



## Ecology and field biology of two dominant *Camponotus* ants (Hymenoptera: Formicidae) in the Brazilian savannah

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*Camponotus renggeri* and *C. rufipes* are very abundant in Brazilian cerrado savannah, where they feed extensively on liquid rewards and commonly associate with plants bearing extrafloral nectaries and honeydew-producing insects. Here, we provide a qualitative and quantitative field account on the natural history and ecology of these two ant species. The study was carried out in a cerrado reserve in south-eastern Brazil across a rainy/hot season (summer) and a dry/cold season (winter). The ants were found in two vegetation physiognomies: all nests of *C. rufipes* were located in the cerrado *sensu stricto* (scrub of shrubs and trees, 3–8 m tall), whereas *C. renggeri* occurred mostly in the cerradão (forest with more or less merging canopy, 10–12 m tall). Both species nested in fallen or erect dead trunks, as well as underground. In addition, *C. rufipes* built nests using dead plant material arranged or not around shrub bases. Colonies of *C. rufipes* were generally more populous than those of *C. renggeri*, and both species had colonies with more than one dealated queen. Both species were active mainly at night and foraged for resources near their nests, mainly extrafloral nectar and hemipteran honeydew (aphids and mealybugs). The average size of the home ranges of *C. renggeri* in cerrado *sensu stricto* and cerradão varied from  $\approx 2.8$  to  $4.0 \text{ m}^2$  and apparently were not affected by season. In *C. rufipes*, however, foraging grounds in cerrado *sensu stricto* showed a twofold increase from dry/cold ( $\approx 4.5 \text{ m}^2$ ) to rainy/hot season ( $\approx 9.8 \text{ m}^2$ ). Our study highlights the importance of natural history data to understand the foraging ecology and role of these ants in cerrado savannah.

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## Introduction

Ants are one of the most diverse and ecologically dominant groups of insects in terrestrial habitats, and their ecological success can be attributed to the variety and efficiency of their foraging habits, eusocial mode of life, local abundance, and the ability to adjust their activity to environmental changes (Hölldobler and Wilson 1990). The genus *Camponotus* (Mayr) is very diverse in species in the Neotropics, and has currently

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1017 described species worldwide (AntWeb 2017). It has a wide geographical coverage, with representatives in the five continents (Bolton 1994). Moreover, *Camponotus* ants use a variety of different strategies regarding nesting habit, colony structure, activity rhythm, foraging, and diet requirements.

*Camponotus* species are considered opportunistic and generalist in relation to their nesting habits and food resources (Silvestre et al. 2003; Blüthgen and Feldhaar 2010). These ants can build their nests underground, in dead branches or rotten trunks, and in plant roots (Brown 2000; Silvestre et al. 2003). The feeding habits reported for some tropical species show that they forage mainly on plant and insect exudates (Oliveira and Brandão 1991; Del-Claro and Oliveira 1999; Pfeiffer and Lisenmair 2000; Santos and Del-Claro 2009), fallen fruits (Christianini et al. 2007; Orr and Charles 2007), and insects (Pfeiffer and Lisenmair 2000; Silvestre et al. 2003; Mody and Lisenmair 2004; Orr and Charles 2007). Some species recruit nestmates to food sources and can behave aggressively to defend them (e.g. *C. socius*: Hölldobler 1971; *C. pennsylvanicus*: Traniello 1977), while others can attack insect herbivores they find on foliage nearby exudate sources (e.g. *C. gigas*: Pfeiffer and Lisenmair 2000; *C. crassus*, *C. rufipes*: Sendoya et al. 2009).

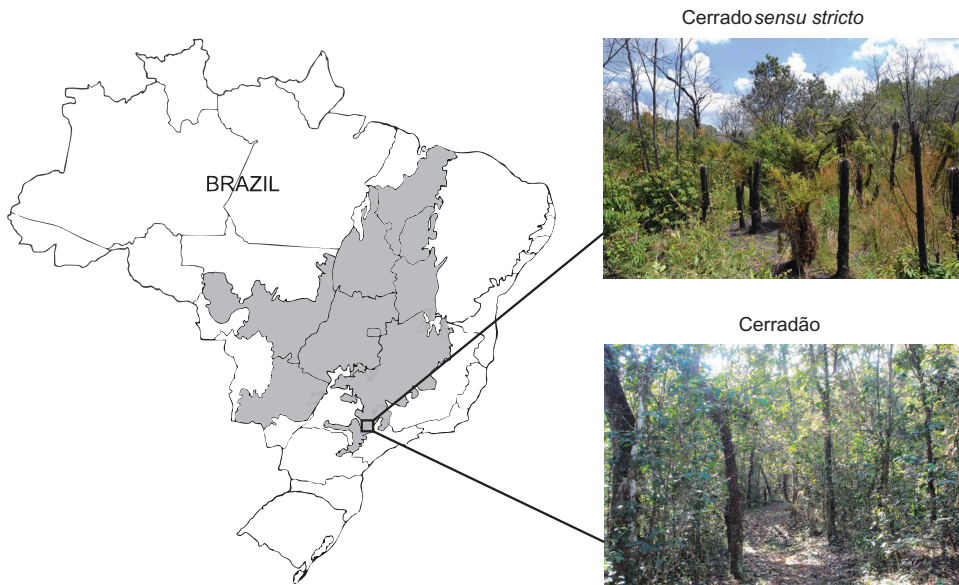
Both *Camponotus renggeri* (Emery) and *C. rufipes* (Fabricius) are dominant ants in the Brazilian savannah belonging to the subgenus *Myrmothrix*. These species can be differentiated by the colour of their legs and tegument: *C. renggeri* has yellowish legs and a shiny black cuticle, whereas *C. rufipes* has reddish legs and an opaque cuticle ranging from black to brown (Hashmi 1973). Their similarities in morphology and the subtle differences in the shades of colours make the differentiation of *C. renggeri* and *C. rufipes* sometimes difficult in the field. In an integrative approach, however, using behaviour, ecology and molecular data, Ronque et al. (2016) confirmed that these ants are two valid species, and that they are genetically divergent along their geographic range in Brazil. Both species feed extensively on liquid rewards and are very abundant in the Brazilian cerrado savannah, where they commonly associate with trophobiont insects (Del-Claro and Oliveira 1999; Kaminski et al. 2010) and with plants bearing extrafloral nectaries (Oliveira 1997; Oliveira and Freitas 2004).

