Behavioral Repertory of the Weaver Ant *Camponotus (Myrmobrachys) senex* (Hymenoptera: Formicidae)

by

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ABSTRACT

Weaver ants are one of the most remarkable examples of social cooperation in nature. However, there are few studies to date on the particular aspects of their social behavior. In this study, we describe the behavioral repertory of *Camponotus* (*Myrmobrachys*) *senex* , a Neotropical weaver ant. A colony collected in the field was transferred to the laboratory for elaboration of an ethogram. Part of the colony: 20 wingless queens, 176 workers, 7 pupae, 30 larvae and 667 eggs, was conditioned in test tubes and put into two plastic boxes. One box was designated as nesting area and the other as foraging area. Both boxes were connected to each other. The ethogram was based on 20 hours of qualitative observations, followed by 50 hours of quantitative behavioral observations, "all occurrence sample" method (*sensu* Altmann 1974). We identified 58 different behaviors (30,651 registers), distributed in 10 behavioral categories. The most frequent categories were: immobility (0.4031%), grooming (0.1393%), exploration (0.1306%) and brood care (0.1035%). Immobility was the most frequent category in all castes and we suggest that immobility might be an energy saving strategy in *C. senex*. Workers displayed a more diversified behavioral repertoire with 57 different acts whereas, queens displayed 34 different acts. The use of male larvae by weaving nests can suggest an additional function for males, in addition to their usual sexual role. It is hoped that new taxonomic and behavioral studies will be carried out in order to obtain a better understanding of labor division in *C. senex*. Our results provide baseline data for future comparisons about evolutionary patterns in nest building behavior in ants as well as to the study of the genus *Camponotus* as a whole.

Key words: ethogram, Formicinae, behavioral ecology, social behavior.

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INTRODUCTION

One of the most notable examples of social cooperation described in nature occurs in the weaver ants (Hölldobler & Wilson 1990). The workers of these species build nests utilizing the silk produced by their larva (Hölldobler & Wilson 1977). Due to this particular behavior it is believed that the social aspect of this group is one of the most advanced within the Hymenoptera (Hölldobler & Wilson 1990). Although weaver ants are abundant in many areas, including the Neotropics, no detailed study regarding their behavioral repertory exists. Behavioral repertoires are unique for several reasons, but mainly for providing a detailed picture of all the activities developed by a species, helping in the comprehension and characterization of its natural history and ecological adaptations (Alcock 1997; Krebs & Davies 1993).

Camponotus (Myrmobrachys) senex Smith 1858 is a weaver ant commonly found in the forests of Central and South America (Schremmer 1979 a, b). Despite this fact, only two studies have been carried out in respect to its weaving behavior and nest structure (Schremmer 1979 a, b). These studies provide few data regarding its natural history and behavioral repertory. Nothing is known about the specific behavior of *C. senex* (Hölldobler & Wilson 1990). Given the importance of investigating the behavior and sociality of weaver ants, in order to obtain a better understanding of the evolution of social behavior in Hymenoptera, this study determined the behavioral repertory of *C. senex*. We hope it could serve as a basis for future comparisons with other ant species.

MATERIAL AND METHODS

One colony of *C. senex* (42x31cm) was collected in the field at Fazenda Marileuza, in the municipality of Uberlândia, Minas Gerais, in Southwestern Brazil (18°57'S; 48°12'W), in April 2002. The colony, containing more than 30 wingless queens and 60,000 individuals, was taken to the laboratory and dissected. For the ethogram (behavioral repertory), a group with 20 wingless females, 176 workers, 7 pupas, 30 larvae and 667 eggs was selected and maintained in captivity. The group was kept in two plastic boxes (40x30x7cm) connected to each other by a transparent plastic tube (20cm long). Inside box A, designated as the nesting area, 12 test tubes (7.4cm in length and 1.0cm in width) were placed horizontally inside the area, each one filled to one third of its length with water soaked pieces of cotton. The ants were placed in this box and naturally searched for shelter in the interior of the test tubes. The box B, designated as the foraging area, contained only a paper filter (15cm diameter). Each box was covered with a glass plate and wrapped in red cellophane to reduce stress caused by ambient light.

