

Behavioural repertoire of termites in corpse management: A comparison between one-piece and multiple-pieces nesting termite species



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ABSTRACT

Corpse disposal is an essential adaptation to social life. This behaviour promotes nest hygiene and prevents the spread of pathogens in the colony of social insects. The current study verified the corpse management in two termite families towards cadavers of different origins. We carried out bioassays with subcolonies of *Cryptotermes brevis* and colonies of *Cornitermes cumulans*, in which corpses of termite workers from the same colony, from another colony and from another species were introduced. The results showed that *C. brevis* consumed the corpses regardless of their origin, but they avoided the chitinous parts of the head. In this species, consumption of dead individuals, besides performing a hygienic function, seems to be a strategy for nitrogen and water acquisition. In the *C. cumulans* species, interspecific and intercolonial corpses were covered with soil and faeces after being groomed. Nestmate corpses were entombed, transported to the nest or ignored after being submitted to grooming. Our findings indicate that a one-piece nesting termite, as *C. brevis*, exhibited a simplified corpse management repertoire in relation to that performed by *C. cumulans*, a multiple-piece nesting species, whose approach was more complex and diverse. Behavioural responses are associated with the nesting of the species.

1. Introduction

The presence of dead individuals inside social insect nests can present a risk of contamination with pathogens, damaging the integrity of the colony (Cremer et al., 2007). Corpse management is considered to be an important characteristic of adaptation to social living and, to prevent prolonged contact with corpses, the social insects perform different undertaking strategies (López-Riquelme and Fanjul-Moles, 2013). These strategies consist of a complex and sophisticated sequence of behavioural patterns elicited by the presence of cadavers of different origins, ages and infection status (Sun and Zhou, 2013). The behavioural responses for disposing of corpses vary among the social insect groups and are dependent on the feeding habit and nest ecology (Neoh et al., 2012). Honey bees remove nestmate corpses from their nest, while ants remove cadavers to the exterior of the nest or to special chambers (Visscher, 1983; Wilson et al., 1958). In some ant species, however, both burial and cannibalism have also been documented (Driessen et al., 1984; Renucci et al., 2011). Likewise, termites perform varied responses that include avoiding contact with the corpse, cannibalism, removal and burial (Sun and Zhou, 2013).

Social insect colony members must be able to distinguish between dead and living individuals before initiating corpse management. Death recognition depends on varied cadaver cues, which can be tactile and,

or chemical (Sun and Zhou, 2013). Two main hypotheses about the recognition through chemical signals are accepted. One of them is that death recognition occurs due to the accumulation of postmortem substances. In several insects, the accumulation of unsaturated acids, e.g. oleic acid and linoleic acid, elicits undertaking responses. According to Wilson (1985), two species of ant, *Pogonomyrmex badius* and *Solenopsis saevissima*, recognise dead individuals due to the emission of fatty acids, especially oleic acid. Studies with other species of ant, as well as bee and termite, corroborate the hypothesis of "fatty acid as warning of death" (Haskins and Haskins, 1974; Howard and Tschinkel, 1976; Ulyshen and Shelton, 2012; Visscher, 1983; Yao et al., 2009). The second hypothesis is that corpse management is triggered by a reduction of vital chemical signs present in the cadaver cuticle, such as the disappearance of dolichodial and iridomyrmecin on the corpse cuticle of the ant *Linepithema humile* (Choe et al., 2009).

One of the termite species studied is *Cryptotermes brevis* (Walker, 1853), whose origin is probably Peru-Chile (Scheffrahn et al., 2009), that is a drywood termite belonging to the Kalotermitidae family. This species is a one-piece nesting termite, i.e., it nests in the piece of wood that serves as food resource (Korb, 2005). The colonies of *C. brevis* live in woods with humidity below 30% and, therefore, these termites obtain humidity from their own food and conserve it through the production of dry faeces (Brazolini et al., 2001)

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The other studied termite is *Cornitermes cumulans* (Kollar, 1832), that is a Neotropical termite belonging to the Termitidae family, which occurs in Brazil, Paraguay and Argentina (Araújo, 1970). This species is a multiple-piece nesting termite, whose colonies live in a well-defined nest separated from the food source (Korb, 2005). It builds mound nests that may reach considerable size and presents large population when compared with those of *C. brevis*.