Despite general information about foliage- and ground-foraging *Camponotus* ants in cerrado (e.g. Schoereder et al. 2010; Frizzo et al. 2012), basic data on the ecology and field biology are clearly lacking for most species, including the abundant *C. renggeri* and *C. rufipes*. The current study provides a natural history and ecological account of these two species in a cerrado reserve in south-east Brazil. More specifically, we provide qualitative and quantitative field data on nesting habits, daily and seasonal activity rhythms, home ranges, as well as on foraging patterns on foliage by *C. renggeri* and *C. rufipes* in the cerrado environment.

## Material and methods

### Study site

The cerrado domain covers approximately 22% of the land surface of Brazil and extends from the southern border of the Amazon forest to the south-east region of Brazil (Figure 1). The so-called cerrados are characterized by a mosaic of different vegetation physiognomies, ranging from extensive grasslands with scattered shrubs



**Figure 1.** Geographic distribution (grey) of the cerrado domain in Brazil (adapted from the Instituto Brasileiro de Geografia e Estatística 2004), and general view of the cerrado physiognomies where the study was carried out. Photograph of cerrado *sensu stricto* courtesy of L. Mota.

to forest woodlands with a sparse understorey of herbs and subshrubs (Oliveira-Filho and Ratter 2002). Fieldwork was carried out at the cerrado reserve near Mogi-Guaçu (22°18'S, 47°11'W), São Paulo state, south-eastern Brazil. The study was undertaken in two vegetation physiognomies, 2 km apart from one another: (1) the 'cerrado *sensu stricto*', which has up to 30% of its vegetation composed of shrubs and trees 3–8 m in height, and (2) the forest-like 'cerradão', which has 50–90% of its vegetation composed of trees up to 10–12 m in height (see Figure 1; further details in Oliveira-Filho and Ratter 2002). The climate of the region is characterized by two well-differentiated seasons: a rainy/hot season (summer) from October to March, and a dry/cold season (winter) from April to September. Annual temperature ranges from 20.5°C to 22.5°C and accumulated rainfall varies from 1100–1200 mm in the rainy/hot season to 250–300 mm in the dry/cold season (data from 1961 to 1990 from the climatological station at the cerrado reserve).

### ***Nesting habits and demographic data***

All nests of *C. renggeri* and *C. rufipes* found in the cerrado *sensu stricto* and cerradão were tagged between December 2011 and August 2012. To locate the nest entrances, workers of the two species attracted to honey and tuna baits placed on the ground and on the vegetation were followed on their way back to their nest. The nests were characterized according to their location, external structure, and building material. Four nests of each species were excavated for demographic data. Colonies of both species were collected, transported to the laboratory, and the numbers of dealated queens, alate females, males, workers, and immature were counted.

## Activity schedule

Data on colony activity were collected during the rainy/hot season (March 2012) and the dry/cold season (August 2012). Samplings were carried out for four colonies of *C. rufipes* located in the cerrado *sensu stricto*, and eight colonies of *C. renggeri* (four in the cerrado *sensu stricto* and four in the cerradão). We recorded the number of workers exiting or entering the nest within a 24 h period, every 2 h in sessions of 30 min. Temperature and humidity at nest entrances were also noted at the beginning of each sampling session. To avoid disturbance of ant foragers, nocturnal observations were performed using red lights.

The influence of air temperature and humidity on colony foraging activity (active/inactive) was assessed by using a logistic regression. We considered a colony to be active when the sum of the number of ants entering and exiting the nest during a 30-minute sampling was higher than three. A pseudo- $R^2$  was calculated using the deviances of the final model as compared with the null model.

## Home range

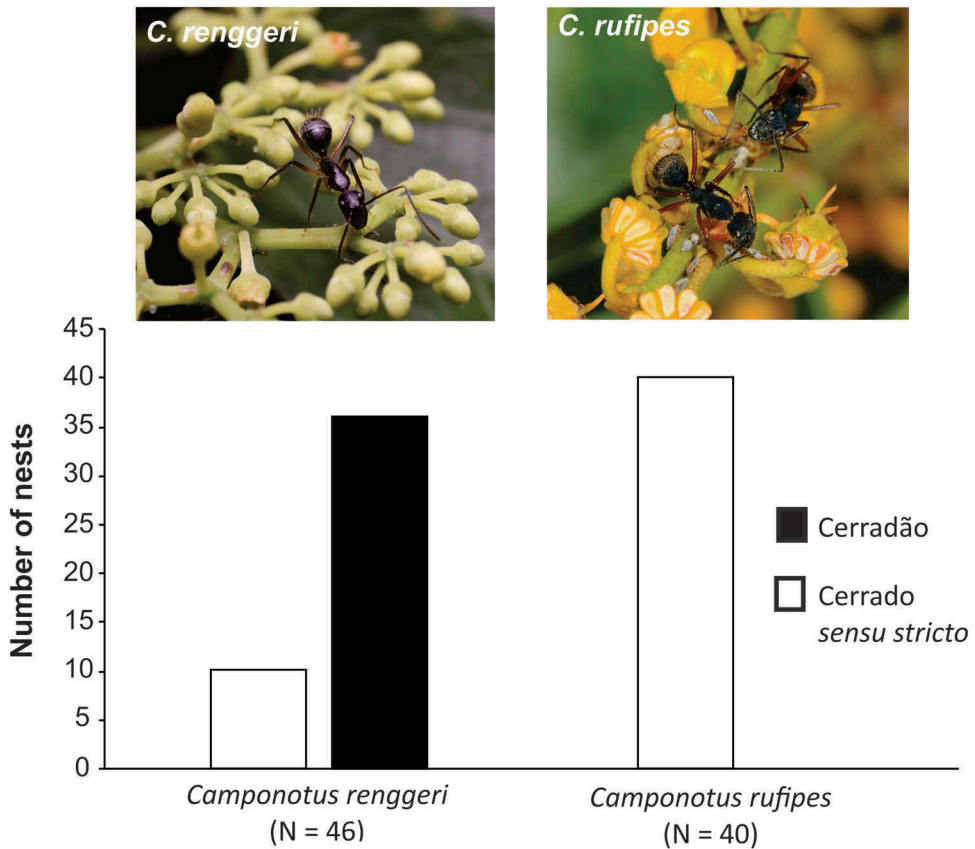
To determine the home ranges of *C. renggeri* and *C. rufipes* colonies during the rainy/hot and dry/cold season, we monitored the foraging activity of four colonies of each species in the cerrado *sensu stricto*, and four colonies of *C. renggeri* in the cerradão (re-sampling of the same individual colony across seasons occurred for one colony of *C. rufipes* and two of *C. renggeri*). Each colony was observed intermittently for 16 h, totalling 192 h of observation in each season. We made the observations after sunset, when the ants were more active. When a worker went out to forage, we followed it and marked with a flag the position of the most distant point it has reached before returning to its nest (any point located on the vegetation was projected onto the ground). We then measured the distance of this point to the nest and determined its geographical direction with a compass. We used R 3.2.5 (R Core team 2015) and the package *adehabitatHR* (Calenge 2006) to calculate through the minimum convex polygon method the area corresponding to the home range of the colonies. All plants visited by the ants were marked and identified, their distance from their respective nest measured, and the presence (or not) of extrafloral nectaries and insect trophobionts on foliage recorded. Ant voucher specimens are deposited at the Museu de Zoologia da Universidade Estadual de Campinas (ZUEC, Campinas, Brazil; registration numbers 2465–2482).

