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Task division and Age Polyethism in colonies of *Mischocyttarus latior* social wasps (Fox) (Hymenoptera: Vespidae)

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Abstract

This paper aimed to study the division of labor between queen and workers, division of labor by age range and sequence of behavioral patterns exercised by females and males from *Mischocyttarus latior* (F.) colonies. Behaviors of 13 dominant females (queens), 68 subordinate (workers) from emergence until they are 77 days and 12 males in 37 colonies were quantified during 545 hours. There were 23 behavioral acts registered divided into five categories. Both dominant females as the workers showed a behavioral repertoire of 23 items, while males only 15. Dominants remain longer on the nest than subordinates and exercise exclusively the behavior of oviposition and rubbing gaster on the nest. Dominants also share 21 behaviors with the workers. Males foraged nectar, preys and water, and exercise other behaviors, mostly related to social activity. All behaviors can be performed by any potentially worker at any age.

Introduction

In Polistini and Mischocyttarini wasps, called "primitively eusocial" which present independent foundation, by haplometrosis (solitary) or pleometrosis (addition of co-founders), there is no morphological differentiation of castes and determining the hierarchyis made based on aggressive interactions (Jeanne, 1972; Gadagkar, 1991).

Giannotti (1999) registered 24 behavioral categories for *Mischocyttarus cerberus styx* (R.), 19 categories for founders (in the pre-emergence), 20 for queens and 18 for workers (post-emergence). Considering the founders and queens, the first appear to be more active, since they carry all the maintenance tasks of the nest and forage more frequently, while the queens remain unmoved more often. Torres et al. (2012) studying the behavioral repertoire related to division of labor in *Mischocyttarus consimilis* Z. registered 30 behavioral acts, of which 23 were executed by queens and 29 workers, and 22 acts common to both castes. The act of starting new cells was the only behavior unique to queens. Behaviors of submission are usually related to workers (Jeanne, 1972; Giannotti, 1999; Giannotti & Machado, 1999; Torres et al. 2009).

Males in social wasps colonies usually perform, mostly, behaviors related to their own survival, although they may perform other activities such as caring for the larvae (Spradbery, 1965; Jeanne, 1972; Raposo-Filho, 1981; O'Donnell, 1999; Sinzato et al. 2003; Giannotti, 2004). Giannotti (2004) considers the possibility that males play a greater number of tasks within the colony in wasp species which they are morphologically similar to the females.

Mischocyttarus latior (F.) is a social wasp present in the Midwest region and common in the Southeast region of Brazil (Richards, 1978; Elpino-Campos et al. 2007; Lima et al. 2010). Their larvae present five instars and the mean duration of the immature stages, from egg laying to adult emergence, is 67.38 ± 9.41 days (Cecílio et al. 2015). The males present length

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of the wing and a similar staining pattern to the females although the legs and lower portion more brownish (Richards, 1978).

The work aimed to study the division of labor between queen and workers, division of labor by age range and sequence of behavioral patterns exercised by females and males from colonies of *M. latior*.

Materials and Methods

The study was conducted in the Campus of Universidade Estadual Paulista Júlio de Mesquita Filho (UNESP) and in the Distrito (district) Ferraz city of Rio Claro, São Paulo, Brazil (22º24'36'' S - 47º33'36'' W), from March 1994 to August 1995.

Prior to the performance of observations, all subjects of the 37 colonies were collected with the help of an insect net and marked on the thorax with model airplanes ink. The same was done with the females as soon as they emerged. To quantify the behavioral categories of the subjects, daily observation sessions of one hour were done, in the hottest periods of the day and hence of greater activity of the wasps, for 77 days. In them, the behavioral acts were recorded for each adult subject (dominant and subordinate females in addition to males) at five minute intervals, totaling 545 hours. It was also registered the position occupied on the nest (on the cells, the side of the nest, behind the nest, in the substrate, out of the nest).

The χ^2 test was applied for two independent samples (Siegel, 1979), in order to verify the significance of the behavioral differences between queens and workers. This procedure also allowed the study of the variation of the different tasks performed by individuals in the colony according to their age range.

Results and Discussion

The behaviors of 13 dominant females were recorded (queens), 68 subordinate (workers) and 12 males, as well as the spatial position occupied on the nest.

Spatial position. Through Fig 1, we can observe the spatial position occupied by wasps. The dominant females remained much longer on the cells (87.2%) that workers, 38.6% ($\chi^2 = 432.42$; $P < 0.001$; G.L. = 1) which indicates the dominance of the first over the subordinates (workers). But behind the nest, there is an inversion and the workers come to occupy 13.3% of the time and queens, only 1.6% ($\chi^2 = 97.32$; $P < 0.001$; G.L. = 1). Regarding the position in the substrate, the workers were 0.8% and queens did not occupy this place at any time. When it is analyzed the location on the side of the nest, it is apparent that the workers remained 19.2% and queens, 4.3% ($\chi^2 = 108.48$; $P < 0.001$; G.L. = 1), showing once more the dominant / subordinate relationship. The workers remained more time out of the nest: 28.1% of the time and queens for only 6.9% ($\chi^2 = 149.65$; $P < 0.001$; G.L. = 1). On the other hand, the males remained 13.0% on the cells, behind the nest 6.4%, 0.5% on the substrate, 17.3% at the side of the nest and 62.9%, outside the nest.