Corpse management have been studied in termites, but there is no record about this subject in the basal Kalotermitidae family. In the Termitidae family, there are reports of corpse management in *Pseudacanthotermes spiniger* dealated female that buried corpses of other females for the purpose of nest hygiene (Chouvenc et al., 2012). Laboratory studies of the competition between two Neotropical termitids, *C. cumulans* and *Procornitermes araujo*, showed that, after confrontation, individuals killed during it were used to block tunnels and to deter other species (Jost et al., 2012).

In the present study, we evaluated the corpse management in *C. brevis* and *C. cumulans* under laboratory conditions to verify the behavioural repertoire and the consequent final disposal of termite corpses. We tested cadavers of different origins, which might replicate natural contexts (for example, confrontation interactions between termites that could result in the death of a nestmate or alien). We hypothesized that termites would perform different corpse management according to the origin of the cadaver and the nesting ecology of the species.

2. Material and methods

2.1. Termites

Ten natural colonies of *C. brevis* were extracted from several pieces of infested furniture collected in different districts of the city of Rio Claro, SP, Brazil (22° 24'S, 47° 33' W). Two nests of *C. cumulans* were collected in Rio Claro, SP, Brazil (22° 23'S, 47° 32' W), transported to the laboratory and maintained at 25 ± 2 °C, > 80% relative humidity (RH) in complete darkness. Each nest was provided with water and food *ad libitum*.

2.2. Preparation of corpses

Undertaking responses to corpses of different origins were tested in subcolonies of *C. brevis* and colonies of *C. cumulans*. Termite workers were frozen to death at -6 °C for 20 min and kept in a covered Petri dish at room temperature for 30 min. After this period, the corpses were introduced into the experimental arenas which were used for the development of the bioassays.

2.3. Experimental set-up

The experimental arena used with *C. brevis* consisted of a circular excavation (35 mm diameter and 8 mm depth) in a *Pinus* sp. wood block (100 × 45 × 25 mm) covered with a glass sheet. A sample from each *C. brevis* colony comprising the primary queen, the primary king, one soldier, pseudergates and nymphs was introduced into this artificial arena (Table 1). After the transference, these subcolonies were acclimated in the dark for a period of 48 h.

The experimental set-up for *C. cumulans* included a nest chamber connected to an observation arena (Fig. 1). A whole nest of *C. cumulans* was placed in a plastic box (53 × 37 × 34 cm) containing moistened sterilised soil and it was called nest chamber. The observation arena, composed of a plastic container (21 × 21 × 7.5 cm), was connected by a plastic tube (0.4 cm internal diameter, 12 cm length) to the nest chamber and contained four fragments of sterilised sugarcane bagasse as food. Each nest was maintained in laboratory conditions during three weeks for acclimation before the experiments. This proceeding allowed termites to discover the food and to mark their trail with faeces.

2.4. Bioassays

To compare the behavioural responses of *C. brevis* and *C. cumulans* towards corpses from different origins, three bioassays were performed, each bioassay based on a different corpse origin as follows: a) intracolony corpse: cadaver from the same colony; b) intercolony corpse: cadaver from the same species collected in other colony; and c) interspecific corpse: dead worker of *Coptotermes gestroi*. We used corpses of conspecific pseudergates and workers in experiments with *C. brevis* and *C. cumulans*, respectively. In each test, the lid or glass sheet was gently removed and one corpse was introduced in the experimental arena, which was then covered to avoid disturbance by airflow. All bioassays were replicated 10 times. The video recording was performed using a videocamera (Sony HDR-CX130 full HD) and started immediately after the corpse introduction. Empirical studies were carried out to determine a 15-minute recording time for bioassays with *C. brevis* and 20-minutes for *C. cumulans*. The bioassays were conducted under red light (methodology of Machida et al., 2001) at 25 ± 2 °C with > 80% RH.