## Results

### Nesting habits and demographic data

A total of 46 nests of *C. renggeri* and 40 nests of *C. rufipes* were tagged. The nests of *C. rufipes* were found exclusively in the cerrado *sensu stricto*, whereas most nests of *C. renggeri* (78.3%) were found in the cerradão (Figure 2). We observed numerous workers travelling between neighbouring nests of *C. rufipes*, indicating that colonies have probably a polydomous structure. We did not observe this behaviour in *C. renggeri*.

The nests of *C. renggeri* and *C. rufipes* were found underground or above ground, in fallen or erect dead tree trunks (Table 1). *Camponotus rufipes* built nests of dry straw,

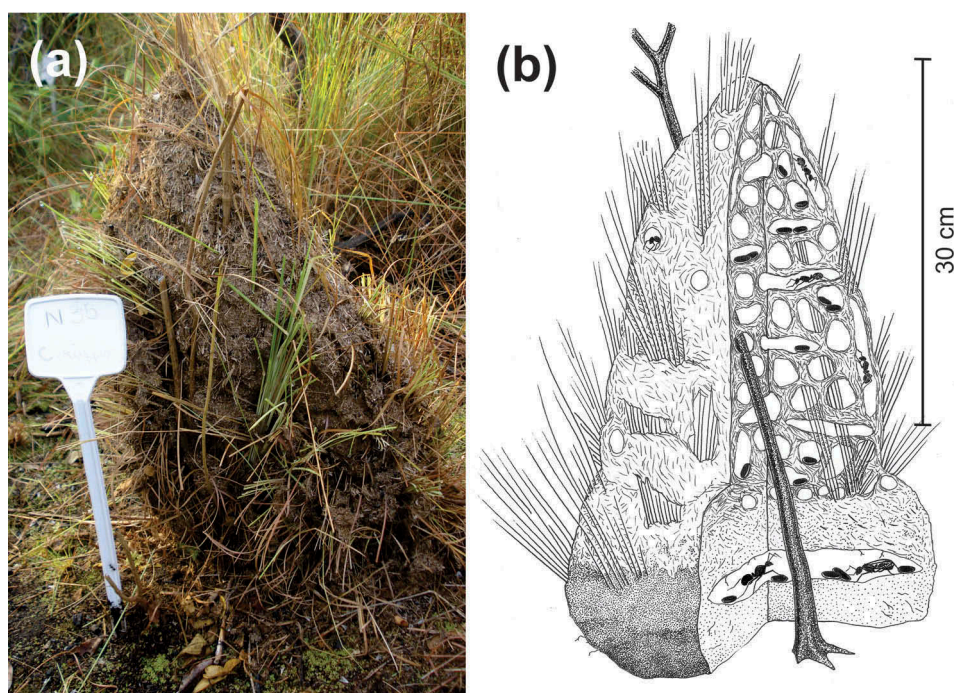


**Figure 2.** Occurrence of *Camponotus renggeri* and *C. rufipes* nests across vegetation physiognomies in the cerrado reserve at Mogi-Guaçu, south-east Brazil. Cerrado *sensu stricto*: scrub of shrubs and trees (3–8 m tall); Cerradão: forest with more or less merging canopy (10–12 m tall; see also Ronque et al. 2016). Ant foragers are shown near flower buds in the vicinity of their nests, where they commonly tend honeydew-producing hemipterans. Photographs courtesy of S. Sendoya.

**Table 1.** Type of nests built by *Camponotus renggeri* and *C. rufipes* in the cerrado reserve at Mogi-Guaçu, south-east Brazil.

Type of nest	Number of nests	
	<i>Camponotus renggeri</i>	<i>Camponotus rufipes</i>
Dry straw	0	11
Dry straw and trunk	0	8
Underground	9	4
Fallen dead trunk	29	10
Erect dead trunk	8	7
Total	46	40

associated or not with plant trunks. Investigation of the internal architecture of nests of dry straw revealed a structure composed of many chambers connected by tunnels (Figure 3). The brood is dispersed among chambers, but most of it occupies a big chamber at the basis of the nest, where dealated and winged queens are also found.



**Figure 3.** Nest of dry straw built by *Camponotus rufipes* in the cerrado reserve at Mogi-Guaçu, south-east Brazil (a), and schematic representation of its internal architecture (b). Drawing by L. Mota.

The workers patrol the whole nest during the day, moving through the tunnels as well on the nest outer surface. Upon nest damage, many workers exit and walk around the nest, stridulating and releasing formic acid. In nests inside fallen or erect trunks, colonies of either species occupy the natural hollow spaces in the dead wood.

The demographic data of colonies of *C. renggeri* and *C. rufipes* is presented in Table 2. The most populous colony was one of *C. rufipes* with 3816 individuals, while colonies of *C. renggeri* usually did not exceed 600 individuals. The colonies of both species presented one or more dealated queens, suggesting that they can be facultatively polygynous.

**Table 2.** Composition of colonies of *Camponotus renggeri* and *C. rufipes* collected in the cerrado reserve at Mogi-Guaçu, south-east Brazil.