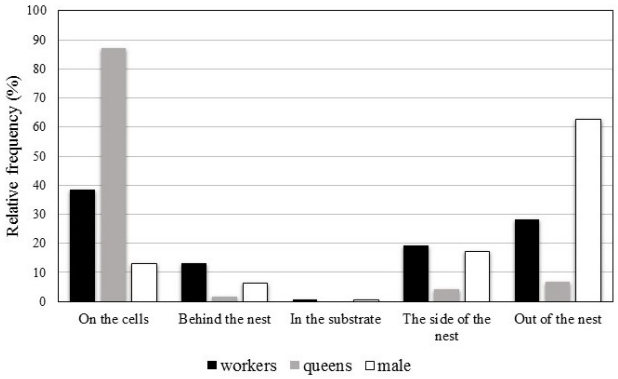

Fig 1. Positions of females (subordinates and dominants) and males on the nests of *Mischocyttarus latior* (Fox, 1898).

Behavioral Repertoire. Table 1 shows the 23 behavioral acts, exercised by individuals of *M. latior* colonies, distributed over five categories, described according to Giannotti (1999), as follows:

I. Social Activity

1. Check cells. The wasps insert their heads on the nest, fumbling with antennas its contents.

2. Check the cells rubbing the gaster against the nest. According to Gamboa and Dew (1981) this behavior may be related to dominance, and represents a kind of communication between adults and larvae.

3. Trophallaxis adult-adult (receiver). Is the receiving of ingluvial liquid among adults (usually nectar of flowers or other sugary substances). As described by West-Eberhard (1969), there is a clear difference in the donor (subordinate) postureto the receiver (dominant), then considered, as two distinct behaviors.

4. Trophallaxis adult-adult (donor). Is the passage of ingluvial liquid among adults (usually nectar of flowers or other sugary substances).

5. Trophallaxis larva-adult. Is the passage of liquid feed (secretion of the salivary gland) from the larva to the adult. It is perceived when the adult, checking cells, makes a longer insertion in a cell containing a larva.

6. Feed larvae. It occurs after chewing, when adults provide a protein juice, which is the principal source of food for larvae.

7. Physically dominate. A wasp in a higher position in the social hierarchy of the colony slightly nibbles or even climbs up on the subordinate.

8. Being physically dominated. Involves the act of the individual to stand passively before the one which dominates or even retreat or fly out of the nest.

II. Oviposition

9. Lay eggs in an empty or newly built cell. The female inserted the gaster in the cell and laid eggs. This behavior lasts 4.5 minutes on average.

III. Nest Maintenance Activity

10. Add material to the cells. As the larvae develop, wasps deposit material in the cell, increasing its height.

11. Ventilate cells. There is a flutter of wings in order to cool the nest. May or may not be associated with the collection of water.

12. Giving alarm. Wasps take a high posture, lifting and opening the wings and directing the antennas to the source of disturbance. Usually they perform a "back-and-forth" movement with the gaster, which is probably related to the dispersion of alarm pheromone.

13. Chewing prey. Wasps chew a piece of solid feed.

14. Apply oral secretion to the nest. The application of this secretion has been observed in the stem and over the top of the nest, making the surface more darkened and shiny, resembling a varnish. This secretion offers more rigidity to these structures and is a protection against parasitoids.

15. Apply gastral glands secretion to the nest pedicel. As studied by Jeanne (1972) and Turillazzi and Ugolini (1979), wasps rub the gaster against the nest pedicel, particularly in the pre-emergence stage, dispersing a secretion that has repellent properties to ants (predators of wasps nests). Depending on the intensity of the stimulus, the wasps vibrate their wings and walk on the nest in fast-moving movements, producing characteristic noises and only after that they attack the disturbing agent.

IV. Foraging activity

16. Unsuccessful foraging. It occurs with the outing of the wasp and subsequent return, without bringing anything to the nest.

17. Prey foraging. It is the act when the wasp leaves the nest to go in search of food, in general caterpillars. When the wasp reaches the nest, it can share or not the material collected with a companion before chewing the prey and give to the larvae.

18. Foraging nectar. The foraging returns without anything visible in the mouth, but always makes trophallaxis with other wasps.

19. Foraging water. The foraging comes back with a visible droplet between the jaws and deposits iton the cells, without dividing it with another wasp. It was observed in warmer weather days, as it is associated with the maintenance of the nest temperature.

20. Wood pulp foraging (nest building material). After an average of 7.5 minutes period, the foraging returns to the nest with a wood pulp acorn in the jaws to add material to the nest cells.

V. Individual Behaviors

21. Immobile on the nest. It occurson the nest or in the substrate, apparently at rest.

22. Self-grooming. The wasp rubs the legs against each other, against the antennae, head, chest, wings, abdomen and finally licks the front legs. It could be partial or total. This behavior is exhibited, mostly, after performing any task on the nest.

