

Research Article

Dynamics of Foraging and Recruitment Behavior in the Asian Subterranean Termite *Coptotermes gestroi* (Rhinotermitidae)

Alberto Arab,¹ Yara carollo Blanco,² and Ana Maria Costa-Leonardo²

¹ Universidade Federal de Alfenas (UNIFAL-MG), Instituto de Ciências da Natureza, 37130-000 Alfenas, MG, Brazil

² Departamento de Biologia, Universidade Estadual Paulista (UNESP), 13506-900 Rio Claro, SP, Brazil

Correspondence should be addressed to Ana Maria Costa-Leonardo, amcl@rc.unesp.br

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The present study investigated the trail-following behavior of the subterranean termite *Coptotermes gestroi* (Wasmann Rhinotermitidae) under laboratory conditions. The results showed that workers were the first to initiate the exploration to the food source. When food was discovered they returned to the nest laying a trail for recruiting nestmates to the food source. In this situation, workers always traveled significantly faster when returning from the arenas. Both workers and soldiers were recruited to the food source; however, the soldier/worker proportion was higher during the first phase of the recruitment. When no food was available, the number of recruited nestmates and the speed on their way back to the nest were significantly lower. The results also showed that scout foragers always laid trail pheromones when entering into unknown territories, and that chemical signals found in the food could induce workers of *C. gestroi* to increase their travel speed.

1. Introduction

The dynamics of the foraging and recruitment process in social insects has been investigated in many species within the Isoptera and the Hymenoptera. While many ants and bees also rely on optical cues, foraging in termites is organized predominantly by chemical signals, such as pheromone trails laid on the substrate for orientation and recruitment. The sternal gland is the only reported source of trail pheromone in termites. Secretions of this gland are considered to function in the recruitment of nestmates to source disturbance within the nest. Termites may also use trail-following pheromones to colonize new food sources [1, 2].

Termite trail-following pheromones are composed of one or few compounds. Up to date, only 9 compounds have been identified as trail pheromones in several termite species. For the termite families in which chemical trail pheromones have been reported, Rhinotermitidae, Termitidae, and Kalotermitidae seem to use mainly neocembrene A, (Z,Z,E)-dodeca-3,6,8-trien-1-ol, (Z)-dodec-3-en-1-ol, and (Z,Z)-dodeca-3,6-dien-1-ol [3–9]. *Nasutitermes corniger* uses in addition to these two compounds, trinervitatriene [8]; *Mastotermidae* uses (E)-2,6,10-trimethyl-5,9-undecadien-1-ol

and Termopsidae uses (E)-2,6,10-trimethyl-5,9-undecadien-1-ol, tricosane, and 4,6-dimethyldodecanal; whereas *Glossotermes oculatus* (Serritermitidae) uses nonecadienone for trail following [10, 11]. Termites also seem to use secretions of the sternal gland as both attractants and orientation signals in their foraging trails [12, 13], but the details of the chemical communication system used by termites are less known than in the Hymenoptera. Nevertheless, behavioral evidence also suggests that additional compounds may act in species specificity and in the differentiation between exploring and foraging trails [14, 15]. Despite the fact that few components have been identified, behavioral evidence suggests that termite trail pheromones are multicomponent systems as shown for some ants [16]. Furthermore, qualitative or quantitative differences in pheromone trails laid by different castes have been suggested as cause for caste-specific polyethism during termite foraging and recruitment [17–19] and for differentiation between foraging and recruitment trails [20].

Subterranean termites (Rhinotermitidae) create ramified tunnel systems above or beneath the soil to locate their cellulosic food. Sometimes these tunnels, which range from tens to hundreds meters in length, connect multiple feeding

sites. The Asian subterranean termite *Coptotermes gestroi* (Rhinotermitidae) is a pest of great economic importance in urban areas of southeastern Brazil. This species was accidentally introduced from marine cargo, probably at the beginning of the 20th century and has rapidly colonized new areas throughout southern Brazil, increasing its economic impact [21]. As discussed elsewhere [22, 23], foragers of *C. gestroi* build several foraging tunnels at random. When the food is located, there is an increase in the number of workers and soldiers in the tunnels that connect the nest directly with the food (recruitment tunnels). At this time, foraging trails could be abandoned by the foragers. The aims of this study were to characterize foraging and recruitment trails on a behavioral level in *C. gestroi* (Wasmann). We examined the response toward two different types of trails, and caste-specific differences toward trails laid by workers or soldiers. Workers of *Reticulitermes santonensis* are able to discriminate trails that connect the nest to food sources from others [15]. Since (Z,Z,E)-dodeca-3,6,8-trien-1-ol is the only compound found in the trail pheromone of *R. santonensis* [24] and *C. gestroi* [25], we hypothesized that differences on the trail following behavior between foraging or recruitment trails could be due to differences in the concentration of the trail pheromone laid by the termites. Although termite trail communication has been studied for decades, detailed knowledge is only fragmentary. Such information would be useful in understanding the foraging behavior and food preference patterns of this species with the objective of improving a pest management strategy against this invasive pest termite.

