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Research Article

Division of Labor in *Pachycondyla striata* Fr. Smith, 1858 (Hymenoptera: Formicidae: Ponerinae)

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Four colonies of the ant *Pachycondyla striata* were used to analyze the specie behavioral repertoire. Forty-six behavioral acts were recorded in laboratory. Here, we present the record the division of labor between the castes and the temporal polyethism of monomorphic workers. The queens carried out many of the behavioral traits recorded in this work however; they performed them less frequently compared to the worker. The workers activity involved chasing and feeding on fresh insects and usingthem to nourish larvae besides laying eggs in the C-posture, an activity also performed by queens, which is similar to that of wasps of the subfamily *Stenogastrinae*. The young workers were involved in activities of brood care, sexuate care, and nest maintenance, and the older workers were involved in defense, exploration, and foraging.

1. Introduction

The evolution of social behavior may be defined as the combination of care for young individuals by adults, overlapping generations, and division of labor in the reproductive and nonreproductive castes [1–4]. The ants are eusocial, and their behavior differs from that one of other social insects in three respects: (a) they have a varied diet, (b) nest building retains characteristics unique to this group, parental care in galleries, and workers performing tasks according to their age or size, and (c) adults remaining long time with their brood [5].

Among the aspects covered in ethologic studies of ants, division of labor (when individuals within a group perform different roles) or polyethism comprehends a widely explored subject and may present two divisions: (a) physical polyethism, when individuals show distinct morphological characteristics to perform specific tasks and (b) temporal polyethism, when the variation of tasks occurs according to age [1, 2, 4, 6]. Therefore, temporal polyethism may occur both in populations of monomorphic workers and in polymorphic workers [7, 8]. The ants of the genus *Pachycondyla* have a wide pantropical distribution with about 270 species being described [9]. The *Pachycondyla species* are diverse in their morphology and their behavior [10].

Pachycondyla striata Smith 1858 [11], classified into the subfamily Ponerinae [12], presents relatively large individuals (13.2–16.7 mm long). The castes are slightly different. The workers are different from the queens by the absence of ocelli and wing scars. This species is distributed through northern Argentina, Paraguay, Uruguay, and Brazil [13–15].

The aim of this study was to verify whether there is division of labor among castes and age polyethism in *P. striata*. The results will contribute to better understanding and interpretation of its social organization and allow comparison with other species of the family Formicidae.

2. Materials and Methods

Four colonies were collected on the campus of the University UNESP—Universidade Estadual Paulista, Rio Claro (22°32′40″S/47°32′44″W), São Paulo State. The ethological analysis began two days after the collection. Observations were done in the foraging area and plaster nest.

Table 1: Composition of the colonies of *Pachycondyla striata*.

Colony	Number of individuals							Date of collection
	eggs	larvae	pupae	workers	winged females	males	queens	
N. 2	—	—	—	20	5	—	—	04/13/2006
N. 3	—	—	37	178	38	33	—	04/14/2006
N. 7	264	65	—	382	7	8	—	08/06/2006
N. 8	30	231	240	384	—	—	1	11/17/2006

The colonies selected in field contained queens and/or winged females. The latter were regarded as queens after wing loss. The colonies were transferred to a laboratory and placed in plastic containers (width: 30.0 cm; length: 48.0 cm; height: 12.0 cm). In each container, there was a plaster nest consisting of three chambers in different sizes, interconnected by tunnels of 1.0 cm in width and 3.0 cm in depth, covered with glass to avoid disturbance and red cellophane paper to prevent the passage of the full spectrum of light.

The diet of the ants consisted of sugar and water in a ratio of 1:1 (offered in test tubes, with cotton wool in the opening), termites, worms, cockroaches, larvae of Coleoptera (*Tenebrio molitor*), flies, and papaya seeds.

Previous observation was performed for 20 hours to obtain behavioral data, with the aim of identifying queens and workers. The ants were differentiated by covering their thorax with quick-drying paint for model airplanes (Revel), allowing the identification of the individuals by age group just after their emergence. Young workers are known for having a paler color in relation to older ones. Later, the scan sampling method described by Altmann [16] was used to qualify the acts.