Species and collection date	Type of nest	No. of dealated queens	No. of alate females	No. of males	No. of workers	No. of immature*	Total
<i>Camponotus renggeri</i>							
26 November 2012	Fallen dead trunk	1	15	15	199	-	230
26 November 2012	Erect dead trunk	-	1	7	217	83	308
5 December 2012	Fallen dead trunk	2	10	59	105	-	176
5 December 2012	Fallen dead trunk	7	17	56	340	146	566
<i>Camponotus rufipes</i>							
19 September 2012	Dry straw	2	80	-	3654	80	3816
26 November 2012	Dry straw & trunk	1	2	-	816	-	819
26 November 2012	Fallen dead trunk	2	82	72	922	647	1725
26 November 2012	Erect dead trunk	-	19	50	251	-	320

\*Eggs, larvae, pupae.

### Daily activity schedule

Regardless of the season, the daily activity of *C. rufipes* colonies was not significantly influenced by temperature (GLM:  $z = 1.726$ ,  $p = 0.084$ ,  $\text{pseudo-}R^2 = 0.029$ ) or humidity ( $z = 0.255$ ,  $p = 0.798$ ,  $\text{pseudo-}R^2 = 0.005$ ). On the other hand, the activity of *C. renggeri* was negatively affected by temperature ( $z = -6.315$ ,  $p < 0.001$ ,  $\text{pseudo-}R^2 = 0.322$ ) and positively affected by humidity ( $z = 5.598$ ,  $p < 0.001$ ,  $\text{pseudo-}R^2 = 0.203$ ).

During both the rainy/hot and dry/cold season the daily rhythm of *C. renggeri* and *C. rufipes* was predominantly nocturnal, with fewer workers active throughout the diurnal part of the nycthemere (Figures 4 and 5). For both species the period of most intense activity began after sunset and ended before sunrise. The number of *C. rufipes* workers entering or exiting their nest was higher in the rainy/hot season than in the dry/cold season (Figure 5). In both *cerradão* and *cerrado sensu stricto* the activity rhythm of *C. renggeri* did not differ between seasons.

### Colony home ranges

The average size of the home ranges of *C. renggeri* in *cerrado sensu stricto* and *cerradão* varied from 2.78 to 4.02 m<sup>2</sup> and apparently was not affected by season (Table 3). In *C. rufipes*, however, foraging ranges in *cerrado sensu stricto* showed a twofold increase from dry/cold (4.55 m<sup>2</sup>) to rainy/hot season (9.83 m<sup>2</sup>) (Table 3).

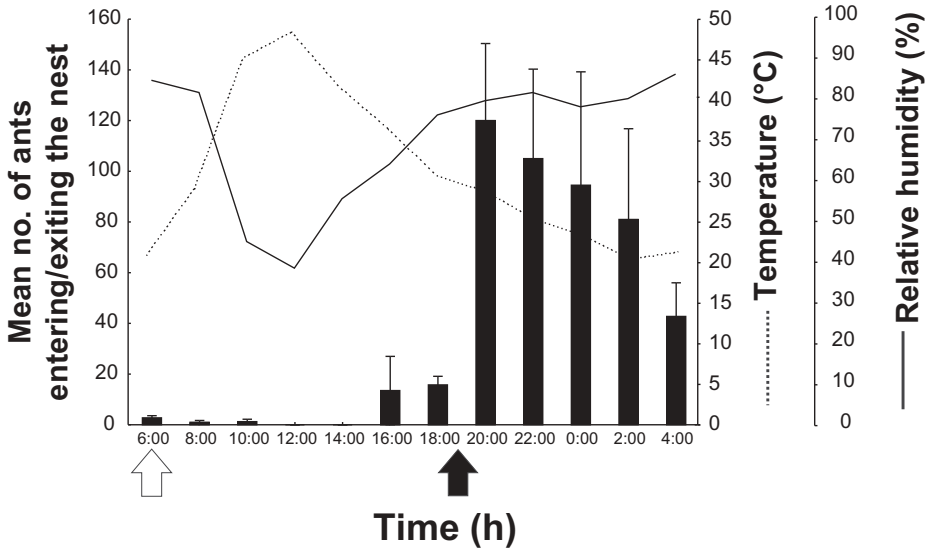
Both ant species foraged for resources nearby their nests. Ant foragers sometimes retrieved solid resources on the ground (e.g. dead arthropods, fallen fruits), but most often climbed onto plants ( $\approx 1$  m high) to collect extrafloral nectar and/or honeydew from aphids and mealybugs (Figure 2), using similar routes on different days. *Camponotus renggeri* foraged on plants up to 2.2 m from their nests in *cerrado sensu stricto* but 70% of the visited plants did not have liquid resources, suggesting that ants probably use foliage to search for new aggregations of trophobionts or other food sources (Figure 6(a)). In *cerradão*, on the other hand, *C. renggeri* foraged up to 1.6 m from their nests and 77% of the visited plants had hemipteran trophobionts (Figure 6(a)). Plants visited by *C. rufipes* were up to 2.8 m from their nests in *cerrado sensu stricto*, and 90% of the plants had trophobionts (aphids and mealybugs) (Figure 6(b)). A list of the plant species visited by *C. renggeri* and *C. rufipes*, and the type of liquid resources found on foliage in *cerrado sensu stricto* and *cerradão* are given on the Supplemental Online Material.