2. Methods

2.1. Collection and Maintenance. Foraging workers and soldiers of *Coptotermes gestroi* (Rhinotermitidae) were collected from natural colonies in Rio Claro city, São Paulo State, Brazil (22°23'43"S, 47°32'39"W). The termites were collected using traps of corrugated cardboard paper placed on the foraging territories of the colonies of each species. The traps were collected after one week and the individuals (workers and soldiers) were confined in 2.5 L glass containers filled with wet sand (at 10% moisture) and stored at 25°C, according to the laboratory maintenance protocols established for this species [19]. Food consisted of 3 × 2 × 1 cm blocks of *Pinus* sp. For bioassays on foraging and recruitment trails; 200 workers and 20 soldiers were transferred into a 500 ml plastic container (artificial nest) and acclimatized for one week until the beginning of the bioassays. Five colonies were used in this study.

2.2. Sternal Glands Extracts. Workers were cold anesthetized (−20°C) and placed in a ventral position on a Petri dish. The fifth sternite containing the sternal gland was gently removed under a stereomicroscope with the aid of microscissors. Samples of 10 glands of workers were transferred to vials and extracted in 100 µL of *n*-hexane for 24 h at room temperature. Preliminary tests showed that a polar solvent such as methanol did not extract compounds that elicited trail following behavior in *C. gestroi*. The material was stored

at −20°C until used for the bioassays. Due to unavoidable contamination with the over-developed frontal gland of the soldiers of this species, the sternal glands of this caste were not used in this study.

2.3. Activity of Sternal Gland Extracts. Activity was evaluated using a Y-choice assay on a 10 cm diameter filter-paper with a 120° angle between each branch. An artificial trail of gland extract (1 µL of extract per 1 cm of trail) was deposited at the base of the Y (3 cm) and on one of the branches (7 cm). In the same way, on the Y base and on the other branch we deposited a hexane extract as control. The distance covered by each individual (worker or soldier) was recorded using the following concentrations of the sternal gland extracts: 0.001 glands/µL (gl/µL), 0.005 gl/µL, 0.01 gl/µL, and 0.1 gl/µL. The maximal response was 10 cm, and the threshold concentration was defined as a trail followed longer than 3 cm. The individuals were previously confined into a device that allowed the exit of one individual at a time. For each replicate, a new filter paper was used in order to prevent trail reinforcement. Thirty replicates were made for each caste and concentration. Data were analyzed by a *t*-test to compare the activity between gland extracts and the control. An ANOVA was used to compare the mean distances covered by both workers and soldiers in response to gland and control extracts. Multiple comparisons among the means were performed using the Tukey HSD test, *P* < 0.05 [26]. All bioassays were made under red-light illumination at constant temperature and relative humidity (25°C, 70% RH).

2.4. Activity and Preference for Foraging and Recruitment Trails. Trail-following behavior was investigated in a setup connected to the above mentioned artificial nest. Termites had access to experimental arenas (200 ml plastic containers) via a glass tube (length, 8 cm; ID, 0.5 cm). Foraging trails consisted of empty arenas. On the other hand, recruitment trails were investigated in the same way but connecting the end of the glass tube to an arena containing blocks of pine wood as a food source. In both situations, we let a single worker lay a trail in the glass tube returning from arenas either with or without food. Access to the glass tube could be opened and closed with a slide in which a hole of 0.5 cm was drilled. The travel speed of the first worker on its way forth and back was evaluated. After trail marking, one worker was allowed to travel through the glass tubes, and its travel speed was evaluated as mentioned before. The total number of termites following both types of trails, offered within 30 min after opening the slide, was also recorded. After each single replicate, the tube was removed and replaced by a new one. Trail-marked tubes were used in the preference bioassays. The experiment was replicated 20 times for each trail type. Data were analyzed by Mann-Whitney *U* test (comparison between foraging and recruitment trails) and Wilcoxon matched-pairs test (comparison of the ways back and forth for each trail type) [26]. In order to determine the persistence of both foraging and recruitment trails, the experiments were also conducted with test tubes marked by the termites 24 h before.