The quantitative observation of the behavioral acts of the individuals in each colony was performed for five minutes, with one-minute intervals. The observation time was one hour a day, four times a week, during six months, for a total of 94 hours. A comparative ethogram for the individuals was developed. Sample coverage was defined by the formula $\varnothing = \mathbf{1} - (\mathbf{N1}/\mathbf{i})$, where **N1** = number of behavioral acts observed once and **i** = total number of behavioral acts, the more this value approaches to 1, the more complete the sample [17]. The behavioral catalog was divided into ten categories and used to build histograms and a dendrogram with clustering method (UPGMA) of Euclidean distance [18] (Table 1).

3. Results

3.1. Division of Labor. When introduced in laboratory, the individuals of *P. striata* immediately occupied the artificial nest. The ants carried the immature from the foraging area and accommodated them in the first and minor chamber for 12 hours. Only after this, they carried them to the last and bigger chamber. In the nest seven, the workers distributed randomly the immature to the chambers and tunnels of the nest.

As previously announced for this study, we considered the existence of two castes morphologically and subtly differentiated, containing monomorphical workers. In Table 2 the different categories, are distributed and quantified and behavioral acts of queens, workers, winged females, and males of *P. striata are defined as well.*

The sample coverage value ($\varnothing$) was 0. 981 meeting the expectations of Fagen and Goldman [17]. The dissimilarity dendrogram informs a great ethological difference between the castes. (Figure 1).

The inactivity of the males into the nest suggests their action to be more prevalent in the mating season, but this was not verified in this study (Table 2).

The behavorial acts supposedly regarded as less derived have been identified in the castes, such as feeding larvae and adults on fresh insects, and laying eggs in the C-posture. Furthermore, the queens performed activities that are exclusively carried out by workers in other more derived species, such as brood care, exploring, foraging, and nest maintenance (Table 2).

The dominance behavior involved both individuals for recruiting and reproductive labor. The latter case, the interaction of dominance occurred between queen and worker and among workers. Some workers developed ovaries to lay eggs. However, this data were not quantified.

3.2. Temporal Polyethism. Some activities were preferably carried out by younger workers or older workers. This suggests division of labor by age (Figure 2).

The younger workers (7 to 56 days of age) stayed in the nest for approximately 27.03 ± 12.72 days (7–56, N = 27). For this time, took they care the pupae, larvae, eggs, males, and winged females (Figure 2). However, some newly hatched ants did not taken care for the young individuals. This might be related the presence of physiological problems, because they died within two or three days.

The older workers (those at more than 56 days of age) performed several categories, but they pointed in the activities out of the nest, as defense, foraging, and exploring (Figure 2). Furthermore, the dominance is a category that deserves attention. It may be linked to the maintenance of the colony, as a measure of protection from the nest and obtaining food, or reproduction.

The intermediate group (queens, virgin queens, and winged females), which is regarded as a caste, showed clear transition tasks. The quantitative results of the group are

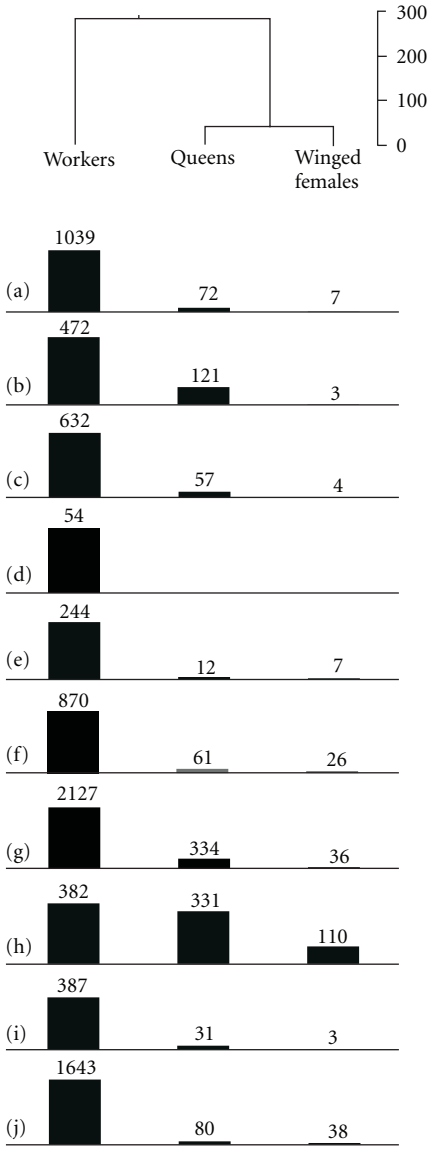

Figure 1: Dissimilarity dendrogram of individuals of *P. striata*. Behavioral categories: (a) feeding, (b) communication, (c) brood care, (d) sexuate care, (e) defense, (f) exploring and foraging, (g) grooming, (h) inactivity, (i) dominance, and (j) nest maintenance.

