

Labor Division in *Melipona compressipes fasciculata* Smith (Hymenoptera: Apidae: Meliponinae)

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Divisão de Trabalho em *Melipona compressipes fasciculata* Smith
(Hymenoptera: Apidae: Meliponinae)

RESUMO - A divisão de trabalho em *Melipona compressipes fasciculata* Smith foi analisada e comparada com outras abelhas eusociais - Meliponini e Trigonini. Os resultados mostraram que existe uma sequência de atividades similar a outros meliponíneos já estudados, a saber: "grooming", trabalho com cerume, construção de células, limpeza da colônia, participação no processo de provisionamento e oviposição (POP), desidratação de néctar, ventilação, vedação de frestas, recepção de néctar, guarda e forrageamento.

PALAVRAS-CHAVE: Insecta, Meliponini, abelhas sem ferrão, divisão de trabalho, abelhas eusociais.

ABSTRACT - Labor division in the stingless bee *Melipona compressipes fasciculata* Smith was analyzed and compared with that of other eusocial bees - Meliponini and Trigonini. The results showed a sequence of activities which was similar to that of other stingless bees already studied, such as: grooming; cerumen work; cell construction; cleaning; the colony; provisioning and oviposition process; ventilation; enclosure gap; nectar reception; and foraging.

KEY WORDS: Insecta, Meliponini, stingless bees, division of labor, eusocial bees.

The existence of physical and temporal castes is one of the most complex and important factors in the social structure of insect colonies (Oster & Wilson 1978). The physical castes include a queen, a small number of males, and the numerically predominant worker caste. The temporal caste consists of temporal labor division in which there is an ontogenetic sequence of activities performed during the workers' lifetime.

In the earliest studies on labor division of honeybees, it was reported that worker activities presented a temporal basis (Butler 1609

apud Winston & Fergusson 1986, Donhoff 1855 *apud* Winston & Fergusson 1986). Further research analyzed the flexibility in temporal labor division and the underlying glandular basis for tasks performance (Rösch 1925 *apud* Winston & Fergusson 1986, Ribbands 1952, Lindauer 1953, Sekiguchi & Sakagami 1966). Recent investigation has involved the colony-level factors which try to determine the reasons why bees perform duties at different times (Free 1961, Kolmes 1985, Winston & Fergusson 1985, among others).

The typical labor division in eusocial bees proceeds in the following sequence: callow, nursing, household, and foraging (Sakagami 1982). However, there is considerable flexibility concerning the age-related trend of activities so that the tasks sequence can be adjusted in relation to the colony external or internal requirements.

Some of the research on labor division in Meliponinae shows the sequence of tasks performed during the workers' lifetime (Basindale 1955, Kerr & Santos Neto 1956, Hebling *et al.* 1964, Darchen 1969). More recently, research has described a temporal sequence of labor division in *Melipona bicolor bicolor* Lepeletier (Bego 1983), *Melipona favosa* Fabricius (Sommeijer 1984), *Frieseomelitta languida* Moure & Camargo (Ribeiro 1989), *Nannotrigona (Scaptotrigona) postica* Latreille (Simões & Bego 1991), *Tetragonisca angustula angustula* Latreille (Grosso 1993) and *Plebeia remota* Holmberg (van Benthem *et al.* 1995), among others.

This is a contribution to add more information on the activity of individual workers in relation to the temporal tasks sequence of *Melipona compressipes fasciculata* Smith, comparing the results with other Meliponinae species.

Materials and Methods

This study was conducted at Ribeirão Preto, S.R, Brazil, from September to December 1991. Two colonies of *M. compressipes fasciculata* from São Luís, MA, were used. Colonies were manipulated only for the introduction of marked workers. A marked cohort of 111 newly emerged workers was introduced into an observation hive. The cohort was obtained by removing combs from another hive so that bees could emerge overnight in an incubator at 28°C to be later introduced into the hive 1-2h after marking. During 14 consecutive days all the workers which emerged were individually marked. These workers were up to 24h old. The general conditions of the colony

were measured based on the number of brood combs and on the number of pollen and honey pots. The 1st observation was carried out in the beginning of the experiment and the 2nd when the experiment was finished (Table 1).

Observation was carried out in both extra and oviposition periods - i.e., 8h of daily observation. The marked workers were recorded as performing one or more tasks through individual observations.

Table 1. General conditions of *Melipona compressipes fasciculata* colonies.