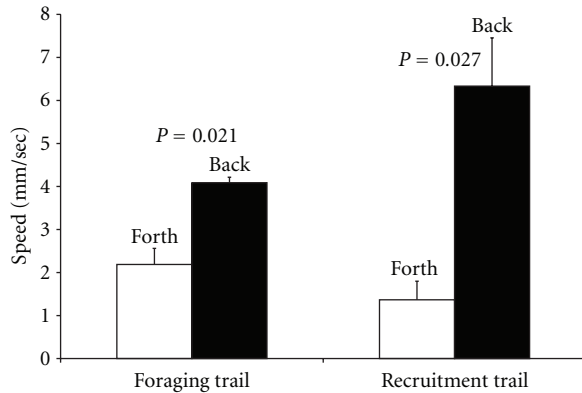


FIGURE 1: Mean travel speed ($\pm$ SD) by trail-laying workers of *Coptotermes gestroi* in a glass tube connected to empty arenas (foraging trail) or wood (recruitment trail). $N = 20$; P values above bars correspond to the Wilcoxon matched-pairs test ($P < 0.05$) for differences between forth and back speed.

To examine the preference of termites to different trail types, the workers were able to deposit a foraging or recruitment trail for 30 min as described above. Both control and test tubes with the trail were then attached simultaneously to the artificial nest in the setup described above. Controls consisted of clean glass tubes. The choice behavior of the first worker following the offered trail was recorded. This experiment was replicated 30 times for each trail type. To evaluate the persistence of trails laid by the termites, we used test tubes marked by the termites one week and one month before the bioassays. The results were analyzed using a binomial Z test [27]. All bioassays were made under red-light illumination at constant temperature and relative humidity (25°C , 70% RH).

3. Results

The worker caste of *C. gestroi* was the first to initiate the exploration towards the new food source. The present data showed that they initiated the exploration in 73% of the assays ($\chi^2 = 24.30$; $df = 1$; $P < 0.001$; Yates correction), independently of the type of foraging situation, that is, with or without food ($\chi^2 = 0.67$; $df = 1$; $P < 0.414$). Afterwards, workers returned to the artificial nest, abdomen pressed to the substrate, chemically marking the initial exploratory trail. The time at which scout workers traveled to the arenas in the glass tube was determined for foraging and recruitment trails. In both situations, workers traveled significantly faster when returning from the arenas (Figure 1). But if wood was offered, travel speed returning to the nest was significantly higher than in the absence of food ($P = 0.047$, Mann-Whitney U test) (Figure 1). This behavior started the recruitment phase. When workers detected both types of trails and followed them. In our bioassays, the first recruited worker traveled significantly faster when returning from the arenas ($P < 0.05$; Wilcoxon matched-pairs test). However, significant differences of the travel speed on the way back and forth with or without

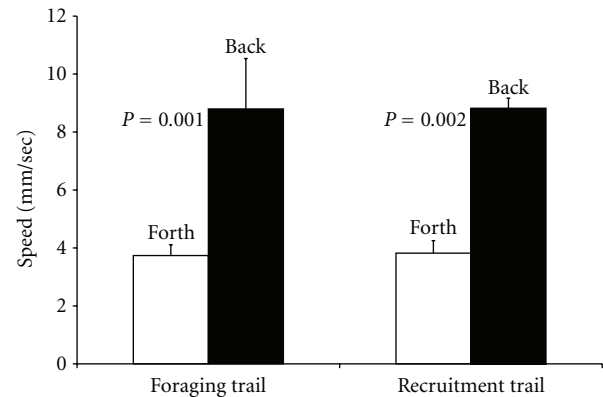


FIGURE 2: Mean travel speed ($\pm$ SD) of the first worker following foraging or recruitment trails. $N = 20$; P values above bars correspond to the Wilcoxon matched-pairs test ($P < 0.05$) for differences between forth and back speed.

food were not detected ($P > 0.05$, Mann-Whitney U test) (Figure 2).