23. Walk. Walking on the nest or in the substrate.

Dominant and Subordinate Behavior. Both the dominant females as the workers showed a behavioral repertoire of 23 items, while the males only 15 ($\chi^2 = 827.75$; $P > 0.001$; G.L = 3).

The number of quantified behavioral categories for some species of social wasps can be variable: *Polistes chinensis antennalis* (F.) presented 34 to 36 behavioral categories in colonies in the stages of pre and post-emergence, respectively (Kasuya, 1983a,b); 37, in *Polistes fuscatus variatus* (F.) (Post et al., 1988.); 31 in *Polybia occidentalis* (O.) (Jeanne et al., 1988.); 27, in *Polistes dominulus* (C.) (Theraulaz et al., 1990), 28, in *Polistes lanio lanio* (F.) (Giannotti, 1992), 24 in *Mischocyttarus cerberus styx* (R.) (Giannotti, 1999), 28 in *P. canadensis canadensis* (L.) (Torres et al. 2009), 30 in *Mischocyttarus consimilis* Z. (Torres et al., 2012) and 42 behavioral acts performed by *Mischocyttarus parallelogrammus* Z. (Togni, 2014).

Standing still occurs in the same way for workers and queens. It is common in other species of the genus that females remain still for a long time on the nest (Giannotti, 1999; Torres et al., 2012). The individual suddenly stops, remaining so for a very variable time, and always with the wings on the gaster, never under. The *M. latior* queens were the ones that remained more time standing still on the nest (42.1%), while the workers stayed 39.2% of the time ($\chi^2 = 1.79$; $P < 0.05$; G.L. = 1). These figures show that, despite the workers having a more active life than queens, it cannot be said that there is a tendency in one or another class to carry out this behavior more times.

The subordinate cleaned up less often than the dominant ($\chi^2 = 58.40$; $P < 0.001$; G.L. = 1). These figures show that queens perform more this behavior as they remain longer on the nest, while the workers are more active, that is, spend a great deal of time on foraging activities. The behavioral sequence of cleaning is equal to queens and workers. The wasp stands immobile on the nest and performs the self-grooming. The average time in queens was 18.41 seconds ± 36.13 (1.57 – 131.82) and for workers, 12.77 ± 15.20 (1.64 – 101.41). More specifically, this cleaning can occur only in the antennae (passing the front legs in the mouthparts and over the same). This latter behavior had an average duration of 6.0 seconds ± 12.81 (3.46 – 36.09) for the workers and 5.03 seconds ± 2.97 (1.57 – 10.71) for the queens. For only in the front legs (rubbing one leg against each other), the average time for workers was 12.68 seconds ± 15.45 (1.64 – 61.41) and for queens, 67.75 seconds ± 34.04 (43.68 – 91.82). For only the rear legs and wings (rubbing one leg against the other, passing over and under the gaster, rubbing the leg again and then passing over the wing, repeating this sequence many times). The average time for workers was 4.75 seconds ± 3.82 (2.37 – 11.50) and for queens, 12.59 seconds ± 16.05 (4.03 – 45.00). A clean sweep, in which all the above described sequences are performed, the average duration for the workers was 28.26 seconds ± 22.46 (2.41 – 42.97) and for the queens, 16.41 seconds ± 10.41 (4.90 – 33.84).

Walking through the nest or in the substrate was a behavior observed mostly for queens and in less number for workers ($\chi^2 = 13.74$; $P < 0.001$; G.L. = 1) demonstrating that as the queens are longer on the nest, they perform more this behavioral act of walking, which may represent a type of patrolling against parasitoids, as Ichneumonidae wasps, which have been observed surrounding the nest. However, this observation would need to be deepened.

Considering the social activities carried out by *M. latior* wasps, there was a greater behavioral frequency for the queens checking cells than to the workers ($\chi^2 = 35.93$; $P < 0.001$; G.L. = 1). This demonstrates that the dominant has greater parental care, besides the fact that it spends most of the time on the nest. Checking cells was a behavior that consisted in the same sequence for both dominant and subordinate, as follows: wasps pass their antennas through the opening of the cell, insert their head in it (sometimes also the thorax) and remove quickly. The duration of this action is very fast, being approximately 1 second.

Although for Gamboa and Dew (1981) the behavior of verifying cells rubbing the gaster against the nest may be related to the dominance, besides representing a kind of communication between adults and larvae, in *M. latior*, there was no significant difference in the frequency of this behavior between queens and workers ($\chi^2 = 1.53$; $P > 0.05$; G.L. = 1).