### Discussion

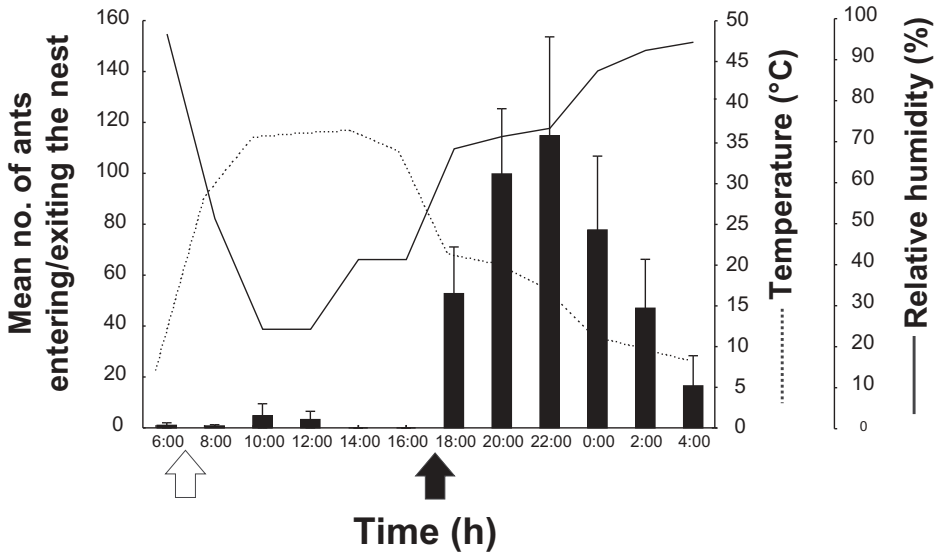
The choice of a nesting location is crucial in the life of an ant colony since the nest serves as a shelter for the queen and brood, and is used to store food (Hölldobler and Wilson 1990). In this study, all nests of *C. rufipes* were located at *cerrado sensu stricto*, whereas nests of *C. renggeri* were mostly found at *cerradão*, indicating that these two species probably differ in their preferences for nesting habitats. Nest site suitability can be mediated by environmental factors such as temperature, humidity, soil type and vegetation (Blüthgen and Feldhaar 2010). The two areas of occurrence of *C. renggeri* and *C. rufipes* are very distinct regarding their vegetation composition and may have influenced the choice of nesting site in these species. *Cerrado sensu stricto* has an open physiognomy consisting mostly of

# *Camponotus renggeri*

(a) *Cerrado sensu stricto*  
Rainy/hot season



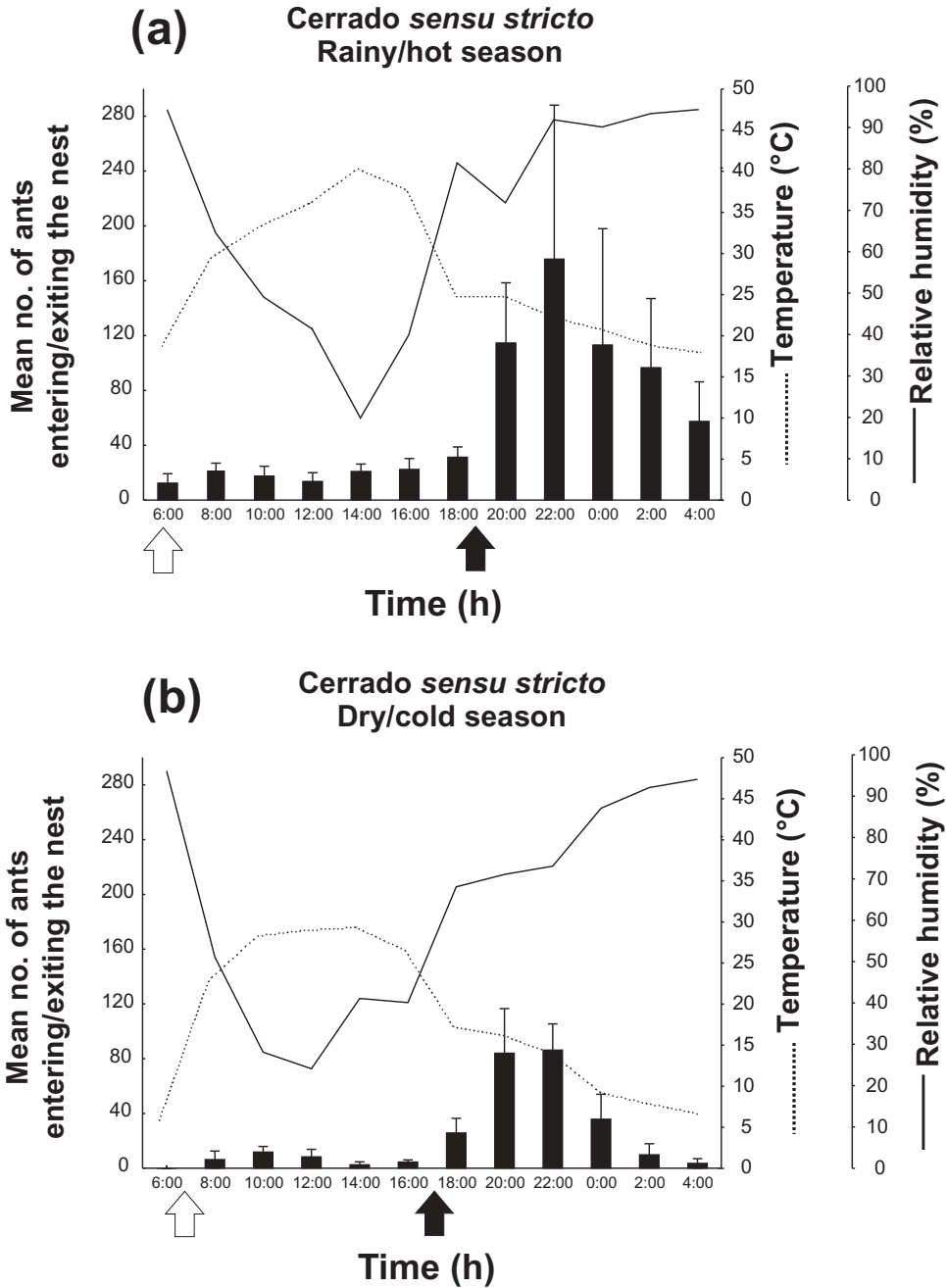
(b) *Cerrado sensu stricto*  
Dry/cold season



**Figure 4.** Daily and seasonal variation in the foraging activity of *Camponotus renggeri* colonies ( $N = 4$ ) in *cerrado sensu stricto* at the Mogi-Guaçu reserve in south-east Brazil. Foraging activity is expressed as the sum of inbound and outbound workers (data are means  $\pm$  SE). Air temperature and humidity were recorded simultaneously during each sampling of ant activity (data are means). The arrows indicate sunrise (white) and sunset (black). The activity pattern by *C. renggeri* in an area of *cerradão* at Mogi-Guaçu is similar to the one shown here.