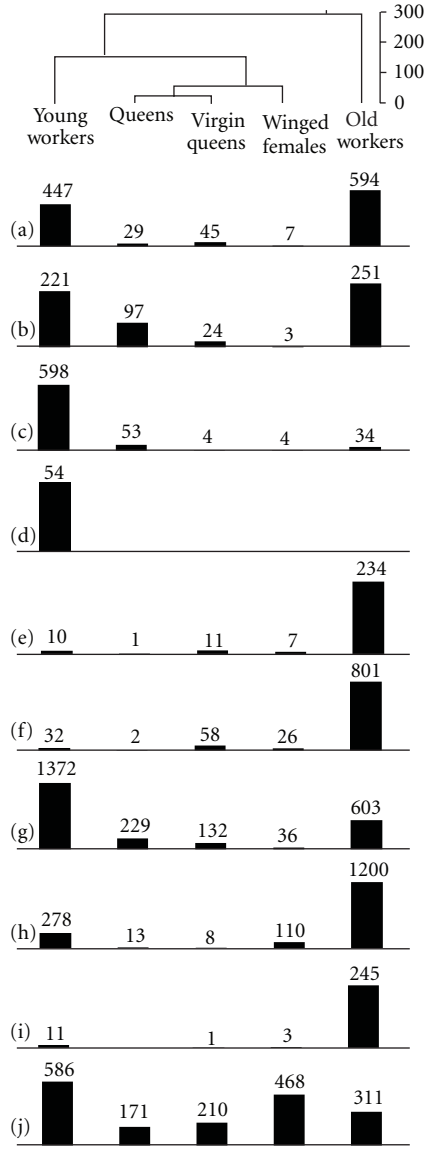

Figure 2: Dissimilarity dendrogram of individuals of *P. striata* showing the division of labor by age. Behavioral categories: (a) feeding, (b) communication, (c) brood care, (d) sexuate care, (e) defense, (f) exploring and foraging, (g) grooming, (h) inactivity, (i) dominance, and (j) nest maintenance.

smaller when compared to workers, and the activties have been concentrated within the nest.

4. Discussion

It is interesting to note that a small portion of behavioral acts is performed by queens within the nest. This type of occurrence is mentioned to the species of *P.* (*Neoponera) villosa*, *P.* (*Neoponera) apicalis*, and *P.* (*Neoponera) obscuricornis* [19]. The queens of *P. striata* presented more care for eggs than to the other immature individuals, while *P. (Neoponera) villosa* spends more energy caring for eggs and pupae, *P. (Neoponera) apicalis* and *P. (Neoponera) obscuricornis* invest more energy in caring for larvae and pupae [19]. The involvement of queens in brood care seems to be a little derived characteristic [20].

Feeding was a behavioral act frequently observed in the queens of *P. striata*, while the queen of *Nothomyrmecia macrops* was seen feeding once [21].

The queens and workers which to perform the laying eggs, retained the position in the form C. *Ectatomma planidens* [22, 23] and *Platythyrea punctata* [24], also acquired the same position.

This is characteristic of wasps of the genera *Listenogaster* [25] and *Eustenogaster* [26]. This condition may be an evidence of an attribute that might have been preserved.

Table 2: Behavioral catalog of *Pachycondyla striata*.