We carried out qualitative observations to define the main categories and behavioural acts exhibited by *C. brevis* towards and near the corpses, which compose the behavioural repertoire of corpse management. The frequency of the following behaviours of *C. brevis* individuals was recorded: antennation, retreat (avoid confrontation), agonism, alarm (oscillatory movement with the whole body), grooming and corpse ingestion. Due to difficulty in differentiating grooming from ingestion, both behaviours were analysed together and their duration was evaluated. Final observations were made 72 h after the beginning of the experiment and, to quantify the consumption, a point was given to each body part that was consumed. Thus, each of the following parts, if ingested, received a point: antenna (two in total), legs (six in total), abdomen, thorax and damaged head; the maximum total was 11 points per cadaver. The three behavioural bioassays were performed once in each of the ten *C. brevis* subcolonies. Tests in the same subcolony were separated by at least one week.

Experimental tests with *C. cumulans* started when one corpse was placed into the region located between the opening of the connector tube and the food in the observation arena, that is, in the trail of the termites to the food. Each bioassay was replicated five times in both nests of *C. cumulans*. Qualitative observations were used to determine the main categories of behaviour exhibited by *C. cumulans* individuals towards and near the corpse, which composed the behavioural repertoire of corpse management. The frequency of the following behaviours was recorded: antennation, retreat, agonism, grooming, alarm, deposition of faeces, deposition of soil and transport of corpse to the nest.

2.5. Data analysis

Data on the frequency of the reported categories of behaviour were compared using a non-parametric Kruskal-Wallis test, followed by a *posteriori* Student-Newman-Keuls test when necessary. A significance level (α) equal to 0.05 was adopted. The behavioural categories that did not present any record were not submitted to statistical analysis. For comparison of differences between two groups, a Mann-Whitney test was used.

3. Results

3.1. Bioassays with *Cryptotermes brevis*

The results showed that a large part of the corpse management repertoire displayed by *Cryptotermes brevis* was performed by nymphs and pseudergates. Soldiers participated through inspection and agonism. Although the soldiers inspected all the corpses, they performed agonism only towards the intercolony and interspecific ones. The royal couple

Table 1
Census of *Cryptotermes brevis* subcolonies used in behavioural bioassays.

Subcolony	Primary queen	Primary king	Nymphs	Pseudergates	Larvae	Soldiers	Eggs	Total Population
1	1	1	3	11	0	1	4	17
2	1	1	6	6	0	1	0	15
3	1	1	4	8	1	1	2	16
4	1	1	9	3	1	1	0	16
5	1	1	5	8	2	1	0	18
6	1	1	7	6	4	1	0	20
7	1	1	5	7	4	1	4	19
8	1	1	5	7	2	1	1	17
9	1	1	4	6	4	1	0	17
10	1	1	4	5	2	1	0	14

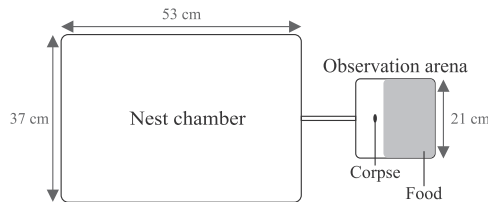


Fig. 1. Experimental set-up for bioassays with *Cornitermes cumulans*. In each replication, a corpse was introduced in the region between the food and the opening of the connector tube of the experimental arena.

did not participate in corpse management.

All of the corpses tested in the bioassays were consumed by the pseudergates and nymphs, regardless of their origin (Fig. 2). Corpse management performed towards intracolony corpses started with the inspection of cadavers through antennation, followed by the individuals exhibiting alarm behaviour. In 40% of the replications with intracolony corpses, pseudergates and nymphs performed agonism. Only the pseudergates and nymphs eventually cannibalised the corpses.

Corpse management of intercolony and interspecific corpses also started with antennation by nymphs, pseudergates and soldiers. Some nymphs and pseudergates exhibited retreat after contact with the corpses, others together with the soldiers attacked alien corpses. During this process of corpse management, some individuals from the quoted castes exhibited alarm behaviour. Finally, nymphs and pseudergates ingested the corpses.