Colony Conditions	Date	
	Sept. 27 1991	Dec. 20 1991
Number of pollen pots	5 (open)	6 (open)
	3 (closed)	12 (closed)
Number of honey pots	5 (open)	6 (open)
	14 (closed)	31 (closed)
Number of young brood combs	3	2
Number of combs with immature in different phases of development	4	2

The activities performed by workers as well as queen/worker interactions were observed according to the following classification: Grooming = a bee cleans any parts of its body with its mouthparts or legs; Cerumen work = removal of cerumen from old brood cells, construction of support pillars, food pots and involucrum; Cell construction = mainly mandibular "manipulation" of cell parts or working inside the cell; Provisioning and oviposition process (POP) = participation in the provisioning and oviposition process of brood cells (Arousal

stage, food discharge, worker oviposition and cell operculation); Cleaning = manipulation of waste material and pieces of cocoon that are carried out of the colony; Enclosure gap = with cerumen and mud; Ventilation = wing beatings; Trophailaxis (Tr) = food exchange from worker to queen; Food reception = from worker to worker; Beg food (B) = from queen to worker; Nectar reception = from worker to worker; Foraging = collection of food and material for nest construction; Insertion (I) = forebody insertion into cell; Escape (E) = worker escapes when the queen approaches; Advance (AD) = simple advance (a worker darts on the queen); Advance-back (AB) = the worker performs advance and back movements in the presence of the queen.

Results and Discussion

The average longevity observed for *M. compressipes fasciculata* was one of 42.5 (Ito 80 days) (Fig. 1). According to Sakagami & Fukuda (1968), the type of survival curve is directly correlated with the division of labor.

Convex curves are found in species with low mortality during the initial phases of life. The high mortality was observed to be true of age brackets in which workers became foragers.

In the other species of Meliponinae bees the following longevities were recorded: *Plebeia (Friesella) schrottkyi* Friese, 30.1 days (Camillo-Atique 1977), *F. languida*, 33.3 days (Ribeiro 1989), *M. bicolor bicolor*, 44.0 days (Bego 1983), *N. (Scaptotrigona) postica* for three colonies studied, 26.3 days, 39.5 days and 32.9 days (Simões & Bego 1991), *M. favosa*, 40.0 days (Sommeijer 1984) and *Melipona scutellaris* Latreille, 27.4 and 34.5 days (H. H. Oliveira & A. Kleinert-Giovannini, pers. inf.) for two different colonies observed. The internal conditions of the colony, observations in different periods of the year, and different morphological and physiological conditions among the species are probably responsible for these variations.

When analyzing our data according to the workers' age sequence, the main aspects described below were observed: the cerumen work is one of the 1st activities performed by workers in *M. compressipes fasciculata*. The

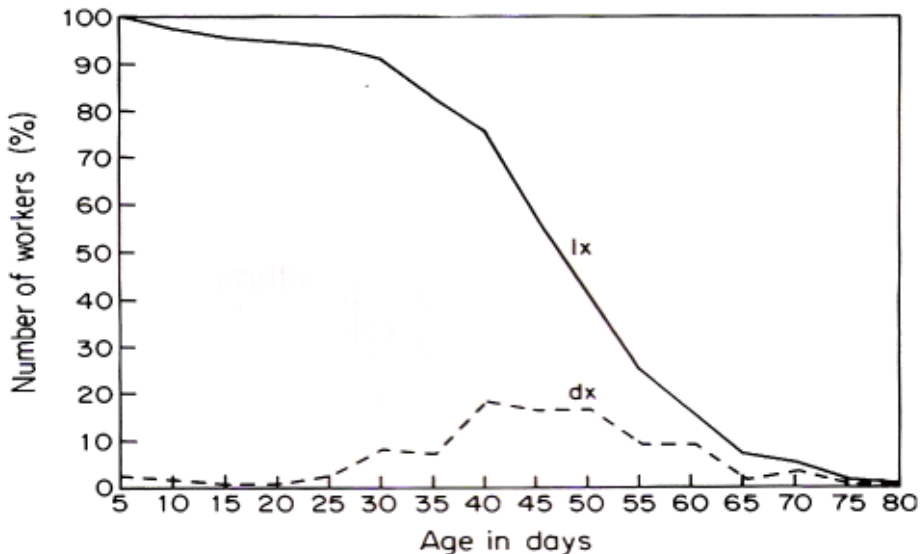


Figure 1. Survival curve (lx) and mortality curve (dx) for workers of *Melipona compressipes fasciculata*.