Category and behavioral acts	Queens	Workers	Winged females	Males
(A) Feeding				
01-Feeding on prey	0.0355	0.0700	0.0128	
02-Intake of liquids	0.0264	0.0587	0.0171	0.0116
44-Cannibalism	0.0030	0.0020	0.0059	
(B) Communication				
03-Antennate workers	0.0755	0.0549	0.0128	0.0516
04-Antennate queens	0.0345	0.0052		
(C) Brood care				
05-Antennate egg	0.0218	0.0129		
06-Antennate larvae	0.0010	0.003		
07-Antennate pupae		0.004		
08-Standing on eggs		0.0006		
09-Standing on larvae	0.0010	0.0014		
10-Standing on pupae		0.0009		0.0058
11-Handling eggs	0.0127	0.0045		
12-Handling larvae		0.0063	0.0043	
13-Handling pupae		0.0015		
15-Feeding larvae		0.0058		
16-Cleaning larvae		0.0085	0.0043	
18-Carrying eggs	0.0063	0.0126	0.0086	
19-Carrying pupae		0.0071		
20-Carrying larvae		0.0031		
22-Standing and holding an egg	0.0045	0.0061		
23-Standing and holding a pupa		0.0012		
24-Egg laying	0.0045	0.0004		
(D) Sexuate care				
14-Handling winged females		0.0003		
17-Cleaning males		0.0059		
21-Carrying males		0.0006		
(E) Defense				
25-Guarding the nest entrance	0.0110	0.0310	0.0210	
(F) Exploring and foraging				
26-Capturing prey	0.0118	0.0582		
27-Walking in the foraging arena	0.0427	0.0478	0.1070	0.0580
28-Tanden running	0.0010	0.0047	0.0043	
(G) Grooming				
29-Self-grooming their antennae	0.1164	0.082	0.059	0.0860
30-Self-grooming their 1st pair of legs	0.0582	0.03	0.0043	0.0660
31-Self-grooming their antennae and 1st pair of legs	0.0282	0.0252	0.0259	0.0233
32-Self-grooming their 2nd and 3rd pairs of legs	0.0591	0.0722	0.0212	0.0290
33-Self-grooming their anus	0.0054	0.0200		0.0260
34-Social grooming	0.0363	0.0062	0.0530	
(H) Inactivity				
38-Inactivity in the nest	0.3700	0.0323	0.4369	0.5000
39-Inactivity in the foraging arena	0.0219	0.0163	0.0350	0.0630
(I) Dominance				
35-Antennal boxing	0.0218	0.0405	0.0027	
36-Blocking	0.0054	0.0005		
37-Immobilization	0.0010	0.0081		0.0160

Table 2: Continued.

Category and behavioral acts	Queens	Workers	Winged females	Males
(J) Nest maintenance				
40-Carrying a dead ant	0.0010	0.1512		
41-Handling a dead ant		0.133		
42-Carrying garbage	0.0010	0.0103		
43-Handling garbage	0.0010	0.0085		
45-Exploring the plaster nest	0.0700	0.0160	0.1639	0.0643
46-Digging in the plaster nest		0.0080		
Total frequency	1	1	1	1
Total categories	9	10	9	8
Total behavioral acts	31	46	19	13

The agonistic behavioral acts were almost always related to reproduction or foraging activities. Antennal boxing occurred with winged females, queens, and workers. This behavior may be related to the recruitment of workers, as the measure was implemented in the nest, and a larger number of workers moved to the foraging arena. The same happens to *P. bertholudi* [27].

In nest 8, after the queen's death, one worker started laying eggs. Afterwards, agonistic encounters became frequent, and another worker that started laying eggs was mutilated. This suggests that *P. striata* presents a reproductive dominance, as does *P. crassinoda* [28]. Agonistic encounters were also reported for *P. (Neoponera) obscuricornis* [29, 30] and *P. bertholudi* [27].

Chagas and Vasconcelos [31] described the fighting behavior between workers of *P. striata* and *P. (Neoponera) obscuricornis* in the field. According to these researchers, this event occurred because *P. striata* invaded the foraging and/or life area of *P. obscuricornis*.

The agonistic behavioral acts observed in *P. striata* were also reported for *Dinoponera quadriceps* [32], *P. (Neoponera) apicalis* [33], *P. (Neoponera) obscuricornis* [29], *Rhytidoponera* sp. 12 [34], *P. inversa* [35], and *P. bertholudi* [27].

We checked that the workers ate larvae, pupae, other workers, and males. Some alive males had their abdominal region pulled off by workers. These behaviors may indicate stress or cannibalism. Wilson [1] reported that dead workers might be used as food or were discarded.

The eggs of *P. striata* collected from the natural environment and those laid by queens and workers in laboratory did not develop. They were predated by dominant individuals or by the whole group under stress. Egg predation was reported in *Ectatomma planidens* [22, 23] and *E. vizottoi* [36] although it has been absent or not observed in *Pachycondyla bertholudi* [37]. The eggs laid by workers are usually eaten by queens and larvae, which represents a stereotyped, conspicuous behavior pattern [1].

