordinate female tries to avoid physical contact with the dominant to preserve its body integrity.

All statistics were conducted using STATSOFT STATISTICA 8.0®. The absolute frequency of dominance behaviors were corrected by the time of observation and the number of individuals which directly participated of the social hierarchy in each colony. Since data did not follow a normal distribution nor the variances were homogenous, we performed non-parametric statistics. The comparisons were tested using Mann-Whitney U test.

RESULTS AND DISCUSSION

In the four pre-emergence colonies of *Mischocyttarus (M.) montei* (I, II, III, and IV), which were founded from previously known colonies (Table 1), the first ranked female was the most dominant individual. These females performed the majority of interactions observed in this phase being responsible for 95.92%, 84.85%, 63.27% and 56.06% of the total number of interactions recorded in their colonies, respectively (Tables, 2, 3, 4 and 5). These results are different from those reported by Noda *et al.* (2001), which have demonstrated that during pre-emergence of *M.cerberus styx,* the totality of dominance acts were performed exclusively by the first ranked females. Similar results were obtained in *M. cassununga* in the pre-emergence stage (Prezoto *et al.* 2004).

According to Prezoto *et al.* (2004) the dominant females in colonies of pre-emergence of *M. cassununga* were by far the most aggressive individuals of the colonies, since they were engaged in ensuring their role as main egg-layers in the nest. Possibly, the differences found between *M. cerberus styx*, *M. cassununga* and *M. montei* are due to the fact that the colonies of *M. montei* observed in pre-emergence were founded by females whose hierarchy was defined in the natal nest, and consequently, the level of genetic relatedness among those females was high (full-sisters). Such characteristics explain the low level of aggressiveness found in the pre-emergence phase of *M. montei.*

Table 2. Absolute frequency of dominance acts registered in colony I (pre-emergence) of *Mischocyttarus (M.) montei*. Rows represent dominance and columns subordination.

Rank	1	2	3	Total
1	-	40	7	47
2	0	-	2	2
3	0	0	-	0
Total	0	40	9	49

Table 3. Absolute frequency of dominance acts registered in colony II (pre-emergence) of *Mischocyttarus (M.) montei*. Rows represent dominance and columns subordination.

Rank	1	2	3	Total
1	-	19	9	28
2	0	-	2	2
3	1	2	-	3
Total	1	21	11	33

Table 4. Absolute frequency of dominance acts registered in colony III (pre-emergence) of *Mischocyttarus (M.) montei*. Lines represent dominance and columns subordination.

Rank	1	2	3	4	5	Total
1	-	11	10	4	6	31
2	0	-	6	2	5	13
3	0	0	-	0	2	2
4	0	0	1	-	1	2
5	0	0	1	0	-	1
Total	0	11	18	6	14	49

Table 5. Absolute frequency of dominance acts registered in colony VI (pre-emergence) of *Mischocyttarus (M.) montei*. Lines represent dominance and columns subordination.

Rank	1	2	3	4	5	Total
1	-	19	13	2	3	37
2	0	-	11	5	5	21
3	2	0	-	4	2	8
4	0	0	0	-	0	0
5	0	0	0	0	-	0
Total	2	19	24	11	10	66

It is interesting to note that despite the fact that these species belong to the same genera, they have unique characteristics that may affect the pattern of social dominance in each species. In *M. cassununga,* it is rare to find a foundation by pleometrosis and the hierarchy is remarkably stable (Murakami & Shima 2006, 2009, 2010). On the other hand, in *M. montei,* most of the colonies are founded by association of few cohorts and new colonies are commonly founded by females whose dominance hierarchy was pre-established during post-emergence in their natal nest. In fact, this occurred in 100% (n=4) of the colonies studied in pre-emergence (Table 1). According to Itô (1987), in species that found their nest mostly by association, such as *M. montei*, the agonistic interactions during pre-emergence tend to be softer. This would be adaptive, since females may tolerate each other in the same nest, the odds of mortality of the main egg-layer, as well as other individuals also essential to the maintenance of colonial functions, would be smaller and the chance of colony success would be higher. However, this proposal was never properly