The observations concerning the ethogram were carried out during the course of one week, from 08:00h to 18:00h, in May 2002. The time of the actual observations was restricted to a few days due to the velocity with which these ants weaved the insides of the test tubes. After two weeks, the silk cover made further behavioral observations impossible. Initially 20 hours of qualitative behavioral observations were carried out, ("*all occurrences sampling*" method, *sensu* Altmann 1974), in order to define the ants main behavioral actions and to establish a worksheet for use in the study. The quantitative observations were conducted in 50 sessions (one hour for each one). These observations followed the "*scanning sample*" method (Altmann 1974).

Ten minutes before the beginning of each session of observation, the cellophane was removed and a food source was offered to the ants. The food source was comprised of 5ml of a standardized diet (Bhatkar & Whitcomb 1970) and five live termites (*Armitermes* sp. Isoptera: Termitidae).

Voucher specimens of the ant species have been deposited in the Museu de Zoologia da Universidade de São Paulo (MZUSP) and the Museu de Biodiversidade do Cerrado (MBC-UFU). The Chi-square test was utilized for comparisons between behavioral categories for workers and queens in the colony (Zar 1984).

RESULTS

In total, 30,651 acts were recorded, distributed between 10 categories and 58 behaviors (Table 1). Workers presented the most diversified behavioral repertoire, with 57 behavioral acts (26,595 observations) and queens displayed 34 behavioral acts (4,056 observations). The most frequent behavioral categories for *C. senex* were: immobility, grooming, exploration and brood care. Immobility was the category most frequently observed in all castes. Other activities such as grooming and brood care were more frequent in workers. Activities most observed for the queens were feeding; grooming and brood care (Table 1).

The results of this study show that workers and queens carry out different activities in the colony. The activities of feeding, communication, brood care and immobility are, comparatively and significantly, more common among queens than among workers ($p<0.001, \chi^2$; Table 2). In contrast, other activities, such as nest building, defense, exploration, grooming and antagonistic relationships are more common among workers than queens ($p<0.001$, χ^2; Table 2). The category

Table 1. Behavioral Repertoire of *Camponotus senex* Smith, 1858 (Formicidae: Formicinae) under captive conditions (50 hours of quantitative observations).

Behavioral category Behavioral act	Worker (N = 176)	Queen (N = 20)	Total
Feeding			
1. Trophallaxis worker	0.0434	0.1425	0.0565
2. Trophallaxis queen	0.0217	0.0030	0.0192
3. Abdominal trophallaxis	0.0011	0.0000	0.0009
4. Feeding larva	0.0009	0.0000	0.0008
5. Feeding on termites	0.0005	0.0000	0.0005
6. Feeding on diet	0.0131	0.0000	0.0114
Communication			
7. Worker antennation	0.0384	0.0604	0.0413
8. Queen antennation	0.0109	0.0229	0.0125
9. Marking trail	0.0010	0.0000	0.0009
Brood Care			
10. Stopped over eggs	0.0173	0.0422	0.0206
11. Stopped over larva	0.0158	0.0402	0.0191
12. Stopped over pupas	0.0007	0.0005	0.0007
13. Manipulating eggs	0.0150	0.0069	0.0139
14. Manipulating larvae	0.0246	0.0084	0.0224
15. Manipulating pupas	0.0016	0.0017	0.0016
16. Manipulating new adults (after hatch)	0.0001	0.0000	0.0001
17. Transporting eggs	0.0025	0.0002	0.0022
18. Transporting larvae	0.0130	0.0010	0.0115
19. Transporting pupas	0.0015	0.0000	0.0013
20. Assisting new adults in the hatching	0.0006	0.0000	0.0005
21. Stopped and holding egg	0.0009	0.0000	0.0008
22. Stopped and holding larva	0.0078	0.0007	0.0069
23. Stopped and holding pupa	0.0001	0.0000	0.0001
24. Egg laying	0.0000	0.0020	0.0003
25. Separating egg masses	0.0019	0.0000	0.0017
Nest Construction			
26. Transporting weaving larva	0.0029	0.0000	0.0025
27. Weaving with larva	0.0162	0.0000	0.0140
28. Cutting particle	0.0012	0.0000	0.0010
29. Carrying particle	0.0005	0.0000	0.0005
30. Inserting particle	0.0005	0.0000	0.0004
Defense			
31. Guarding nest entrance	0.0195	0.0000	0.0169
32. Stopped and observing	0.0040	0.0002	0.0035
33. Aggressive display	0.0087	0.0032	0.0080
34. Flicking formic acid	0.0010	0.0000	0.0008
35. Attacking (mandibles + acid)	0.0010	0.0000	0.0008
36. Drumming	0.0103	0.0000	0.0089