After 20 min, a significantly greater number of workers arrived to the food source (recruitment trail) ($P < 0.05$; Mann-Whitney test). On this type of trail, the maximum number following within 30 min rose to above 23 (Figure 3(a)). The number of workers recruited in the foraging trails stabilized after 10 min of starting the bioassay. Eventually, the termites would build a covered gallery inside the glass tube, leading from the artificial nest containing the termites to the food. Soldiers were also observed following the trails and their number increased significantly after 15 min in recruitment trails ($P < 0.05$; Mann-Whitney U test) (Figure 3(b)). During the first phase of the trail-following behavior (5–20 min), the soldier/worker proportion was approximately 1 : 1 in recruitment trails. In foraging trails, this proportion was significantly lower ($P < 0.05$; Mann-Whitney U test). But the soldier/worker proportion on the recruitment trail decreased after 15 min, as the number of recruited workers increased (Figure 3(c)). The total number of termites participating in the recruitment process represented a small proportion (about 10%) of the total number of termites confined in the artificial nests.

The preference of both foraging and recruitment trails over control trails indicates that foragers of *C. gestroi* always laid trails when exploring for food sources, even in the absence of food. When both types of trails were tested simultaneously, workers significantly preferred recruitment trails over foraging trails, indicating that the signal laid by the termites is different between these types of trails (Table 1). Recruitment trails laid by *C. gestroi* showed a high persistence in the glass tubes. When we offered a trail marked one week and one month before the choice bioassays, workers also showed a strong preference for their own trails over the control (Table 1).

The trail-following activity elicited by sternal gland extracts was higher than those of the control extracts in *C. gestroi* ($t = 18.43$, $df = 1$, $P < 0.0001$; t -test). The residual activity of the control extracts was probably