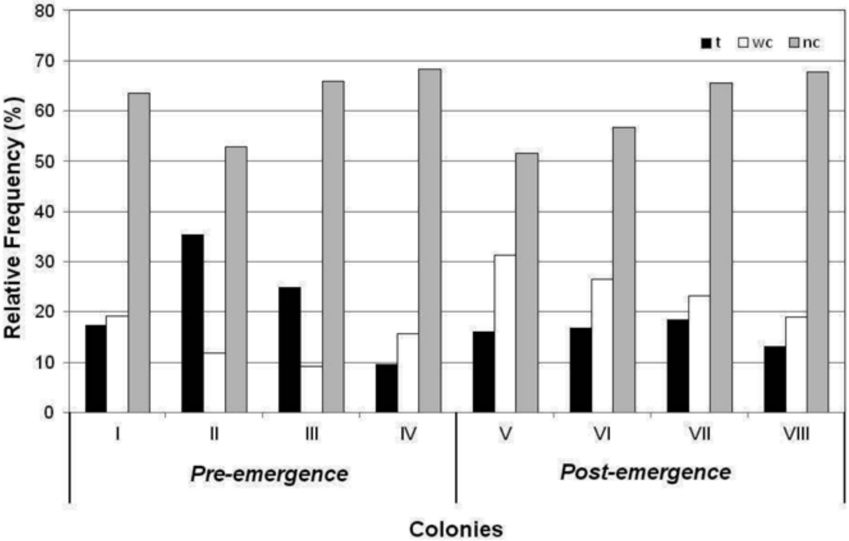

Fig. 2. Relative frequency of dominance acts performed by the females of *Mischocyttarus (Monogynoecus) montei* in the different phases of colony development (t – *trophallaxis*; wc – dominance acts involving direct physical contact; nc – dominance acts without physical contact).

tested. It is clear that the females of *M. montei* try to avoid direct contact, and the interactions without physical contact are much more common than those involving direct contact (Fig. 2). Another fact that may explain the low level of aggressiveness in pre-emergence colonies of *Mischocyttarus (M.) montei* is the characteristics of the foundations observed in the colonies studied; every colony was founded by an association of females from a pre-existent colony in post-emergence, so the hierarchy was already established. This type of foundation is common in this species (Oliveira 2003, 2007) and must be an important feature to guarantee the success of pre-emergence colonies.

Itô (1985) reported that aggressive interactions in pre-emergence colonies of *Ropalidia fasciata*, *Polistes versicolor*, *Mischocyttarus angularis* and *M. basimacula* were significantly less intense than in *P. canadensis*. In *M. angulatus,* no agonistic interactions were recorded during the pre-emergence stage and *P. versicolor* sustained a low level of aggressiveness even during post-emergence stage. In *M. angularis* and *M. basimacula,* the intensity and frequency of dominance acts increased during post-emergence. Noda *et al.* (2001) found the same pattern for *M. cerberus styx*; the absolute frequency of dominance acts was greater in post-emergence. In *M. drewseni*, as the first foragers emerge, the frequency of dominance acts increases and the dominant females establish its reproductive superiority during the first 10-15 days after the emergence of foragers. After the establishment of dominance, the frequency of acts decreased significantly once the hierarchy was already established (Jeanne 1972).

Tables 6, 7, 8 and 9 show the absolute frequency of dominance and subordination interactions during the post-emergence phase of *M. montei.* It is clear that the absolute frequency of agonistic interactions is greater than in the pre-emergence stage; this fact was also reported by other authors (Noda *et al.* 2001; Prezoto *et al.* 2004 and Murakami & Shima 2006). In post-emergence, the first ranked female performed a considerable share of the dominance behaviors recorded, represented by 60.6%, 45%, 35% and 61.7%, respectively. These values, however, were consistently smaller than in pre-emergence. The only exception occurred in colony VII, where the 2nd ranked female performed slightly more dominance acts than the first one; however, she was heavily dominated by the dominant female (Table 8).

In post-emergence, the number of individuals increases, more cells are available to lay eggs and consequently the competition for reproductive domi-

Table 6. Absolute frequency of dominance acts registered in colony V (post-emergence) of *Mischocyttarus (M.) montei*. Lines represent dominance and columns subordination.