Table 1. Cont. Behavioral Repertoire of *Camponotus senex* Smith, 1858 (Formicidae: Formicinae) under captive conditions (50 hours of quantitative observations).

Behavioral category Behavioral act	Worker (N = 176)	Queen (N = 20)	Total
Exploring			
37. Patrolling in foraging area	0.0428	0.0000	0.0371
38. Patrolling nest area (inside tubes)	0.0859	0.0380	0.0795
39. Inspecting the substrate while stopped	0.0124	0.0005	0.0108
40. Inspecting the substrate while walking	0.0034	0.0010	0.0031
Immobility			
41. Stopped in the nest area (inside tubes)	0.3731	0.4739	0.3864
42. Stopped in the foraging area	0.0193	0.0000	0.0167
Grooming			
43. Autogrooming 1st pair of legs	0.0309	0.0306	0.0309
44. Autogrooming antenna + 1° pair of legs	0.0534	0.0434	0.0521
45. Autogrooming 2nd pair of legs	0.0203	0.0032	0.0180
46. Autogrooming 3rd pair of legs + abdomen	0.0109	0.0084	0.0105
47. Autogrooming anus	0.0082	0.0071	0.0081
48. Allogrooming worker	0.0092	0.0424	0.0136
49. Allogrooming queen	0.0027	0.0000	0.0024
50. Carrying dead individual	0.0033	0.0000	0.0028
51. Carrying refuse	0.0011	0.0000	0.0010
Antagonistic Relations			
52. Attack against an individual	0.0196	0.0121	0.0186
53. Biting the head of another individual	0.0005	0.0012	0.0006
54. Biting another individual from behind	0.0001	0.0005	0.0001
55. Fighting over larva	0.0009	0.0012	0.0009
Other			
56. Vibrating 1st pair of legs + head	0.0003	0.0000	0.0003
57. Vibrating 1st pair of legs	0.0015	0.0000	0.0013
58. Cannibalism: eating larva	0.0004	0.0005	0.0004
Total	**1.0**	**1.0**	**1.0**

entitled "others" which includes the acts of "vibrating the first pair of legs plus the head", "vibrating the first pair of legs only" and "cannibalism", did not show a significant difference between the castes ($p<0.001$, χ^2; Table 2).

General comments regarding some behavioral acts described for *C. senex* (see Table 1):

A – Abdominal trophallaxis: in this act, described by Wilson (1976), the queen exudes a drop of liquid from its anus, which is quickly collected by the workers. The exuded liquid can be ingested or transported and placed on the substrate by the workers of *C. senex*.

Table 2. Behavioral categories for queens and workers of *Camponotus senex* Smith, 1858 (Formicidae: Formicinae) under captive conditions (50 hours of quantitative observations).

Behavioral categories	Worker (N = 176)	Queen (N = 20)	Total	χ^2	*p*
Feeding	0.0807	0.1455	0.0892	389.92	p<0.001
Communication	0.0503	0.0833	0.0547	11.26	p<0.001
Brood Care	0.1034	0.1038	0.1035	422.78	p<0.001
Nest building	0.0213	0.0000	0.0185	0	p<0.001
Defense	0.0444	0.0035	0.0390	46.46	p<0.001
Exploration	0.1445	0.0394	0.1306	91.48	p<0.001
Immobility	0.3923	0.4739	0.4031	98.39	p<0.001
Grooming	0.1400	0.1351	0.1393	390.99	p<0.001
Antagonistic Relations	0.0209	0.0150	0.0202	17.56	p<0.001
Other	0.0022	0.0005	0.0020	8.44	p>0.05
Total	**1.0**	**1.0**	**1.0**		

B – Nest building: the behavior of weaving in this category is especially restricted to the group of weaver ants (Hölldobler & Wilson 1990). The act most commonly observed was weaving with the larva. Workers manipulated the larva between their mandibles, touching the mouth of the larva into desired points on the substrate. At these points the larva exuded silk which bound structures together forming the nest. Particles can be added to the silken mesh. In this study, the particles cut and carried during the experiment were pieces of filter paper from the foraging arena. In nature the ants remove small particles of tree bark and soil, especially fragments of vegetative material (Schremmer 1979 a, b).