With respect to trophallaxis, taking into account the receiver behavior, it was found that queens receive a greater amount of food than workers ($\chi^2 = 36.31$; $P < 0.001$; G.L. = 1), confirming the dominant/subordinate relationship. In relation to the donation behavior, it was observed that both the workers and the queens, donate food ($\chi^2 = 0.21$; $P > 0.05$; G.L. = 1), with no significant difference. Both for dominant and subordinate the behavior sequence to adult-adult trophallaxis as receiver was the same. The individual walked on the nest, quickly invested in the wasp that was effecting the donation, performed an antennal beat on the head of those who donated (probably to whoever was donating enter the proper position), acquired a dominant stance on it (who received was up and who donated below). Thus performed the exchange of materials and generally cleaned-up (mainly antennas), for approximately 2.99 seconds ± 1.08 (2.06 – 4.96) for queens and 5.49 seconds ± 2.99 (2.10 – 10.46) for workers. For the latter, this value was considered for both the receiving behavior as for the donation. To queens it was not verified the sequence of donation behavior to others.

There was no significant difference in frequency of the trophallaxis larva-adult between subordinates and dominants ($\chi^2 = 0.16$; $P > 0.05$; G.L. = 1). Both castes receive "larval salivary" and, likewise, it was found that both varieties feed larvae (workers, 1.5%, and queens 0.7%), with no significant difference ($\chi^2 = 1.66$; $P > 0.05$; G.L. = 1). The individual walked on the nest, checked the contents of the cell with antennas, placed the head and chest in it and performed trophallaxis with the larva. The average time was 5.83 seconds ± 5.57 (2.14 – 22.96).

For queens and workers, the behavior sequence to perform trophallaxis between larva and adult was the same. They approach the opening of the cell, make an antennal recognition, insert a part of the body (head and thorax), perform trophallaxis with the larva and usually clean the mouth parts after the act. For the dominants, the average time was 7.10 seconds ± 5.43 (2.13 – 26.47) and for the workers it was 4.97 seconds ± 3.55 (1.87 – 15.58).

In relation to dominance, as we have already seen, the queens dominate a larger number of times (12.5%) and the workers only 1.1% ($\chi^2 = 330.80$; $P < 0.001$; G.L. = 1), confirming what was found in the literature (Pardi, 1948; West-Eberhard, 1969; Giannotti & Machado, 1999; Torres et al. 2012), emphasizing that such behavior is used as a "method" of domination. And as expected, it was found that the workers are physically dominated in a greater number of times, while this behavior in queens almost never happens (0.6%) ($\chi^2 = 25.10$; $P < 0.001$; G.L. = 1). When it occurs, the subordinate does so only investing against the dominant without showing too much aggression. This action usually occurs when there is competition for dominance in the colony. It is seen that in *M. latior* queens, dominance behavior occurs in two ways: it can walk towards the worker and then nibble it, or walk towards it and attack, though without physical contact (this assault can happen more than once to the same individual in the same act to master). Among workers, this behavior occurs in much the same way; the only difference is the less aggressiveness with which the action is carried by these.

Considering the nest maintenance activities, ventilate cells and chew prey were the most executed by both queens and workers. The dominants presented 0.4% of the behavior to ventilate cells and the subordinate 0.4% ($\chi^2 = 0.00$; $P > 0.05$; G.L. = 1), so this is not significant. Ventilate cells occurred once for dominants by 2.75 seconds. The behavioral sequence was as follows: they vibrated frantically the antennas, directing the body towards the cells and intensely shaking the wings. For workers, the act occurred, on average, for 0.82 seconds ± 0.16 (0.60 – 1.00). For them, the sequence occurred without vibration of the antennas and sometimes between the cleaning-up behavior.

It was observed a greater number of queens (0.8%) chewing preys than workers (0.4%), but the values were not significant ($\chi^2 = 2.19$; $P > 0.05$; G.L. = 1). As the larvae were developing, it was seen that both the queens added material into the cells (1.7%) as the workers (0.3%) ($\chi^2 = 28.42$; $P < 0.001$; G.L. = 1).

Considering the defensive behavior, "to alarm" was the same for both castes (0.1%) ($\chi^2 = 0.03$; $P > 0.05$; G.L. = 1). Apply oral secretion on the nest was the only task performed exclusively by workers (0.1%). As for applying gastral glands secretion on the nest pedicel, this behavior was observed in both queens (0.2%) and workers (0.0002%) ($\chi^2 = 4.31$; $P < 0.05$; G.L. = 1), suggesting a behavior related to the permanence time in the colony. The alarm behavior occurs in the same way for both workers and queens. When individuals perceive a threat against the nest, they perform the

following behavioral sequence: immobile on the nest, raise their wings, raise the body, flap their wings causing a loud noise, move through the colony flapping wings and legs against the nest, what causes the sound to be even more intense, and finally attack the disturbing agent. The average time for this behavior (beginning of the act until rest) was 13.78 seconds ± 4.36 (10.69 – 16.87).

With respect to behavioral acts related to the foraging activity, the workers foraged prey much more often than queens ($\chi^2 = 33.45$; $P < 0.001$; G.L. = 1) since this activity requires more time out of the nest and therefore the queen rarely exercises.

Forage nectar is also a much more frequent behavior for workers than for queens ($\chi^2 = 165.87$; $P < 0.001$; G.L. = 1), thus proving the high rate of this activity by workers. Foraging water was a behavior most often done by workers than queens ($\chi^2 = 54.25$; $P < 0.001$; G.L. = 1), showing again the high rate of foraging activity of workers within a colony.