Rank	1	2	3	4	5	6	7	8	Total
1	-	65	34	15	8	6	6	3	137
2	1	-	29	16	8	2	5	1	61
3	0	1	-	2	3	4	3	0	13
4	0	0	0	-	0	0	5	0	5
5	1	0	0	2	-	0	0	2	5
6	0	0	0	0	1	-	0	0	1
7	0	0	0	1	0	0	-	1	2
8	0	0	0	0	1	0	1	-	2
Total	2	66	63	36	21	12	20	7	226

*The 1st ranked female disappeared from the colony, the 2nd assumed the post of dominant, and after that the 2nd lost its post to the 3rd. After the stabilization of the new rank, the data was collected.

Table 7. Absolute frequency of dominance acts registered in colony VI (post-emergence) of *Mischocyttarus (M.) montei*. Rows represent dominance and columns subordination.

Rank	1	2	3	4	5	6	Total
1	-	36	27	6	7	8	84
2	1	-	46	11	11	4	73
3	1	1	-	9	5	2	18
4	3	1	0	-	1	3	8
5	0	0	0	0	-	0	0
6	0	0	0	0	0	-	0
Total	5	38	73	26	24	17	183

*The 1st ranked female disappeared from the colony and its post was occupied by the 2nd ranked female. After the stabilization of the new rank, the data was collected.

nance is more intense. However, when comparing the absolute frequencies/hour/individual between the two phases, no statistical differences were found (Mann-Whitney Z=0.28, p=0.77) (Fig. 3). Such results may be explained by the fact that in post-emergence, more individuals participate of dominance and subordination interactions, including typical foragers (Tables 6-9). This may have diluted the number of interactions in post-emergence, explaining the finding of no statistical difference between the two phases. In fact, 92% (646/701) of the total dominance acts displayed in post-emergence were performed by the three higher ranked females of each colony. It is also worth mentioning that, although the relative frequency of dominance acts were not

Table 8. Absolute frequency of dominance acts registered in colony VII (post-emergence) of *Mischocyttarus (M.) montei*. Rows represent dominance and columns subordination (F indicates foragers).

Rank	1	2	3	4	5	6	F(n=4)	Total
1	-	30	12	9	2	2	4	59
2	2	-	20	13	4	5	20	62
3	0	0	-	6	5	1	9	21
4	0	0	0	-	1	2	5	8
5	0	0	0	0	-	0	1	1
6	0	0	0	0	0	-	0	0
F(n=4)	0	3	0	0	5	1	2	11
Total	2	33	32	28	17	11	41	162

Table 9. Absolute frequency of dominance acts registered in colony VIII (post-emergence) of *Mischocyttarus (M.) montei*. Rows represent dominance and columns subordination. (F indicates foragers)

Rank	1	2	3	4	F(n=5)	Total
1	-	32	17	10	15	79
2	0	-	12	7	11	30
3	1	0	-	0	8	9
4	0	0	0	-	5	5
F(n=5)	0	1	0	1	3	5
Total	1	33	29	19	42	128

statistically different between the two phases, our data showed that the median frequency (%) of dominance interaction involving physical contact was statistically higher in the post-emergence ($Freq_{PE}$=13.66%; $Freq_{PO}$=24.80%; Z=2.02, p=0.04) (Fig. 2). These results showed that the competition for reproductive dominance in *M. montei* during post-emergence stage is more intense than in pre-emergence. The exchanges in social rank occur more frequently during post-emergence phase. The dominant supersedure occurred in 50% (n=2, Colonies I and II, Tables 6 and 7) of the colonies studied in this phase. Queen supersedure was reported by some authors, especially in *Polistes*, during the late post-emergence, when the competition for reproductive dominance is stronger (Strassamann 1981; Miyano 1986). Recently, Murakami and Shima (2009) reported a case of dominant supersedure in *M. cassununga*, however, the authors classified this as a very rare event. In

M. montei, exchanges are common (Oliveira 2003; 2007), indicating a less stable hierarchy when compared to *M. cassununga*. This fact may explain the reason why a group of females leaves the natal nest and founds a new nest in the neighborhood. This is caused by a conflict which affects the productivity of the colony through cannibalism of eggs and larvae (in prep.). When this occurs, the only way to maintain the development of the natal nest in post-emergence is the colonial fission, in which the most dominant female and the typical foragers remain in the natal nest, while the higher ranked females (usually involved in the colonial conflict) leave the nest.