C – Drumming: described by Markl and Fuchs (1972), consists of drumming some parts of the body, in this case the gaster against the substrate. This behavior is commonly observed when a worker comes across termites.

D – Inspecting the substrate while stopped or walking: these acts were with the individual maintaining its mandible and antennas aligned with the substrate. This behavior is probably a result of the ants habit of investigating chemical trails in the environment (Hölldobler & Wilson 1990).

E – Antagonistic relationship: In this category acts related to confrontations between individuals were noted. The most common act was to attack other individuals, which consisted of running rapidly in the direction of the other individual, like chase behavior (Pie & Del-Claro 2002). Some confrontations lasted minutes, in one encounter between two workers each bit the other on their respective mandibles. In these confrontations no worker deaths were registered.

F – Vibrating first pair of legs and head or only first pair of legs: In this act, the individual vibrates one or both of the structures aforementioned, on the horizontal plane, remaining in this state for seconds or even minutes.

DISCUSSION

Ethograms are utilized in the study of ants in order to generate a deeper and more comprehensive knowledge of social behavior and it has had satisfactory results for many species (Wilson 1976, Brandão 1978, Traniello & Jayasuriya 1985), within which can now be included *C. senex*. Behavioral repertoires can also provide specific data related to the division of caste and work in the colony and to polymorphism or polyethism (Wilson 1980, Wilson 1984, Pratt 1994).

Behavioral repertoires have been developed among several groups of ants, as for instance, in Formicinae (Brandão 1978, Wilson 1984), Ponerinae (Paiva & Brandão 1989, Henriques & Moutinho 1994, Pratt 1994, Oliveira *et al.* 1998), Myrmicinae (Wilson 1976, Del-Claro *et al.* 2002) and in Aneuretinae (Traniello & Jayasuriya 1985). The ants possess behavioral repertoires that vary from species to species, but in general, the species present between 30 to 40 behavioral acts (see Table 3 and Brandão 1978, Wilson 1984, Paiva & Brandão 1989, Jaisson *et al.* 1992, Henriques & Moutinho 1994). Up to now, no ant species had shown a diversity of behavioral acts like those observed for *C. senex*. The behaviors observed in this species indicate that it possesses a complex behavioral repertoire that could be related to its life style as a species of weaver ant. The specificity seen in ants such as the behavioral specificity of castes, cooperation in nest building and heterogeneity and sophistication in communication, are pointed out as factors pertaining to a complex society, as seen in *Oecophylla* (Anderson & McShea 2001). Such factors appear to be present in *C. senex* and are commonly observed in other weaver ant species. For example, the recruiting system in *Oecophylla longinoda* is given as the most advanced among ants (Hölldobler & Wilson 1978), which suggests that complex behavioral systems do indeed occur in the weaver ants.

Comparison between workers activities and those of the queens ratified these observations. Although queens did execute a quantity of behavioral acts similar to those of the workers, the frequency with which each act was conducted varied significantly for a majority of the categories listed. In many aspects this variation is expected, for example, in the exploratory activities, because while the queens are limited to the interior of the nests, the workers travel both in and out of the colony, foraging, exploring and patrolling the area surrounding

Table 3. Review of diversity of behavioral acts in some ants species.