Antennation behaviour displayed by *C. brevis* on corpses from different origins did not significantly differ (Kruskal-Wallis test: $H_2 = 2.133, P = 0.344$). With all corpse types, antennation was the most common behavioural category recorded (mean \pm SE in percentage: $46.9 \pm 5.3\%$ of all behaviours recorded in bioassays using interspecific corpses, $38.8 \pm 7.1\%$ with intercolony corpses and $65.4 \pm 4.5\%$ with intracolony corpses). In addition, the alarm behaviour was not significantly different among the different corpses ($H_2 = 5.9114, P = 0.052$).

Our analysis also revealed that agonistic behaviour towards corpses

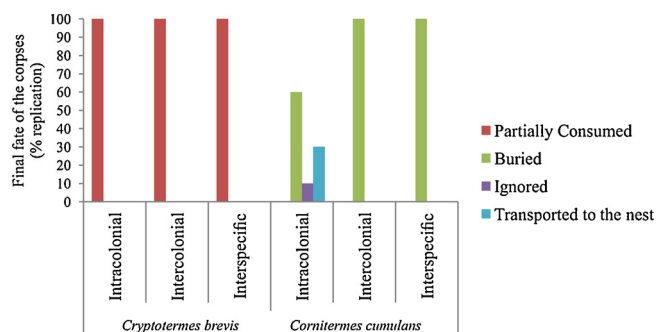


Fig. 2. Final fate of the corpses from different origins in bioassays with *Cryptotermes brevis* and *Cornitermes cumulans*.

significantly differed between those of intracolony and intercolony origin ($H_2 = 9.284, P = 0.0254$), as well as between intracolony and interspecific corpses ($P = 0.0036$) (Fig. 3a). The agonistic behaviour was observed in 40% of replications with intracolony corpses, in 90% with intercolony corpses and 100% with interspecific corpses. Nymphs and pseudergates did not retreat when coming into contact with intracolony corpses. Additionally, there was significant difference in the frequency of retreat between intercolony and interspecific corpses (Mann-Whitney test: $U = 3.477, N1 = N2 = 10, P = 0.0005$) (Fig. 3b). The time spent on grooming or corpse consumption did not differ significantly among corpses from different origins (Kruskal-Wallis test: $H_2 = 3.073, P = 0.251$). Final observations of corpses (72 h after the beginning of the experiment) showed that the consumption of cadavers significantly differed between intracolony and interspecific cadavers ($H_2 = 8.355, P = 0.0068$) and between intercolony and interspecific cadavers ($P = 0.039$). The data indicated that *C. brevis* had tendency to consume conspecific corpses.

3.2. Bioassays with *Cornitermes cumulans*

Our set-up for *C. cumulans* allowed the corpse to be placed on the foraging trail, consequently only forager individuals found the corpse. Thus, the observations revealed that workers of *C. cumulans* actively participated in the corpse management. They inspected and performed the final corpse disposal, which could be based on three options: corpse transport towards the nest, corpse entombment or avoidance of the corpse (Fig. 2). Whereas, the soldier participation included inspection and agonism of corpses and they guarded the area while workers were entombing the corpse.

Interspecific corpses were covered with soil and faeces by workers of *C. cumulans*. Immediately after the corpse introduction into the experimental arena, workers and soldiers approached and inspected the corpse with their antennae. Several workers exhibited retreat behaviour after contact with the cadaver. However, some workers and soldiers showed agonistic behaviour and other workers groomed the corpse. Approximately 4 min after introduction of the corpse, a worker deposited the first droplet of faeces on the cadaver. Subsequently, about 5 min after the beginning of the experiment, some workers started to cover the corpse with soil and faeces. On two occasions, the deposition of food fragments (sugar cane bagasse) on the cadaver was recorded. During the entombment process, workers and soldiers also showed alarm behaviour; this was characterised by an oscillatory movement of the body or the head.