This colonial fission, which is different from a natural dispersion, once reproductive individuals are not being produced yet, is adaptive, since it allows the natal nest to keep developing to the natural decline. Additionally,

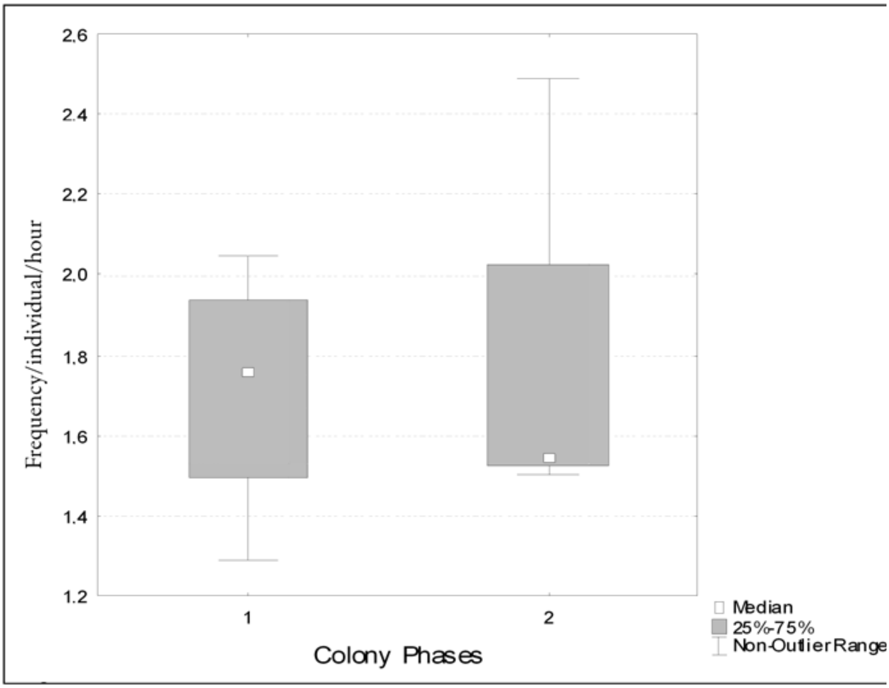

Fig. 3. Box-plots indicating the median, 25th and 75th percentiles and non-outlier range of the frequency/individuals/hour of dominance interactions in the two phases of colonial development. 1 – pre-emergence, 2 – post-emergence. The results of the Mann-Whitney test were not significant (Z=0.28; p=0.77).

this pattern allows the foundation of new colonies by highly related females, ensuring a low level of conflict during pre-emergence stage. If such fission, related to the dispersion of the higher ranked females, did not occur, the colony would decline prematurely. Therefore, such a mechanism is adaptive, as it allows the species to maximize its dispersion without the cost of derailing the natal nest. There are few studies in the literature regarding this pattern of fission in social wasps. Gadagkar and Joshi (1985) reported that the high level of aggression found in *Ropalidia cyathiformes* before the colony fission could be a consequence of the reproductive competition among nestmates. The authors suggested that the high level of aggression decreased the level of brood production. These results were similar to those found in *M. montei* (in prep). Most of the studies available in the literature are related to the natural dispersion of the colonies; Litte (1977) showed that the females of three nests of *Mischocyttarus mexicanus* dispersed and regrouped in small groups during the fall (proper time for the dispersion of reproductive females). The authors also reported that all wasps within each group were derived from the same natal nest.

Finally, we conclude that: (1) the colonial fission caused by a conflict during post-emergence phase, but not by natural dispersion, may promote the foundation of new colonies by females with defined social dominance hierarchy, which may explain the low level of dominance interactions found in pre-emergence; (2) the fact that no statistical difference was found in the relative frequency of dominance interactions between the phases of development indicate that, in post-emergence, more females participated in these interactions, including typical foragers, which diluted the frequency of interactions in post-emergence. However, the median relative frequency of interactions involving physical contacts was statistically higher in post-emergence, and these interactions were displayed mostly by the three higher ranked females of each colony; (3) *M. montei* have two types of colonial foundation: (a) by a fission caused by a conflict, such characteristics are adaptive since it prevents that the natal nest declines prematurely; (b) by natural dispersion, after production of reproductive individuals. In both cases, the colonies are maintained by females with high level of relatedness (this was inferred as all females were marked and observed continuously) increasing the odds of colonial success.

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