The value found for wood pulp collection was 1.8% for the workers and 2.5% for queens ($\chi^2 = 1.87$; $P > 0.05$; G.L. = 1) and although it most frequently occurs among the queens, such behavior was not significant. Giannotti and Machado (1999) considered that the collection of pulp is the main foraging activity exercised by queens of *P. lanio lanio*. According to West-Eberhard (1969) the dominant females are in charge of the construction of new cells, some of them laying eggs right in sequence, similar to what was observed for *P. canadensis*. For the author, the occasional foraging trips are aimed at collecting material for nest building (pulp and water). Giannotti (1999) noted that in wasps of the species *M. cerberus styx*, both founders as queens, collected wood pulp more intensively than the workers. These data differ from those observed by Torres et al. (2009) to *P. canadensis canadensis*, whose queens only collected prays and still in a much smaller proportion than the workers. On the contrary, *Polistes versicolor* O. in the foundation phase collected all the features except prey, having an equal proportion between queens and workers in wood pulp collection (Sinzato & Prezoto, 2000).

The return to the nest without success was another prevalent behavior in the workers, and little seen in queens ($\chi^2 = 35.44$; $P < 0.001$; G.L. = 1) since the workers go out of the nest more often to forage and therefore are more subject to an unsuccessful output.

There was no any particular behavioral sequence for the act of foraging. The individual went out flying straight from the nest, or it happened to walk on the colony and fly, or walked off the substrate and then flew. It has been observed only once, a worker making two wing beats prior to leaving for the field. In one of the leavings of a dominant for foraging nectar, the time observed was 139.52 seconds and a leaving for water foraging of a worker, this time was 9.21 seconds. It was also verified for the subordinates, the average times of 12.97 seconds ± 2.49 (10.10 – 14.55) to collect nectar and 0.28 seconds ± 0.12 (0.19 – 0.36) for unsuccessful foraging. It was observed that there occurs an induction via dominance for the leaving for foraging. This usually occurred after the foraging worker performed trophallaxis with other workers or with the queen and after feeding the larvae and cleansed. After these acts, the dominant or even other workers (hierarchically superior to the foraging worker), invested on it and practically forced it to make a new exit to the field.

The oviposition and rubbing of the gaster on the nest were unique behaviors of the dominant females, which presented 21 behaviors in common with the workers. This differs from *M. consimilis*, whose queens had just the act of starting new cells as the sole activity and the workers had seven unique behaviors (Torres et al., 2012). As for the males, they played no unique behavior (Table 1). This shows that there is not a clear division of labor between castes, but between the genders.

Male Behavior. It was observed that males foraged nectar, prays, water, and that many times there was an unsuccessful return (Table 1). Only the foraging of pulp to build new nest cells was not observed in males. Other behaviors observed for males of the present species involved social activity: check the cells, adult/adult trophallaxis (donor), larva/adult trophallaxis, adult/adult trophallaxis (receiver), feeding larvae, being physically dominated (and physically dominate. They performed an activity related to the maintenance of the colony (apply oral secretions to the nest, besides standing still, performing self-grooming of the body and walk the nest. The males are usually food receivers, both adults and larvae (Giannotti, 2004). However, it is noteworthy that there was adult/adult trophallaxis behavior (donor), even if a small percentage. O'Donnell (1995) reported the collection of nectar and later trophallaxis by males of *Polistes instabilis* S., even considering that the activities carried out on the nest by them have been at low rates. It is likely that this behavior is related to the fact that there is a need for food donations to females so they continue being accepted in the colony. According to O'Donnell (1995), production costs of males are compensated, in part, for any investments that they can make through their work.

In the colonies, males get food from various sources, including regurgitation of workers and salivary secretions of the larvae (Spradbery, 1965). The males of *Mischocyttarus drewseni* S. and *Mischocyttarus mastigophorus* R. also request, for their own consumption, nectar and macerated insects from the foraging workers that are returning (Jeanne, 1972 and O`Donnell, 1999 respectively). The *Mischocyttarus extinctus* Z. males also request proteic and glucidic food fromthe foraging workers. It was found that the males of this species leave the colony to forage; this fact could be followed because the colony was two meters away from the forage area. They frequented these areas because, probably, it was the place where we found matings, in addition to foraging (Raposo-Filho, 1981).

In addition to requesting food from foragers, *M. latior* males play a greater participation in the activities of the nest, as it occurs with *P. lanio lanio* (Giannotti, 2004). However, *M. latior* also plays foraging activities, not happening with this species.

Table 1. Ethogram of females (subordinates and dominants) and males of *Mischocyttarus latior* (Fox, 1898).