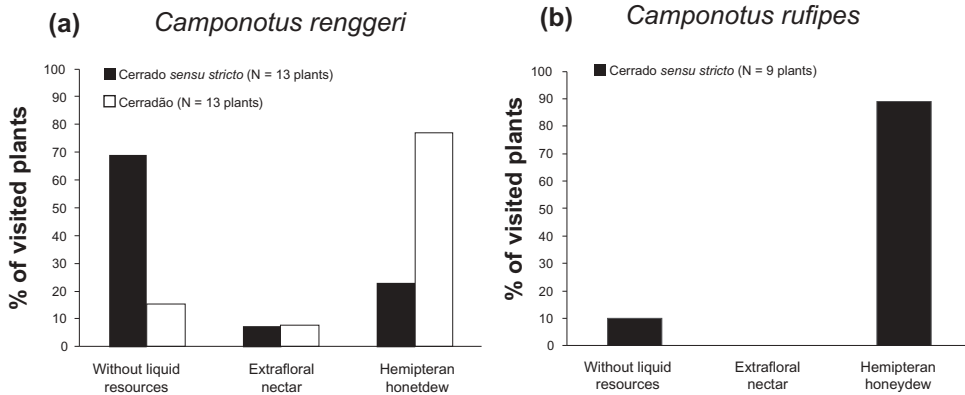
# *Camponotus rufipes*



**Figure 5.** Daily and seasonal variation in the foraging activity of *Camponotus rufipes* colonies ( $N = 4$ ) in cerrado *sensu stricto* at the Mogi-Guaçu reserve in south-east Brazil. Foraging activity is expressed as the sum of inbound and outbound workers (data are means  $\pm$  SE). Air temperature and humidity were recorded simultaneously during each sampling of ant activity (data are means). The arrows indicate sunrise (white) and sunset (black).

**Table 3.** Home ranges of *Camponotus renggeri* and *C. rufipes* across seasons in a cerrado reserve at Mogi-Guaçu, south-east Brazil.

Species and cerrado physiognomy	Season	Mean no. $\pm$ SD of foragers sampled ( $N = 4$ colonies)	Mean area. $\pm$ SD of home ranges ( $m^2$ ) ( $N = 4$ colonies)	Minimum and maximum size of home ranges ( $m^2$ )
<i>Camponotus renggeri</i> Cerradão	Rainy/hot	57.25 $\pm$ 7.71	4.02 $\pm$ 3.61	1.1–8.9
	Dry/cold	46.25 $\pm$ 9.74	3.25 $\pm$ 2.71	1.0–6.7
Cerrado <i>sensu stricto</i>	Rainy/hot	60.75 $\pm$ 5.56	2.98 $\pm$ 1.28	1.8–4.8
	Dry/cold	51.50 $\pm$ 3.41	2.78 $\pm$ 1.76	1.2–4.3
<i>Camponotus rufipes</i> Cerrado <i>sensu stricto</i>	Rainy/hot	84.25 $\pm$ 22.03	9.83 $\pm$ 2.57	6.4–10.5
	Dry/cold	68.50 $\pm$ 12.44	4.55 $\pm$ 3.41	1.2–9.3

**Figure 6.** Frequency distribution of plants with or without liquid resources visited by *Camponotus renggeri* (a) and *C. rufipes* (b) in different vegetation physiognomies, in a cerrado reserve at Mogi-Guaçu, south-east Brazil.

shrubs, with low crown cover and a fair amount of herbaceous vegetation between shrubs and trees. On the other hand, cerradão has a dense canopy with 50–90% of crown cover composed of trees and sparse herbaceous stratum (Figure 1). The type of vegetation may thus mediate the availability of material for nest construction, such as fallen trunks used by *C. renggeri* in cerradão, or grass for construction of nests of dry straw by *C. rufipes* in cerrado *sensu stricto*. Moreover, the more dense canopy cover of cerradão results in milder temperatures and higher humidity in this area compared to cerrado *sensu stricto* (Oliveira-Filho and Ratter 2002), which probably also influence the nesting preferences by *C. renggeri* and *C. rufipes* (Ronque et al. 2016).

In tropical habitats, ants show a huge variety of nest types since these environments are heterogeneous in their composition and frequently encompass different vegetation formations that provide a wide availability of nest sites (Wilson 1959; Liefke et al. 1998; Brown 2000). In Brazilian cerrado, the nesting habit of *Camponotus* species is related to the availability of dead trunks and plant biomass (Silvestre et al. 2003), as reported for the abundant *C. crassus* that nests in fallen branches (Morais and Benson 1988). In our study we observed that both *C. renggeri* and *C. rufipes* use natural cavities in fallen or erect dead trunks as nesting sites or excavate cavities in the soil to build underground

nests (see also Ronque et al. 2016). In addition, we found that *C. rufipes* frequently builds nests with dead plant material consisting of many interconnected chambers (Figure 3). Nests made of plant fragments with similar internal structure have also been described for *C. rufipes* by Weidenmüller et al. (2009) in the Chaco region of Argentina. Species of the genus *Camponotus* are known to build different types of nests in various types of vegetation physiognomies worldwide (Brown 2000; Blüthgen and Feldhaar 2010). While some species use the available spaces in the environment for nesting, such as natural cavities in dead trunks (e.g. *C. pennsylvanicus* in temperate forests of the USA: Traniello 1977), others dig their nests in the soil (e.g. *C. gigas* in Bornean tropical forests: Pfeiffer and Lisenmair 2000; *C. socius* in temperate forests of the USA: Tschinkel 2005), or build silk nests on the vegetation (*C. senex* in Brazilian cerrado: Santos and Del-Claro 2009).

In addition to nest architecture, demography is also an important part of the structure of a colony with important consequences for colony organization and reproduction (Steiner et al. 2010). The demography of ant colonies varies widely; while some species can have colonies with 20 million workers, others may contain only 10 workers (Hölldobler and Wilson 1990). The demographic structure is also variable among species of *Camponotus*. For instance, whereas *C. senex* in the Brazilian cerrado has colonies with up to 5000 individuals (Santos and Del-Claro 2009), *C. gigas* colonies in Borneo can contain up to 7000 individuals (Pfeiffer and Lisenmair 2000). Much smaller colonies are found in New Guinean rainforest species, such as *C. confusus* and *C. papua*, which have up to 200 and 300 workers per colony, respectively (Wilson 1959). In our study, we found that the nests of *C. renggeri* in dead trunks were much smaller than those built by *C. rufipes* with dead plant material. This corroborates the general tendency of ant species nesting in limited space (e.g. preformed cavities in fallen trunks or rotten logs) to produce smaller colonies than those that excavate cavities in the soil or build their nests in the vegetation (Hölldobler and Wilson 1990).