The intercolony cadavers were submitted to a process similar to that observed with interspecific corpses, which resulted in the corpse entombment. The undertaking responses always started with the inspection of cadavers by workers and soldiers. After the inspection, some workers also groomed the corpse. Following the activities described above (about 3 min after the introduction of the corpse), a worker deposited the first faeces droplet. Approximately one minute after this event, workers began to cover the corpse intermittently with soil and

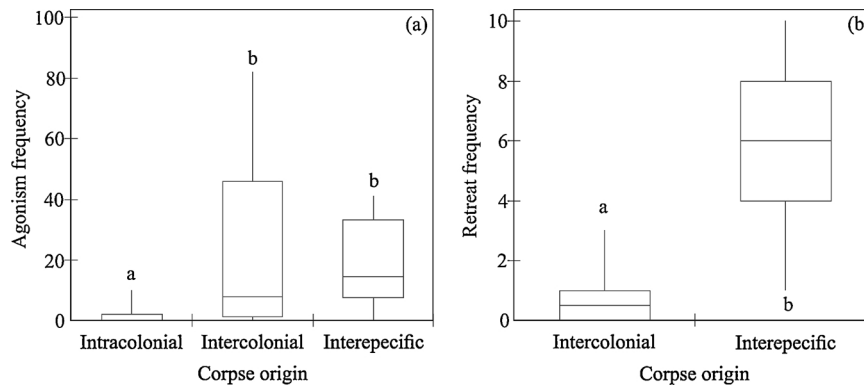


Fig. 3. Box and whisker plots of *Cryptotermes brevis* behaviour towards corpses from different origins. Horizontal bars indicate median values, boxes show the lower and upper quartiles of the data sets. (a) Agonism behaviour (b) Retreat behaviour. Different letters indicate statistical differences ($P < 0.05$).

faecal material. Throughout the corpse management, some soldiers and workers exhibited alarm behaviour, but this behaviour was more frequent during the corpse covering process.

Workers of *C. cumulans* performed varied corpse management activities on dead nestmates. In 30% of the replications, a worker grasped the corpse using its mandibles and transported it to the nest chamber. In 10% of replications, workers groomed the corpse and then abandoned it. In 60% of replications, workers covered the corpses with soil and faeces after had groomed them (Fig. 2).

Antennation behaviour performed by *C. cumulans* workers and soldiers was not significantly different among treatments (Kruskal-Wallis test: $H_2 = 5.7089$, $P = 0.0576$). In contrast, agonistic behaviour significantly differed among corpses from different origins (Kruskal-Wallis test: $H_2 = 24.075$, $P < 0.001$) (Fig. 4a). Workers never attacked nestmates corpses, only soldiers did it. Workers also did not retreat after contact with intracolony corpses. The display of this behaviour towards corpses significantly differed between those of intercolony and interspecific origins (Mann-Whitney test: $U = 3.5907$, $N_1 = N_2 = 10$, $P = 0.0003$) (Fig. 4b). Additionally, time spent on grooming the corpses differed only between interspecific and intercolony cadavers (Kruskal-Wallis test: $H_2 = 6.5213$, $P = 0.0111$). Furthermore, the data showed that there was a wide variation in time invested in grooming nestmate corpses among the replications.

Corpse marking with faeces droplets was statistically similar among the cadavers of different origins ($H_2 = 5.4474$, $P = 0.0656$). Intracolony corpses that were transported into the nest or abandoned were not marked with faeces. To perform the faeces deposition, the worker rotated its body, pointed the end of the abdomen and expelled a faeces droplet on an undefined area of the cadaver.

The soil deposition behaviour significantly differed among all treatments ($H_2 = 19.311$, $P = 0.0001$). Interspecific corpses received 3

times more soil deposition than intercolony corpses and 10 times more than intracolony cadavers. Alarm behaviour displayed by workers and soldiers differed mainly between the presence of intercolony and interspecific corpses ($H_2 = 7.685$, $P = 0.0061$). Additionally, workers exhibited a repeated longitudinal movement in the anterior-posterior direction of their bodies and the soldiers performed a head-banging movement towards corpses from all origins.