Behavioral Acts	Individuals in the Colony					
	Subordinates (n=68)		Dominants (n=13)		Males (n=12)	
	n	(%)	n	(%)	n	(%)
I Social Activity						
1. Check cells (CC)	182.0	4.2*	92.0	8.8*	26.0	3.9
2. Rub gaster on nest (RN)	1.0	0.0	2.0	0.2	0.0	0.0
3. Trophallaxis adult-adult (receiver) (TR)	59.0	1.3*	44.0	4.2*	9.0	1.3
4. Trophallaxis adult-adult (donor) (TD)	85.0	1.9	1.0	0.1	12.0	1.8
5. Trophallaxis larvae-adult (TL)	90.0	2.1	49.0	4.7	12.0	1.8
6. Feed the larvae (FL)	65.0	1.5	7.0	0.7	7.0	1.0
7. Dominate physically (DP)	49.0	1.1*	131.0	12.5*	6.0	0.9
8. Be physically dominated (BD)	156.0	3.6*	6.0	0.6*	12.0	1.8
II Oviposition						
9. Oviposit (OV)	0.0	0.0	1.0	0.1	0.0	0.0
III Nest Maintenance Activity						
10. Add material to cells (AM)	15.0	0.3	18.0	1.7	0.0	0.0
11. Ventilate cells (VL)	17.0	0.4	4.0	0.4	0.0	0.0
12. Give alarm (GA)	5.0	0.1	1.0	0.1	0.0	0.0
13. Chew prey (CP)	18.0	0.4	8.0	0.8	0.0	0.0
14. Apply buccal secretion to the nest (AB)	6.0	0.1	0.0	0.0	2.0	0.3
15. Apply gastral glands secretion (AG)	14.0	0.3	1.0	0.1	0.0	0.0
IV Foraging Activity						
16. Unfruitful Foraging (UF)	175.0	4.0*	3.0	0.3*	155.0	23.1
17. Foraging preys (FR)	175.0	4.0*	4.0	0.4*	39.0	5.8
18. Foraging Nectar (FN)	861.0	19.6*	19.0	1.8*	234.0	34.9
19. Foraging Water (FW)	351.0	8.0*	15.0	1.4*	7.0	1.0
20. Foraging Pulp (FP)	80.0	1.8	26.0	2.5	0.0	0.0
V Individual Behaviors						
21. Immobile on the nest (IN)	1718.0	39.2	441.0	42.1	92	13.7
22. Self-grooming (SG)	200.0	4.6*	114.0	10.9*	39.0	5.8
23. Walk (WA)	63.0	1.4*	61.0	5.8*	18.0	2.7
Total	**4385.0**	**100.0**	**1048.0**	**100.0**	**670.0**	**100.0**

*Values presenting significant difference among behaviors of dominants and subordinates.

Behavior According to Age. Table 2 shows the frequency of 17 behaviors performed by workers of *M. latior* at intervals of 1 to 11 weeks (up to 77 days):

One week range (1 to 7 days): It is verified that the most accomplished behavior by subordinates was to immobile on the nest (50.19%) and secondly, the forage (32.27%).

Two weeks range (8 to 14 days): It was observed a high foraging index (71.43%), showing that this is a typical behavior for workers of this age, as they gained more experience within the colony.

Three weeks age range (15 to 21 days): The activity of forage is the most accomplished behavior by workers, with 46.56% of the time, although there was a drop compared to the previous range. Second, the body self-grooming behavior was shown, with 13.30%, perhaps by the fact that the wasp had remained longer in the colony.

Four-week age range (22 to 28 days): It was found the highest percentage of foraging behavior (76.89%), reaffirming what has been said above that the experience is an important factor for the exit of workers to field. These data are similar to those found for workers of *P. lanio lanio* in a study by Giannotti and Machado (1994), where it was found that the foraging begins only in the second week and reaches its peak only in the fifth. The difference is that in this case, *M. latior* starts to perform foraging activities in the first week, with the peak of foraging in the fourth week.

Five weeks age range (29 to 35 days): There is a decrease in the foraging activity (45.74%) over the previous; still remained the most accomplished work, followed by theimmobile on the nest (31.91%).

Six weeks age range (36 to 42 days): There is a big drop in foraging activity (6.58%) and an increase in the standing still activity (59.87%), which was the most frequently performed.

Table 2. Frequency (%) of behaviors performed by workers of *Mischocyttarus latior* (Fox, 1898) at intervals of weeks.