Both *C. renggeri* and *C. rufipes* had more than one queen in some of their colonies, suggesting that the two species can be facultative polygynous (Ronque et al. 2016). Polygyny can be related with nest site instability/fragility, and increased numbers of queens in facultative polygynous species is associated with the scarcity of nesting sites (Debout et al. 2007; Steiner et al. 2010). Polygyny in *C. renggeri* and *C. rufipes* may be related to the fragility and instability of their nests, since both species nest in fallen trunks on the cerrado ground. Indeed, we observed that mechanical damage to fallen trunks led to a massive outflow of *C. renggeri* brood carrying workers. In such cases the presence of more than one queen may increase colony survival. Whether or not the number of queens in *C. renggeri* and *C. rufipes* colonies is associated with nest site instability remains to be investigated.

We regularly observed *C. rufipes* workers travelling between nests, suggesting that this species could have polydomous colonies; this could be tested by evaluating the aggression level between workers from neighbouring nests (Ellis et al. 2017). Polydomy could be related to polygyny if fragmentation of one colony in several subunits can be secured by sufficient reproductive females serving each subunit, which increases the probability of colony survival (Debout et al. 2007). Multiple nest sites can also increase a colony's foraging area and/or reduce the risk of colony extinction through predation, allowing improved efficiency in resource defence (Holway and Case 2000; Debout et al. 2007). Polydomy can be an asset in the surrounding environment of *C. rufipes* colonies

that exploit aggregated and renewable food sources such as aggregations of trophobionts, because ants can establish their nests near these resources (Holway and Case 2000; Oliveira and Del-Claro 2005).

The daily activity of ants is related to their tolerance to environmental fluctuations throughout the day (Heinrich 1993), and temperature is considered a primary control of their activity (e.g. Porter and Tschinkel 1993; Cerdá et al. 1998). However, humidity is closely related to temperature and consequently also influences the daily cycle of foraging in ant colonies (Levings 1983). For instance, it was observed for *Pheidole militicida* (Hölldobler and Möglich 1980), *Formica polyctena* (Rosengren 1977), *Prenolepis imparis* (Talbot 1943) and *Atta capiguara* (Caldato et al. 2016) that there is a rise in foraging activity when humidity increased at high temperatures. Temperature and humidity significantly influenced the activity rhythm of *C. renggeri* and the foraging activity of this species throughout the year was mainly nocturnal, with few workers exiting the nests during the diurnal part of the nycthemere. A nocturnal activity pattern is more frequent in ants of tropical regions in order to avoid high daytime temperatures and low humidity. For instance, it has been recorded in *Camponotus gigas* in Bornean tropical forests (Pfeiffer and Lisenmair 2000; Orr and Charles 2007), *Dinoponera gigantea* in Amazonia (Fourcassié and Oliveira 2002), *Odontomachus chelifer* and *O. hastatus* in Atlantic rainforests (Raimundo et al. 2009; Camargo and Oliveira 2012).

The daily activity of ants can also be based on an endogenous rhythm entrained by environmental signals, such the alternation of light/dark period. In many ant species, however, environmental conditions and/or colony needs can overlap with the circadian rhythm (Hölldobler and Wilson 1990; Heinrich 1993). Although the foraging activity of *C. rufipes* was mainly nocturnal, temperature and humidity did not influence significantly the daily cycle of foraging in this species, suggesting that its activity rhythm may be more endogenous than influenced by environmental factors.

The presence of competitors, predators or parasitoids, and resource availability are among the factors that can also affect daily activity in ants (Carroll and Janzen 1973). Competition for renewable liquid resources on foliage (extrafloral nectar, insect honeydew), apparently promotes segregation of daily activity among exudate-feeding *Camponotus* species. For instance, Del-Claro and Oliveira (1999) found that whereas *C. rufipes* tends trophobionts over 24 h, *C. renggeri* tends them only at night. Segregation in foraging periods between dominant *Camponotus* species at extrafloral nectaries has also been reported in coastal Mexican dunes for *C. planatus* and *C. atriceps* (= *abdominalis*) (Oliveira et al. 1999).

In tropical environments the resources can fluctuate in time and space, which may lead ants to alter their foraging grounds across seasons (e.g. McGlynn et al. 2003). In the current study *C. renggeri* had similar home ranges throughout the year, whereas *C. rufipes* had foraging grounds that increased twofold in the rainy/hot season. Greater home ranges in the growing season have also been reported for the poneroids *Pachycondyla striata* (Medeiros and Oliveira 2009) and *Gnamptogenys moelleri* (Cogni and Oliveira 2004) in Atlantic rainforests, and are likely due to increased brood quantity in the colonies during the hot season, requiring augmented food intake by foragers. The foraging grounds of *C. renggeri* and *C. rufipes* are very small compared to other *Camponotus* species. For instance, Yamamoto and Del-Claro (2008) found that foragers of *C. sericeiventris* can cover an area of approximately 138 m<sup>2</sup>, travelling up to 10 m from

their nests. Pfeiffer and Lisenmair (2000) estimated that the foraging area of one polydomic colony of *C. gigas* is  $\approx 8000 \text{ m}^2$  in a Bornean rainforest. Variation in home range areas among ant species can be attributed to numerous factors such as differences in colony size, resource availability, interference competition, and associated costs of defence (Hölldobler 1987; Breed et al. 1990; Gordon 1995; McGlynn et al. 2003).

The current field account on the natural history and ecology of *C. renggeri* and *C. rufipes* helps us understand how these ants organize their foraging activities to exploit available resources, and provides a general picture of their interactions with plants and arthropods in cerrado savannah. Ants are exceptionally abundant and diversified in the tropics (Brown 2000), but the biology and ecology of most species remain largely unknown. Our study illustrates how natural history and behavioural data can be combined to reveal basic biological features and foraging patterns of two important ant species, and we hope that it can encourage further research on ants in threatened cerrado.