4. Discussion

The royal couple of *C. brevis* subcolonies did not participate in corpse management, even when the cadaver was an alien or a nestmate. The corpse management in mature colonies of social insects, as well as other maintenance and hygiene behaviours, is generally carried out by the worker caste (Wilson, 1971; Wilson et al., 1958). However, in incipient termite colonies, the royal couple performs tasks to ensure their own survival and of their progeny. Laboratory experiments with incipient pleometrotic colonies of *P. spiniger* (Termitidae) showed that corpses of dealated female were groomed and buried (Chouvenc et al., 2012). Nevertheless, in established colonies with available workers, the royal couple does not perform the corpse management, as observed in *C. brevis*.

C. brevis nymphs and pseudergates performed the final corpse disposal, and the soldiers participated in the process by discriminating between cadavers of different origins and being aggressive toward corpses from another colony and another species. There is no description in the literature of corpse management by pseudergates or other castes in Kalotermitidae.

Another comparison is that *C. cumulans* soldiers inspected the cadavers, displayed agonistic behaviour and guarded the area while workers were entombing the corpse. The same result was observed in

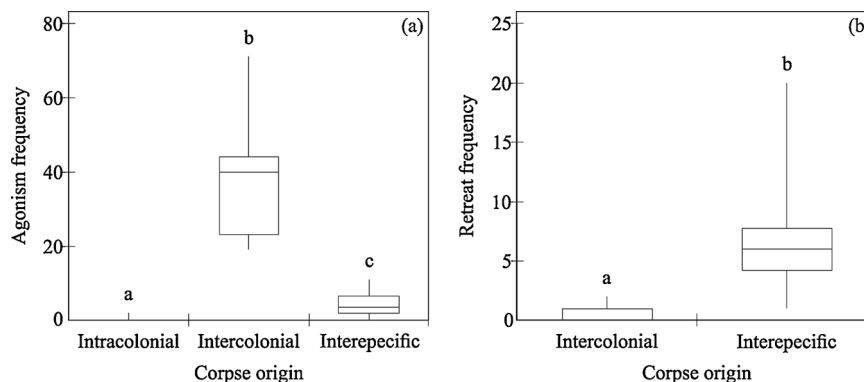


Fig. 4. Box and whisker plots of *Cornitermes cumulans* behaviour towards corpses from different origins. Horizontal bars indicate median values, boxes show the lower and upper quartiles of the data sets. (a) Agonism behaviour (b) Retreat behaviour. Different letters indicate statistical differences ($P < 0.05$).

colonies of the *Reticulitermes flavipes* (Rhinotermitidae) subterranean termite, in which the soldiers guarded the entrance of the experimental arena while the workers performed the management of the intracolony corpses (Sun et al., 2013). According to the authors, these soldiers occasionally inspected the conspecific corpses with their antennae, but did not exhibit agonistic responses, although they attacked congeneric termite corpses. Therefore, soldiers do not directly participate in the corpse management, but are able to identify the origin of dead individuals and provide defence to the workers while they perform the corpse disposal. The behaviour of guarding the foraging area during the entombment, as performed by *C. cumulans*, seems to be adaptive for a multiple-piece nesting termite.

The behavioural repertoire of corpse management performed by *C. brevis* and *C. cumulans* was initiated with antennation. This behaviour was also observed in bees, wasps, ants and in other termites (Neoh et al., 2012; Sun et al., 2013; Visscher, 1988). To start the corpse management it is imperative that the colony members distinguish dead individuals from living ones (Sun and Zhou, 2013). Ulyshen and Shelton (2012) reported that in *Reticulitermes virginicus* termite the recognition of corpses involves the synergism between chemical (oleic acid) and tactile cues (shape and texture). The action of fatty acids as chemical cues of cadavers had been described in ants, cockroaches and bees (Rollo et al., 1994; Visscher, 1983; Wilson et al., 1958). The stimuli are detected by the insects through chemosensory sensilla on the antennae. According to Chouvenc et al. (2012), in dealated females of *P. spiniger* the combination of several chemical components elicited undertaking responses, including various fatty acids, indole and phenol. In the present study, *C. brevis* and *C. cumulans* performed corpse management immediately after the introduction of cadavers from different origins, which suggests that the cues to dead recognition were present in all tested cadavers.