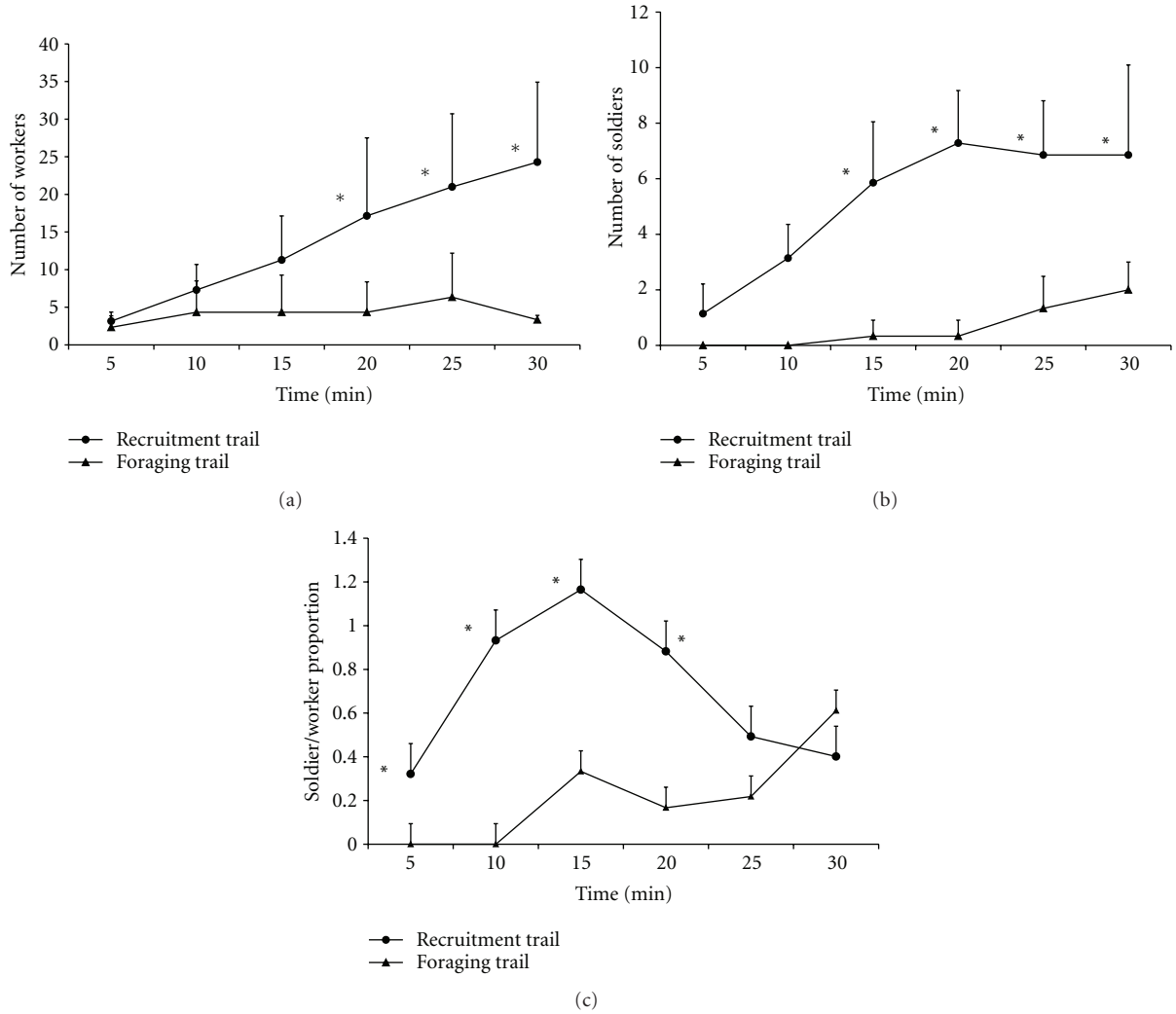


FIGURE 3: Mean number ($\pm$ SD) of workers (a), soldiers (b), and proportion of soldiers and workers (c) of *Coptotermes gestroi* following a foraging or recruitment trail within 30 min. $N = 20$. Asterisks indicate significant differences between types of trails ($P < 0.05$; Mann-Whitney test)

TABLE 1: Trail-following preference* of *Coptotermes gestroi* workers on foraging and recruitment trails.

Time after trail marking	Foraging trail		Recruitment trail		P
	Marked	Unmarked	Marked	Unmarked	
30 min	20	8			0.002
30 min			24	6	<0.0001
30 min	6		24		<0.0001
1 week			18	8	0.009
1 month			20	5	<0.0001

* The results were analyzed using the binomial test ($P < 0.05$); $N = 30$.

due to contamination of trail pheromones after removal of the sternal glands. Trail-following behavior was affected by the concentration of sternal gland extracts. Activity of both workers and soldiers increased significantly with increasing concentrations of the sternal gland extracts

(workers: $F = 201.59$; $df = 3$; $P < 0.0001$. Soldiers: $F = 174.75$; $df = 3$; $P < 0.0001$; ANOVA). Both castes registered their maximum activity at the concentration of $0.01 \text{ gl}/\mu\text{L}$, and their activity threshold was observed at $0.001 \text{ gl}/\mu\text{L}$. Concentrations higher than $0.01 \text{ gl}/\mu\text{L}$ clearly reduced the trail-following activity of the individuals (Figure 4).

4. Discussion

Foraging behavior in termites is a collective process mediated by semiochemicals produced by exocrine glands of both workers and soldiers. The sternal gland is the only known source of trail pheromones in termites, and secretions of this gland are considered to function in the recruitment of nestmates from nest to feeding sites. *Coptotermes gestroi* and other subterranean termites have a similar foraging behavior in the presence of a new food source. The behavior of termite workers when the scouts look for a new food source was described by Arab et al. [19] for *C. gestroi*, Reinhard

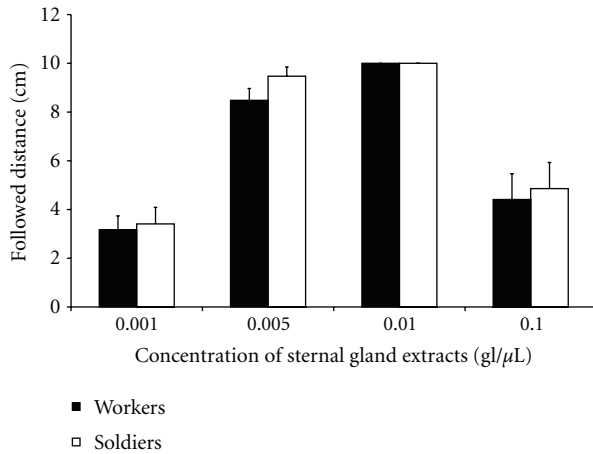


FIGURE 4: Termite activity elicited by sternal gland extracts of *Coptotermes gestroi*. Values indicate mean followed distance ($\pm$ SD) by workers and soldiers. $N = 30$.

and Kaib [15] for *Reticulitermes santonensis*, and Traniello and Busher [18] for *N. costalis*. The results of these studies and the present one showed that: (1) both castes (mainly workers) initiate the exploration to new food sources; (2) trail pheromone is laid on the substrate; (3) both castes are recruited from the nest; (4) the number of individuals recruited depends on the presence of food; (5) soldier/worker proportion is higher at the first stage of the recruitment process.