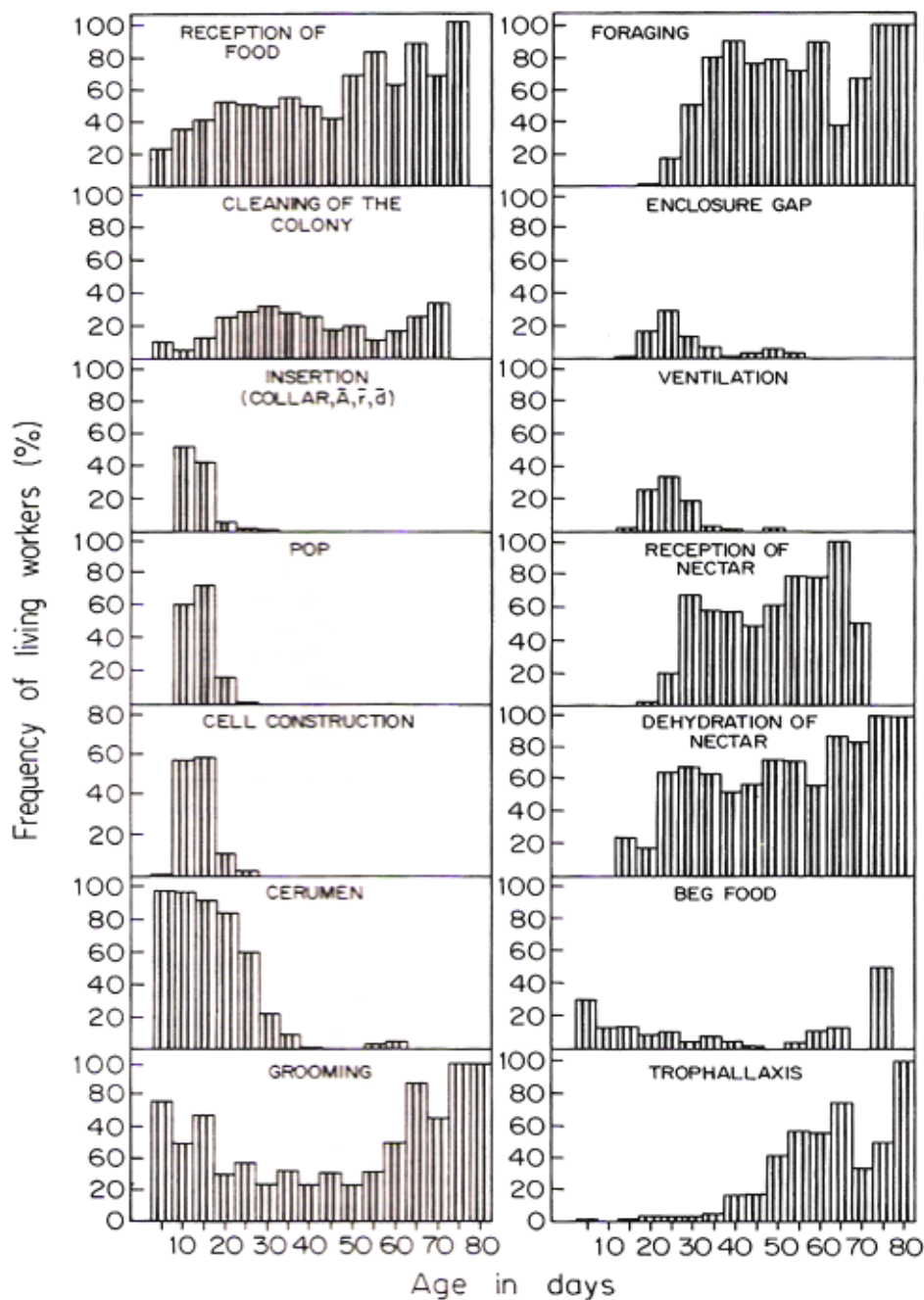


Figure 2. Frequency of workers of *Melipona compressipes fasciculata* engaged in various activities according to respective age in brackets.

grooming task and colony cleaning are activities that overlap almost completely. Duties as reception, nectar dehydration and foraging are performed only after the bees have participated in the cell construction and oviposition process. Trophallaxis and food reception occur all during the workers' lives. It is important to consider that trophallaxis is more conspicuous when bees are older, and that nectar reception starts when they are young. Beg food is performed throughout the bees' lifetime (Fig.2).