Nymphs, pseudergates and soldiers of *C. brevis*, and workers and soldiers of *C. cumulans* exhibited alarm behaviour towards corpses of different origins. Additionally, this behaviour was more frequent during the entombment process in *C. cumulans*. According to Neoh et al. (2012), the *Microcerotermes crassus* and *Globitermes sulphureus* termites also exhibited alarm responses during the corpse management. The same behaviour displayed by workers and soldiers of *R. flavipes* towards congeneric corpses seemed to facilitate the recruitment of other workers and soldiers (Sun et al., 2013). *C. cumulans* may have also recruited individuals to perform the collective activity of covering the corpses with soil and faeces.

Pseudergates and nymphs of *C. brevis* and workers of *C. cumulans* exhibited retreat behaviour, especially in the presence of corpses from another colony or different species. Neoh et al. (2012) described that in *G. sulphureus* termite workers inspected nestmate corpses and, afterwards, avoided them. Foraging workers of *Coptotermes gestroi* changed their tunnelling pattern when they found soldiers corpses of *Heterotermes tenuis* in order to avoid confrontation and to isolate dead termites (Lima and Costa-Leonardo, 2012). Additionally, workers of *Reticulitermes hesperus* avoided areas where there were termites which had been killed by insecticides (Smith and Rust, 1991). According to Dukas (2001), *Apis mellifera* avoided flowers where there were corpses of nestmates or the extract of their cadavers. This author infers that the activity of avoiding places where there were corpses and, thus, the preference for sites with safe characteristics is a strategy to prevent predation. Therefore, the retreat behaviour of *C. brevis* and *C. cumulans* seems to be a strategy to avoid contamination, especially by alien corpses.

The corpse management exhibited by nymphs and pseudergates of *C. brevis* resulted in the consumption of termite cadavers regardless of their origin. According to Potrikus and Breznak (1981), cannibalism and necrophagy promote the recycling of nutrients. In addition, cannibalism is considered a consequence of stress, such as nitrogen deficiency (Collins, 1983; Lee and Wood, 1971). Thus, the consumption of dead individuals may occasionally contribute to a greater survival of

the colony through nitrogen intake. However, several authors report that the primary function of cannibalism is not the recycling of proteins, but the hygiene of the nest and this is reinforced by observations that few species kill and consume nestmates (Collins, 1983; Lima and Costa-Leonardo, 2007). Despite these conflicting views, the consumption of cadavers can help the survival of the *C. brevis* colony, because these termites obtain water from food and corpse consumption can aid in the transfer of water to the active individuals in the nest.

Some studies also showed that the consumption of the corpses is a hygiene strategy, because it destroys the source of pathogens. When termites ingest this material, they inhibit the development of entomopathogens due to the antimicrobial action of their guts. This was observed in *R. flavipes*, in which the inhibition of *Metarhizium anisopliae* fungal development was due to fungistatic action of the termite digestive tract (Chouvenc et al., 2009b). According to Rosengaus and Traniello (2001), the *Zootermopsis angusticollis* dampwood termite consumed nestmates contaminated with the fungus *M. anisopliae*, indicating that contamination with pathogens did not prevent cannibalism (Rosengaus and Traniello, 2001).

Workers of *C. cumulans* displayed the same corpse management towards intercolonial and interspecific cadavers, which consisted of grooming and entombment of the corpses. This same response was described by Sun et al. (2013) for *R. flavipes* towards corpses of congeneric *R. virginicus* termite, which were covered with nest soil, faeces and chewed mulch. The use of faecal material and soil from the nest promotes an important antifungal action (Chouvenc and Su, 2012; Rosengaus et al., 1998a).