The present data indicate behavioral differences in the way that termites react to the different trail types. Travel speed of *C. gestroi* scout workers was always higher on the way back to the nest. This probably is due to the fact that scout foragers always laid trail pheromones when entering into unknown territory, and thus are able to follow their own trail back to the nest. These results also indicate that the subsequent discovery of a food source by workers also increases their travel speed. When food is discovered, the travel speed on the way back to the nest was higher in recruitment trails as compared to the foraging situation (without food). According to Clément et al. [28] and Reinhard et al. [29], wood volatiles can induce trail-following behavior in subterranean termites. However, in the subterranean termites, the presence of food does not seem to elicit the building of underground tunnels, instead, workers of *C. gestroi* build tunnels randomly in their foraging territories [30, 31]. Probably, chemical signals found in the food or other factors, such as chewing behavior [32] or the presence of a full gut in the returning termites could induce workers of *C. gestroi* to increase their travel speed, therefore, maximizing the foraging performance when food is discovered.

Recruitment trails of *C. gestroi* were more preferred and attractive to workers than foraging trails. They were followed by more termites than foraging trails. A higher attraction of recruitment trails compared to foraging trails has also been described for *Trinervitermes bettonianus* (Termitidae), *R. flavipes* (Rhinoitermitidae), and *Nasutitermes costalis* (Termitidae) [12, 20, 33]. The difference between

the two types of trails may be connected to qualitative or quantitative differences, that is, termites could either release more pheromone to lay a recruitment trail or release additional pheromone components. Qualitative differences of the trail pheromone can be more expected in the Termitidae, since the trail pheromone identified in some species of this family is a blend constituted by at least two components, which can be modulated to elicit different responses on nestmates. Conversely, only ((Z,Z,E)-dodeca-3,6,8-trien-1-ol) has been identified in the trail pheromone of workers of *R. santonensis* and *C. gestroi*, suggesting that preference for trail types in these species could be modulated by differences of the concentration of the trail pheromone laid by nestmates. Further components in the trail pheromone of these species have not yet been identified. Workers of *R. santonensis* termites pressed their abdomen onto the ground in a dotted way in foraging trails. In contrast, for recruitment trails the abdomen was dragged over the surface, resulting in a continuous trail. During dragging, more sternal gland secretion could be applied [1, 15]. Direct observations were unable to detect differences in trail pheromone deposition; however, activity bioassays showed that higher concentrations of sternal gland extracts elicited a higher activity in both workers and soldiers of *C. gestroi*, as demonstrated by Grace et al. [34] for *R. hesperus*.

Long-lasting, low-volatility trail pheromones could be useful for trail orientation when termites forage in tunnels built underground or on the surface [25] and references therein, and trail information could be modulated by the concentration of the trail pheromone. However, (Z,Z,E)-dodeca-3,6,8-trien-1-ol is a volatile and unstable molecule [8] and cannot remain active for long periods. Since the present bioassays showed that recruitment trails remain active after one month, it is possible that other signals play a role in modulating this type of communication in *C. gestroi*. Many termite species add feces, saliva, and other secretions to the trail. This could explain why foraging trails can be reused after several years in some termite species [20].

Caste-specific polyethism during foraging and recruitment has been observed in some termite species [18]. Scout individuals are specialized in exploring for food sources and recruiting nestmates by laying chemical trails [15]. The present results for *C. gestroi* show that workers initiate the exploration to new food sources. Then, both soldiers and workers are recruited; however, soldier/worker proportion was higher at the first stage of the recruitment. This caste-specific difference in recruitment behavior has been observed in other termites [15] and corresponds to the different roles of the two castes during the search for food [30]. In *C. gestroi*, workers initiate foraging most of the times, and the soldier/worker proportion remained high during the first phase of the foraging (5–20 min). This behavior could be associated with the defensive role of soldiers in the exploration to an unknown territory and was more evident in the presence of food (recruitment trails), thus suggesting that the trail pheromone could also modulate the defensive behavior of soldiers in colonies of this species.

The comparison of this research with other similar studies provided a better understanding of how a termite

colony organizes the process of foraging and recruitment. Recently, detailed research on the chemical composition of the trail pheromone of several species has been conducted (reviewed in [35, 36]). However, behavioral bioassays have not been performed in parallel to verify the presence of additional signals in the foraging behavior of termites. Future studies involving foraging bioassays will be necessary in order to expand the understanding of caste-specific roles in the trail-following behavior of termites.

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