The activities observed by different authors do not agree with those defined for *M. compressipes fasciculata*, which makes the comparison of results difficult. It is important to emphasize the fact that labor division is dynamic and that it varies with species, colonies, and colonial needs (Sekiguchi & Sakagami 1966, Simões & Bego 1979,1991, Bego

1983). Thus, the internal conditions related to the number of workers available to perform each task, the queen's laying rate, stored food, the age of colony members, etc. are important factors in establishing such dynamic. External conditions such as seasonality (Ceccato 1970, H. H. Oliveira & A. Kleinert-Giovannini pers. inf), availability of food resources and nest construction material, etc. can also influence colony dynamic.

A important point is the overlap of duties. A determined worker can perform more than one activity at the same time in all the species observed. The frequency of bees' performing different activities throughout their lives (Fig. 3) were: 99.1% worked with cerumen; 76.6% worked in cell construction; 52.3% participated in the oviposition process; 95.5% did grooming; 75.7% were involved in the colony cleaning; 0.9% worked with mud; 7.5% were involved in the resin work; 55.5% worked in ventilation; 41.2% worked in enclosure gap; 58.3% worked in nectar reception; 89.5% worked in nectar dehydration; 88.1% worked in foraging; and 0.9% worked in guarding.

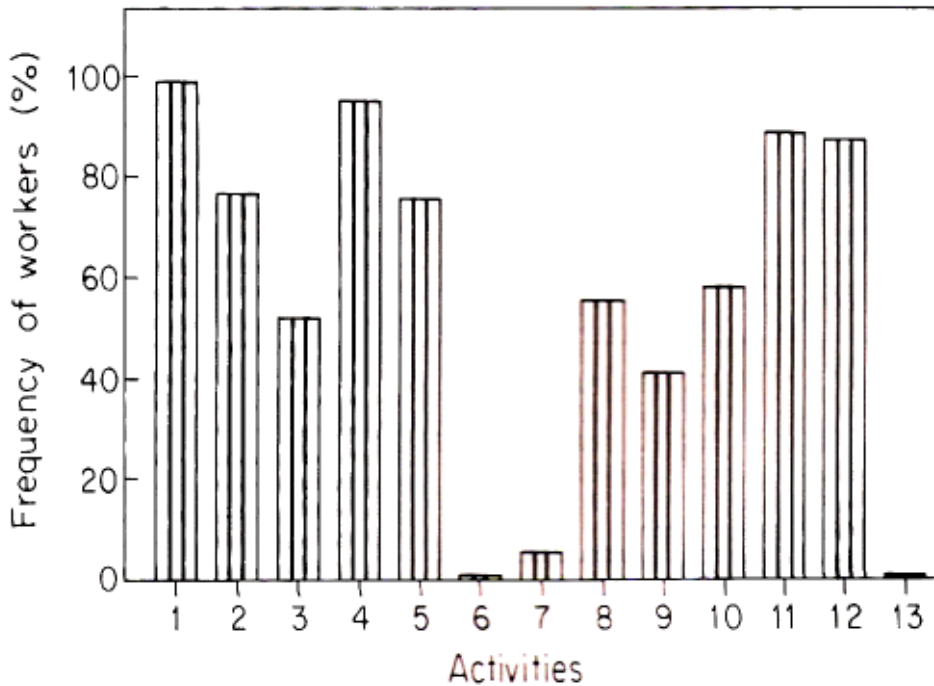


Figure 3. Frequency of workers of *Melipona compressipes fasciculata* performing different activities in the colony. 1 = cerumen; 2 = cell construction; 3 = oviposition process; 4 = grooming; 5 = colony cleaning; 6 = mud work; 7 = resin work; 8 = ventilation; 9 = enclosure gap; 10 = néctar reception; 11 = nectar dehydration; 12 = foraging; and 13 = guarding.