Age interval (week)	Behavioral Acts																
	Foraging Activity	Individual Behaviors			Nest Maintenance Activity							Social Activity					
	FA	IN	SG	WA	AG	CP	FL	AM	VL	AB	CC	TR	TD	TL	DO	SD	RN
1	32.3	50.2	2.3	1.6	0.3	0.2	1.1	0.3	0.1	0.0	4.6	1.0	1.1	1.3	0.4	3.2	0.0
2	71.4	10.7	2.2	0.5	0.5	0.0	2.2	2.2	0.0	0.0	2.7	0.9	3.6	2.2	0.0	0.5	0.5
3	46.6	6.5	13.3	5.8	1.8	1.3	1.8	0.0	0.4	0.9	7.8	2.4	1.6	4.2	3.3	2.4	0.0
4	76.9	13.3	2.7	0.0	0.0	0.0	1.3	0.0	0.0	0.0	1.8	0.4	2.7	0.4	0.0	0.4	0.0
5	45.7	31.9	5.3	1.6	0.0	0.0	0.5	0.0	0.0	0.0	6.4	1.6	0.5	4.3	1.1	1.1	0.0
6	6.6	59.9	5.9	0.0	0.0	2.6	0.7	0.0	2.0	0.0	5.3	3.3	7.2	0.0	1.3	5.3	0.0
7	32.8	60.7	1.1	0.5	0.0	0.0	0.0	0.0	0.0	0.0	2.2	0.5	0.0	1.1	0.0	1.1	0.0
8	0.0	79.0	0.0	5.3	0.0	0.0	0.0	5.3	0.0	0.0	5.3	0.0	5.3	0.0	0.0	0.0	0.0
9	6.5	79.0	1.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.2	0.0	0.0	3.2	0.0	6.5	0.0
10	16.7	52.6	7.7	2.6	0.0	0.0	2.6	0.0	0.0	1.3	7.7	2.6	2.6	2.6	0.0	1.3	0.0
11	35.7	45.9	0.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	12.3	1.0	1.0	0.0	1.0	1.0	0.0

The second most performed behavior was the performance of adult/adult trophallaxis as donor (7.24%), probably by the fact that the subordinates are reducing the foraging and increasing the work inside the colony, as they are not so young anymore, tending to have dominant behaviors in the colony.

Seven weeks age range (43 to 49 days): A high value is observed in standing still (60.75%), despite the frequency of foraging behavior have increased (32.80%).

Eight weeks age range (50 to 56 days): The foraging rate decreases to zero, while the standing still in the colony was the second highest among all intervals, with 78.95% of the time. At this age, the workers performed only just four tasks: checking cells, adult/adult trophallaxis (donor), adding materials to the cell and walking, all these with a frequency of 5.26%.

Nine weeks age range (57 to 63 days): The largest value of standing still within the colony occurred in this interval (79.03%), while forage and being physically dominated was observed in only 6.45% of the time.

Ten weeksage range (64 to 70 days): There was an increase in self-grooming jobs and checking cells, both with 7.69%; these behaviors probably occurred due to the subordinated being for a longer time on the nest.

Eleven weeks age range (71 to 77 days): There was an increase in foraging activity (35.71) and a decrease in standing still behavior (45.92%). The checking of cells was the behavior more frequently found among all other studied intervals.

It can be seen that there was a greater distribution of behaviors within the colony in the first three intervals analyzed and, by means of these data, it is verified that all behaviors can be potentially performed by any worker at any age, as observed in *P. lanio lanio* (Giannotti & Machado, 1994). Thus, for a also eusocial basal wasp as *M. latior*, this behavioral plasticity that exists between the workers is essential for the survival of small colonies of social wasps such as *Mischocyttarus* and *Polistes* (Giannotti, 1999).

Conclusion

Dominants remain longer on the nest than subordinates and exercise exclusively the behaviors of oviposition and rubbing gaster on the nest. They share most of the behaviors with the workers and the main differences between the frequency of behaviors are related to foraging activity and social activity. The males developed various activities unrelated to their own survival and all behaviors can be potentially performed by any subordinate of *M. latior* at any age.

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References

Cecílio, D. S. S., Da Rocha A. A. & Giannotti, E. (2015). Post-embryonic Development of *Mischocyttarus latior (*Fox) (Hymenoptera, Vespidae). Sociobiology, 62: 446-449. doi: 10.13102/sociobiology.v62i3.400

Elpino-Campos, A., Del-Claro, K., & Prezoto, F. (2007). Diversity of Social Wasps (Hymenoptera, Vespidae) in Cerrados fragments of Uberlândia, Minas Gerais State, Brazil. Neotropical Entomology, 36: 685-692. doi: 10.1590/S1519-566X2007000500008

Gadagkar, R. (1991) *Belonogaster, Mischocyttarus, Parapolybia* and independent-founding *Ropalidia*. In K. G. Ross & R.W.

Matthews (Eds.), The social biology of wasps (pp. 149-190). Ithaca and London: Comstock Publishing Associates.

Gamboa, G.J. & Dew, H.E. (1981). Intracolonial communication by body oscillations in the paper wasp, *Polistes metricus*. Insectes Sociaux, 28: 13-26.

Giannotti, E. (1992). Estudos biológicos e etológicos da vespa social neotropical *Polistes* (*Aphanilopterus*) *lanio lanio* (Fabricius, 1775) (Hymenoptera, Vespidae). Rio Claro: UNESP.

Giannotti, E. (1999). Social organization of the eusocial wasp *Mischocyttarus cerberus styx* (Hymenoptera, Vespidae). Sociobiology, 33: 325-338.

Giannotti, E. (2004). Male Behavior in Colonies of the Social Wasp *Polistes lanio* (Hymenoptera, Vespidae). Sociobiology, 43: 551-555.

Giannotti, E. & Machado, V.L.L. (1994). Longevity, life table and age polyethism in *Polistes lanio* (Hymenoptera, Vespidae), a primitive eusocial wasp. Journal of Advanced Zoology, 15: 95-101.