Oophagy is indispensable to the social Hymenoptera [1]. It is important because workers do not regurgitate food either for larvae or for queens, so they can use their own resources to produce immature oocytes [38]. This event seems restricted to some genera in the subfamily Ponerinae [38].

In the presence of a large number of eggs, the workers gathered them and stood still on them. They standing motionless on eggs, pupae, and larvae. This may suggest warming and protection of the immature individuals. When the number of eggs in the nest was small, the ants of this species kept the eggs clustered between their mandibles.

The behavioral act *tandem running* was carried out to recruit workers into the foraging arena. Medeiros and Oliveira [39] observed this as well. This behavior is common in several species such as *Pachycondyla (Brotoponera) tesserinoda* [40] and *Pachycondyla obscuricornis* [31].

The larvae of *P. striata* display a characteristic behavior to order food. They shake their necks and heads several times towards the ventral region of their body until a worker answers. This behavior is similar to that one of larvae of *Gnamptogenys striatula* [41]. The workers moved the larvae towards the prey. In some cases, the workers held the prey between their mandibles, while the larvae inserted their head into the sectioned part of the mealworm and fed on hemolymph. The workers feed preferentially larvae closer to them. Asking for food was a behavioral act observed more often in larvae in the last instar. The workers touched the buccal apparatus of the larvae with their mandibles open, but it was not possible to see the food transfer or the projection of the glossa of the workers. A similar behavioral act was described for *P. crassinoda* [28].

Small pieces of mealworm were placed in the ventral region of the larvae of ants by the workers. The larvae curved their necks and fed in the same manner as described for *Gnamptogenys horni* [42], *Ponera pennsylvannica* [43], and *Pachycondyla crassinoda* [43]. According to Wilson [1] and Traniello and Jayasuriya [44], feeding larvae on small fragments of prey is a less derived characteristic.

P. striata use their stinger to paralyze their prey. The sting might be stimulated by sudden movements of the prey, similar to way what happens to workers of *P. caffraria* [45]. According to Traniello and Jayasuriya [44], using the stinger to paralyze prey is a less derived characteristic.

The state of inactivity or deep sleep exhibited by *P. striata* is similar to one that described by Cassill et al. [46]. Many workers remained motionless in foraging area. This category may reflect the restricted space of the arena or, as Miguel and Del-Claro [47], the state, containment of spent

energy. The inactivity behavior was observed in *Pachycondyla (Neoponera) villosa*, *P. (Neoponera) apicalis*, *P. (Neoponera) obscuricornis* [19], *P. crassinoda* [48], *Nothomyrmecia macrops* [21], *E. planidens* [22, 23], and *E. opaciventre* [47].

The monomorphic workers of *P. striata* present specialized task division, forming work groups to performing tasks linking to individuals with similar ages. Young individuals provide parental care, whereas older individuals carry out the activities of defense, exploration, and foraging.

Young workers stayed in the nest for 56 days, but some left earlier. They were recruited into the foraging area according to the necessity of food or to substitute the dead workers. In the first 45 days after emergence, *Ectatomma tuberculatum* performs tasks progressively according to the age of the individuals [49]. The same happens to workers of *Platythyrea lamellosa*, which after hatching (0–5 days of age) present association with pupae and later take care of eggs and larvae, performing specific tasks influenced by their age [50]. Unlike *P. striata*, newly hatched individuals of the species *Pachycondyla caffraria* (0–5 days of age) present four types of behavioral acts and are capable of foraging early at this age [51]. Each colony of this species has precise requirements as to carbohydrates and proteins, appropriate for labor division, which happens in relatively fixed proportions between hunting foragers and those which collect water with sugar [45]. Workers of *P. striata* were seen at the carbohydrate source in a very small frequency. This activity was included in the behavioral act of taking water in from the cotton wool. *P. striata* preferred to capture other insects to provide protein intake.

This research shows the profile of social organization of *P. striata*. We see that many behavioral acts are common for species of the subfamily Ponerinae. Although there is a narrow dimorphism in castes of *P. striata*, there is a great difference of division of labour between them. The age is a factor that controls the performance of tasks in workers.

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