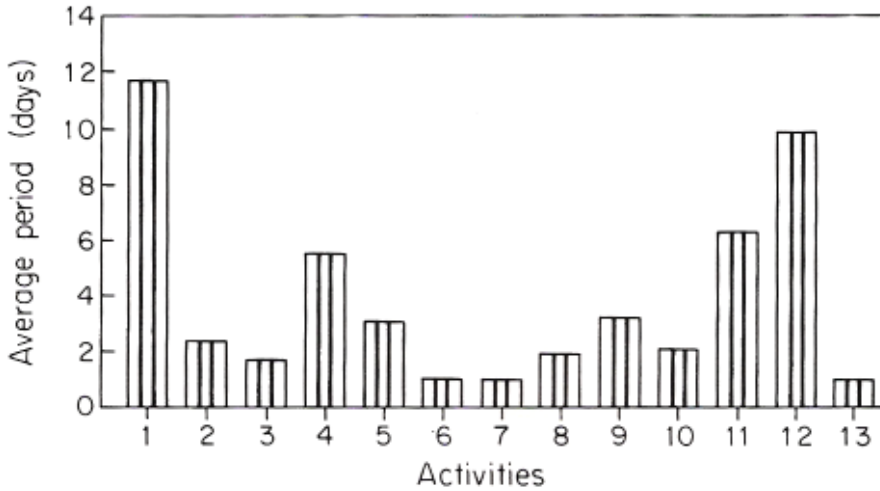


Figure 4. Average period (in days) for each activity performed in *Melipona compressipes fasciculata*. 1 = cerumen; 2 = cell construction; 3 = oviposition process; 4 = grooming; 5 = colony cleaning; 6 = mud work; 7 = resin work; 8 = ventilation; 9 = enclosure gap; 10 = nectar reception; 11 = nectar dehydration; 12 = foraging; and 13 = guarding.

seen working with resin; 55.9% ventilated the nest; 41.4% performed the enclosure gap of the colony; 58.6% performed nectar recep-

tion; 90.1% dehydrated nectar; 88.3% worked as foragers and 0.9% performed the guarding task. The *M..bicolor bicolor data* (Bego 1983)

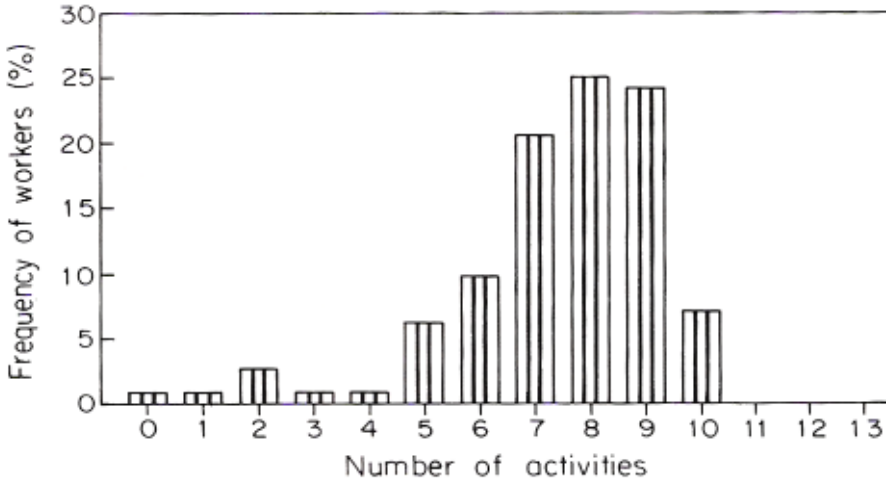


Figure 5. Frequency of workers in relation to the number of activities performed in *Melipona compressipes fasciculata*. 0 = no activity; 1 = cerumen; 2 = cell construction; 3 = oviposition process; 4 = grooming; 5 = colony cleaning; 6 = mud work; 7 = resin work; 8 = ventilation; 9 = enclosure gap; 10 = nectar reception; 11 = nectar dehydration; 12 = foraging; and 13 = guarding.

are different when compared with those of *M. compressipes fasciculata* as to colony cleaning. *N. (Scaptotrigona) postica* (Simões & Bego 1991), *M. bicolor bicolor* (Bego 1983) and *F. schrottkyi* (Camillo-Atique 1977) present lower frequency of workers as to foraging activity differently from *M. compressipes fasciculata*. As to guarding, the species above, including *F. languida* (Ribeiro 1989), presented higher frequency than that observed for *M. compressipes fasciculata*.

The average period for each activity performed by workers (Fig. 4) indicated that the duration of cerumen work was of ca. 12 d; cell construction = 2 d; oviposition process = 2 d; grooming = 6 d; colony cleaning = 3 d; mud work = 1 d; resin work = 1 d; ventilation = 2 d; enclosure gap = 3 d; nectar reception = 2 d; nectar dehydration = 6 d; foraging = 10 d and guarding = 1 day. In *N. (Scaptotrigona) postica* (Simões & Bego 1991) obtained similar results, except for nectar dehydration.