Giannotti, E. & Machado, V.L.L. (1999). Behavioral castes in the primitively eusocial wasp *Polistes lanio* Fabricius (Hymenoptera, Vespidae). Revista Brasileira de Entomologia, 43:5-190.

Jeanne, R.L. (1972). Social biology of the Neotropical Wasp *Mischocyttarus drewseni*. Bulletin of the Museum of Comparative Zoology, 144: 63-150.

Jeanne, R. L., Downing, H.A. & Post, D.C. (1988). Age polyethism and individual variation in *Polybia occidentalis*, an advanced eusocial wasp. In R.L.Jeanne (Ed.), Interindividual Behavioral Variability in Social Insects (pp. 323-357). Colorado: Westview Press.

Kasuya, E. (1983a). Behavioral ecology of Japonese paper wasps, *Polistes* spp. II. (Hymenoptera: Vespidae). Ethogram and internidal relationship in *P. chinensis antennalis* in the founding stage. Zeitschrift fur Tierpsychologie, 63: 303-317.

Kasuya, E. (1983b). Behavioral ecology of Japonese paper wasps, *Polistes* spp. IV. (Hymenoptera: Vespidae). Comparison of ethogram between Queens and Workers of *P. chinensis antennalis* in the Ergonomic Stage. Journal of Ethology, 1: 34-45.

Lima, A.C.O., Castilho-Noll M.S.M., Gomes B.& Noll, F.B. (2010). Social Wasp Diversity (Vespidae, Polistinae) in a Forest Fragment in the Northeast of São Paulo State Sampled with Different Methodologies. Sociobiology, 55: 613-626.

O'Donnell, S. (1995). Division of labor in post-emergence colonies of the primitively eusocial wasp *Polistes instabilis* de Saussure (Hymenoptera: Vespidae). Insectes Sociaux, 42: 17-19.

O'Donnell, S. (1999). The function of male dominance in the eusocial wasp, *Mischocyttaurs mastigophorus* (Hymenoptera: Vespidae). Ethology, 105**:** 273-282.

Pardi, L. (1948). Dominance order in *Polistes* wasps. Physiological Zoology, 21: 1-13.

Post, D.C., Jeanne, R.L., Erickson-JR, E.H. (1988). Variation in behavior among workers of the primitively social wasps *Polistes fuscatus variatus*. InR.L.Jeanne (Ed.), Interindividual Behavioral Variability in Social Insects (pp. 283-321).Colorado: Wsetview Press.

Raposo-Filho, J.R. (1981). Biologia de *Mischocyttarus* (*Monocyttarus*) *extinctus* Zikán, 1935 (Polistinae, Vespidae). Rio Claro, UNESP.

Richards, O.W. (1978). The social wasps of the Americas, excluding the Vespinae. London: British Museum (Natural History).

Siegel, S. (1979). Estatística não paramétrica para ciências do comportamento. São Paulo: Mc Graw-Hill.

Sinzato, D.M.S. & Prezoto, F. (2000). Aspectos comportamentais de fêmeas dominantes e subordinadas de *Polistes versicolor* Olivier, 1791 (Hymenoptera: Vespidae) em colônias na fase de fundação. Revista de Etologia, 2: 121-127.

Sinzato, D.M.S., Prezoto, F. & Del-Claro, K. (2003). The role of males in a neotropical paper wasp, *Polistes ferreri* Saussure, 1853 (Hymenoptera, Vespidae, Polistinae). Revista Brasileira de Zoociências, 5: 89-100.

Spradbery, J.P. (1965). The social organization of wasp communities. Symposium of the Zoological Society, London, 14: 61-96.

Theraulaz, G., Pratte, M. & Gervet, J. (1990). Behavioural profiles in *Polistes dominulus* (Christ) wasp societies: a quantitative study. Behaviour, 113: 223-250.

Togni, O.C. (2014). Biologia e ecologia comportamental da vespa eussocial primitva *Mischocyttarus* (*Megacanthopus*) *parallelogrammus* (Hymenoptera, Vespidae). Rio Claro, UNESP.

Torres, V.O., Antonialli-Junior, W.F&Giannotti, E. (2009). Divisão de Trabalho em colônias da vespa social neotropical *Polistes canadensis canadensis* Linnaeus (Hymenoptera, Vespidae). Revista Brasileira de Entomologia, 53: 593-599.

Torres, V.O., Montagna, T.S., Raizer, J. & Antonialli-Junior, W.F. (2012). Division of labor in colonies of the eusocial wasp, *Mischocyttarus consimilis*. Journal of Insect Science, 12: 1-15.

Turillazzi, S., Ugolini, A. (1979). Rubbing behaviour in some European *Polistes* (Hymenoptera: Vespidae). Monitore Zoologico Italiano (N.S.), 13: 129-142.

West-Eberhard, M.J. (1969). The social biology of Polistine wasps. Miscellaneous Publications, Museum of Zoology, University of Michigan, 140: 1-101.