Furthermore, corpse burial can be a defence mechanism, since cadavers can obstruct galleries by creating barriers (Li et al., 2010). According to the authors, corpses resulting from agonistic interactions between *C. gestroi* and *C. formosanus* termites were buried, blocking tunnels that were not subsequently opened. Sealing tunnels can prevent agonistic encounters and future mortality, besides defining boundaries between adjacent termite colonies.

Dealated females of *P. spiniger* groomed corpses of other females and then buried them (Chouvenc et al., 2012). According to Lamberty et al. (2001), the saliva of these females contains peptides with antibiotic and antifungal properties, suggesting that the grooming activity associated with the physical isolation of corpses is an important part of the strategy for preventing dispersal of opportunistic pathogens among colony members. Neves and Alves (2000) observed that the grooming performed by *C. cumulans* workers removed conidia of the *Beauveria bassiana* and *M. anisopliae* fungi from the nestmate cuticles. The grooming behaviour, along with the antifungal activity of the termite guts, provides an effective individual and also inter-individual defence against fungi (Chouvenc et al., 2009a). Allogrooming has an important function in the control of disease in termites (Rosengaus et al., 1998b). Accordingly, the grooming behaviour exhibited by *C. cumulans* can promote the removal of pathogens in the corpse before its physical isolation in the foraging area.

C. cumulans showed different strategies for disposal of dead nestmates: The cadavers were buried at the foraging site, abandoned after being groomed or transported into the nest. Sun et al. (2013) reported that the *R. flavipes* also transported intracolony corpses into the nest and proposed that these corpses were probably cannibalised later. In contrast, Torales (1982) found corpses inside the nests of *C. cumulans* which were whole or with missing thorax and abdomen. In the latter case, the heads were clustered with soil grains and faeces inside chambers of a nest in the laboratory. According to the author, these chambers, called a "cemetery", were coated with abundant faecal material and their openings were often sealed with heads of workers and soldiers. Likewise, Neoh et al. (2012) also found carcasses confined in a sealed cavity in nests of the *M. crassus*.

The workers of *C. cumulans* marked corpses of different origins with faecal material before covering them with soil. According to Torales (1982), *C. cumulans* begins the construction process by depositing a

droplet of faecal material. This same material is used between successive soil deposits. Other termite species, such as the subterranean *C. gestroi* and *Heterotermes* spp., also mark the surface used for transit and food with faecal pellets (Fontes and Araújo, 1999). Faecal marking of foraging trails of the *Nasutitermes corniger* termite has a chemical signalling function, which, through pheromonal activity, helps the orientation of foraging individuals (Silva, 2008; Stuart, 1969). Faecal marking probably has a similar function in *C. cumulans*.

The corpse management repertoires of *C. brevis* and *C. cumulans* have some similar behaviors, which are related to the cadaver recognition: antenation, retreat, alarm and agonism. However, those species perform different final disposals.

C. brevis consumed the corpses. One-piece nesting termites do not leave the nest to forage, so to find a corpse, this must be introduced inside the nest, which turns impracticable to ignore it, as it would maintain the threat within the nest. It is also impossible for them to bury corpses, for they live in the wood. Thus, corpse consumption is a strategy of hygiene and also defense, as shown in response to alien corpses. Furthermore, this consumption allows nitrogen and water intake, which benefits the colony. Likewise, corpse management repertoire of *C. cumulans* has behaviours that may be adaptive for its type of nest. Multiple-piece nests are more elaborated and possess several chambers, some of them internally coated with faecal material (Torales, 1982). Therefore, it is possible to confine the corpses in sealed cavities of the nest, or it may isolate the corpse by entombment within the feeding area, which may be a strategy of defending it.

The present study shows that one-piece nesting termite, as *C. brevis*, exhibits a simplified corpse management repertoire, which ends with the cadaver consumption, regardless its origin. Conversely, a multiple-piece nesting species, as *C. cumulans*, presents a diverse behavioural repertoire, which may include recruitment of individuals to perform corpse entombment, with a variation in time spent and amount of soil according to the cadaver origin; avoidance of some intracolony cadavers; or individually transporting some of the intracolony corpses into the nest, which shows the complexity of this last approaches.

Conflict of interest

The authors declare that they have no conflict of interest.

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