As to the frequency of workers of *M. compressipes fasciculata* related to the num-

ber of duties carried out (Fig. 5), most of them performed from 7 to 9 activities, 20.7% (7), 25.2% (8) and 24.3% (9). Only a small number of bees did not perform any duties and, finally, no bees carried out all the activities. In *M. bicolor bicolor* (Bego 1983), most bees performed from 4 to 6 tasks, 26.0% (4), 36.0% (5) and 27.0% (6). Inherwork, Bego (1983) considered a total of 7 activities. In addition, all marked bees performed more than one duty. Only 1.5% performed all the tasks. As to *F. languida* (Ribeiro 1989), most bees did from 4 to 6 duties, 22.5% (4), 25.0% (5) and 17.5% (6). 1.0% of the total number of workers did not perform any tasks and 2.0% did all duties.

The frequency of queen/worker interactions in relation to workers' age in the extra-oviposition period showed that escape occurred until 60 d, simple advance until 45 d and advance-back until 40 d. The highest frequency occurred during the age period in which the workers participated in the oviposition process, except for the escape behavior that

Table 2. Frequency (%) of workers that performed interactions with the queen in the extra-oviposition period in *Melipona compressipes fasciculata*.

Age (days)	Interactions						
	E	AD	AB	I	Tr	B	T
0 - 5	10.8	0.9	49.6	0.9	3.6	20.7	111
6 - 10	4.6	12.0	83.3	17.6	12.0	13.9	108
11 - 15	7.6	31.1	80.2	8.5	2.8	9.4	106
16 - 20	12.4	29.5	63.8	2.9	7.6	2.9	105
21 - 25	5.8	15.4	42.3	0	7.7	2.9	104
26 - 30	6.9	7.9	14.9	0	1.0	0	101
31 - 35	8.7	5.4	3.3	0	2.2	1.1	92
36 - 40	1.2	3.6	1.2	0	0	0	84
41 - 45	4.7	1.6	0	0	0	0	64
46 - 50	2.2	0	0	0	0	0	46
51 - 55	0	0	0	0	0	0	28
56 - 60	5.6	0	0	0	0	0	18

E= escape; AD= advance; AB= advance-back; I= insertion; Tr=trophallaxis; B= beg food. T= total number of living workers in each age bracket.

was very intensive until the last days of the bees' lives. Forebody insertion in collared cells occurred until 20 d, and was coincident to the age of the workers which participated in the oviposition process. Trophallaxis and beg food occurred until 35 d; the highest fre-

quency in relation to the fonner was from 6 to 10 d of life and to the later it was from 1 to 5 d of the workers' lives (Table 2). In general, results showed that the behavior related to queen/worker interactions were not limited to 1 younger workers.

Table 3. Frequency (%) of workers that performed interactions with the queen in the oviposition process in *Melipona compressipes fasciculata*.

Age (days)	Interactions						
	E	AD	AB	I	Tr	B	T
0 - 5	0	0	15.3	0	0	0	111
6 - 10	0.9	2.8	70.4	39.8	2.8	4.6	108
11 - 15	0	4.7	45.3	41.5	3.8	6.6	106
16 - 20	0	1.0	11.4	6.7	1.0	0	105
21 - 25	0	0	0	0	0	0	104
26 - 30	0	0	0	1.0	0	0	101
31 - 35	0	0	2.2	0	0	0	92

E= escape; AD= advance; AB= advance-back; I= insertion; Tr= trophallaxis; B= beg food. T= total number of living workers in each age bracket.

The frequency of interactions in relation to workers' age in the oviposition period shows that escape occurs in the interval from 6 to 10d, simple advance from 6 to 20d, advance-back until 35 d, forebody insertion into the cell from 6 to 30 d, beg food from 6 to 15 d, and trophallaxis from 6 to 20 d (Table 3).

Our results showed that in *M. compressipes fasciculata*, the POP tasks comprise mixed activities, i.e., the bees did not perform continuously the same kind of duty. Being so, they performed these tasks without presenting any kind of constancy in a particular work. As for labor division in general, however, *M. compressipes fasciculata* data showed a pattern similar to that of several other stingless bees studied up to now related to the sequence of activities: grooming, cerumen work, cell construction, colony cleaning, participation in the provisioning and oviposition process (POP), nectar dehydration, ventilation, enclosure gap, nectar reception, guarding and foraging

(Kerr & Santos Neto 1956, Hebling *et al.* 1964, Darchen 1969, Russo 1976, Camillo-Atique 1977, Bego 1983, Sommeijer 1984, Ribeiro 1989, Simões & Bego 1991, Grosso 1993 and van Benthem *et al.* 1995).

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