Species	Sub - family	Number of act behavior	Reference
Ectatomma permagnum	Ponerinae	40	Paiva and Brandão 1989
Zacryptocerus varians	Myrmicinae	40	Wilson 1976
Pheidole pallidula	Formicinae	39	Sempo and Detrain 2004*
Formica perpilosa	Formicinae	38	Brandão 1978
Pheidole pubisventris	Formicinae	37	Wilson 1984*
Aneuretus simini	Aneuretinae	35	Traniello and Jayasurya 1985
Pachycondyla crassinoda	Ponerinae	33	Henriques and Moutinho 1994
Nothomyrmecia macrops	Nothomyrmecinae	31	Jaisson and others 1992
Gnamptogenys horni	Ponerinae	31	Pratt 1994
Pheidole guilelmimuelleri	Formicinae	31	Wilson 1984*
Pheidole megacephala	Formicinae	31	Wilson 1984*
Camponotus sericeiventris	Formicinae	28	Busher and others 1985
Pachycondyla stigma	Ponerinae	23	Oliveira and others 1998
Camponotus senex	Formicinae	58	This paper

*Just for workers

the nest (Hölldobler & Wilson 1990). Other behaviors such as feeding appear to reflect one more special distinction of the reproductive caste, due to the smaller quantity of queens to workers. There are many more workers to attend one queen than queens that could possibly be attended or have food solicited from them. The observed differences have a real biological significance, which sometimes reflects itself onto the specific role of each caste in the colony. Other times these differences are owed to the density differences between individuals of different castes. We suggest that further studies, taxonomic and behavioral, be conducted so that the division of labor in the colonies of *C. senex* can be better understood.

Immobility in ants appears to follow a general pattern, where a large part of the colony remains in this state. Most likely, this immobile state is an attempt, by the colony, to minimize energy costs. *C. senex* showed close to 40% of the colony in this state of immobility, comparatively one of the highest percentages registered for ants (Jaisson *et al.* 1992). In fact, *C. senex* like other weaver ants spend a great deal of their time in the construction and maintenance of their nests and they possess the largest investment of silk in the construction of its nests among all weaver ants (Santos & Del-Claro unplublished data). This may justify the high percentage of immobility within the colony.

Antagonistic behavior in ants deserves attention and specific study regarding its function. Conflicts between queens, queens and workers and workers and workers in the colony are observed in some ant species (Bourke 1991, Henriques & Moutinho 1994) and they might be related, for example, to the establishment of the hierarchy of dominance (Oliveira & Hölldobler 1990). Abdominal trophallaxis, added to the observations of antagonistic interactions queens and workers, suggests that this phenomenon can also occur in *C. senex*. In Ponerinae, the ability of higher-ranking workers to obtain the liquid from the queen' anus confers to them an advantage in faster gonadal development, through the hormones contained within the liquid. In the absence of the queen, these workers assume the reproductive function in the colony, giving rise only to males due to the lack of prior fecundation (Oliveira & Hölldobler 1990).

Cannibalism, although not yet well understood, was observed in some species (Wilson 1976, Paiva & Brandão 1989, Bourke 1991) and might be related, for example, to dominance or stress in the colony (Carlin 1988, Hölldobler & Wilson 1990). The cannibalism of larva by queens of *C. senex*, occurred after the transfer of the ants to the artificial nest, probably a result of stress brought on by the transfer.

Drumming observed in *C. senex* and in other species (Markl & Fuchs 1972), may serve the ant in allowing it to evaluate the size of prey, or even the presence of prey on the abaxial surface of a leaf. We suggest that the behavior of vibrating the first pair of legs and the head, observed only in *C. senex* is a variation of the drumming or jerking (Hölldobler & Wilson 1990), towards the perception of vibrations produced on the substrate possibly having a mechanoreceptive function. Other invertebrates make use of appendages in contact with substrate to detect the presence of predators or prey, making this activity vital to the organism survival (Polis 1990). In *C. senex*, the drumming is used as a defense mechanism, recruiting workers out of the nest and noisily advising others against predatory attacks (Santos & Del-Claro unplublishing data).

Although it is one of the most common ant genera, especially in the Neotropics, there are relatively few behavioral studies utilizing ethograms for *Camponotus* (Busher *et al.* 1985, Satoh 1991). The results shown here represent the first detailed investigation regarding the distribution of activities of a weaver ant colony, ultimately, serving as a model for other weaver ant species as well as for the genus *Camponotus*; one of the most distributed ant groups in the world.

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