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## References

- AntWeb. 2017. San Francisco: California academy of sciences. [accessed 2017 Feb 4]. <https://www.antweb.org/description.do?subfamily=formicinae&genus=camponotus&rank=genus>.
- Blüthgen N, Feldhaar H. 2010. Food and shelter: how resources influence ant ecology. In: Lach L, Parr CL, Abbott KL, editors. Ant ecology. Oxford: Oxford University Press; p. 115–136.
- Bolton B. 1994. Identification guide to the ant genera of the world. Cambridge: Harvard University Press.
- Breed M, Abel P, Bleuze TJ, Denton SE. 1990. Thievery, home ranges, and nestmate recognition in *Ectatomma ruidum*. *Oecologia*. 87:117–121.

- Brown WL. 2000. Diversity of ants. In: Agosti D, Majer J, Alonso E, Schultz TR, editors. *Ants: standard methods for measuring and monitoring biodiversity*. Washington: Smithsonian Institution Press; p. 45–79.
- Caldato N, Forti LC, Bouchebti S, Lopes JFS, Fourcassié V. 2016. Foraging activity pattern and herbivory rates of the grass-cutting ant *Atta capiguara*. *Insect Soc.* 63:421–428.
- Calenge C. 2006. The package *adehabitat* for the R software: a tool for the analysis of space and habitat use by animals. *Ecol Model.* 197:516–519.
- Camargo RX, Oliveira PS. 2012. Natural history of the Neotropical arboreal ant, *Odontomachus hastatus*: nest sites, foraging schedule, and diet. *J Insect Sci.* 12:1–9.
- Carroll CR, Janzen DH. 1973. Ecology of foraging by ants. *Annu Rev Ecol Syst.* 4:231–257.
- Cerdá X, Retana J, Cros S. 1998. Critical thermal limits in Mediterranean ant species: trade-off between mortality risk and foraging performance. *Funct Ecol.* 12:45–55.
- Christianini AV, Mayhé-Nunes AJ, Oliveira PS. 2007. The role of ants in the removal of non-myrmecochorous diaspores and seed germination in a Neotropical savanna. *J Trop Ecol.* 23:343–351.
- Cogni R, Oliveira PS. 2004. Patterns in foraging and nesting ecology in the neotropical ant, *Gnamptogenys moelleri* (Formicidae, Ponerinae). *Insect Soc.* 51:123–130.
- Debout G, Schatz B, Elias M, McKey D. 2007. Polydomy in ants: what we know, what we think we know, and what remains to be done. *Biol J Linn Soc.* 90:319–348.
- Del-Claro K, Oliveira PS. 1999. Ant-Homoptera interactions in a Neotropical Savanna: the honeydew producing treehopper *Guayaquila xiphias* (Membracidae), and its associated ant fauna on *Didymopanax vinosum* (Araliaceae). *Biotropica.* 31:135–144.
- Ellis S, Procter DS, Buckham-Bonnett P, Robinson EJH. 2017. Inferring polydomy: a review of functional, spatial and genetic methods for identifying colony boundaries. *Insect Soc.* 64:19–37.
- Fourcassié V, Oliveira PS. 2002. Foraging ecology of the giant Amazonian ant *Dinoponera gigantea* (Hymenoptera, Formicidae, Ponerinae): activity schedule, and spatial foraging patterns. *J Nat His.* 36:2211–2227.
- Frizzo TLM, Campos RI, Vasconcelos HL. 2012. Contrasting effects of fire on arboreal and ground-dwelling ant communities of a Neotropical Savanna. *Biotropica.* 44:254–261.
- Gordon DM. 1995. The development of an ant colony's foraging range. *Anim Behav.* 49:649–659.
- Hashmi AA. 1973. A revision of the Neotropical ant subgenus *Myrmothrix* of genus *Camponotus*. *Studia Entomologica.* 16:1–140.
- Heinrich B. 1993. *The hot-blooded insects*. Cambridge (MA): Harvard University Press.
- Hölldobler B. 1971. Recruitment behavior in *Camponotus socius* (Hym. Formicidae). *Z Vergl Physiol.* 75:123–142.
- Hölldobler B. 1987. Communication and competition in ant communities. In: Kawano S, Connell JH, Hidaka T, editors. *Evolution and coadaptation in biotic communities*. Tokyo: University of Tokyo Press; p. 98–124.
- Hölldobler B, Möglich M. 1980. The foraging system of *Pheidole militica* (Hymenoptera: formicidae). *Insect Soc.* 27:237–264.
- Hölldobler B, Wilson EO. 1990. *The Ants*. Cambridge (MA): Harvard University Press.
- Holway DA, Case TJ. 2000. Mechanisms of dispersed central-place foraging in polydomous colonies of the Argentine ant. *Anim Behav.* 59:433–441.
- Instituto Brasileiro de Geografia e Estatística. 2004. Map of Brazilian biomes. [accessed 2017 Jul 10]. <http://mapas.ibge.gov.br/tematicos.html>.
- Kaminski LA, Freitas AVL, Oliveira PS. 2010. Interaction between mutualisms: ant-tended butterflies exploit enemy-free space provided by ant-treehopper associations. *Am Nat.* 176:322–334.
- Levings SC. 1983. Seasonal, annual, and among-site variation in the ground ant community of a deciduous tropical forest: some causes of patchy species distributions. *Ecol Monogr.* 53:435–455.
- Liefke C, Dorow WHO, Hölldobler B, Maschwitz U. 1998. Nesting and food resources of syntopic species of the ant genus *Polyrhachis* (Hymenoptera, Formicidae) in West-Malaysia. *Insect Soc.* 45:411–425.

- McGlynn TP, Shotell MD, Kelly MS. 2003. Responding to a variable environment: home range, foraging behavior, and nest relocation in the Costa Rican Rainforest ant *Aphaenogaster araneoides*. *J Insect Behav.* 16:687–701.
- Medeiros FNS, Oliveira PS. 2009. Season-dependent foraging patterns: case study of a Neotropical forest-dwelling ant (*Pachycondyla striata*; Ponerinae). In: Jarau S, Hrcncir M, editors. Food exploitation by social insects: ecological behavioral, and theoretical approaches. Abingdon: Taylor & Francis Group; p. 81–95.
- Mody K, Lisenmair E. 2004. Plant-attracted ants affect arthropod community structure but not necessarily herbivory. *Ecol Entomol.* 29:217–225.
- Morais HC, Benson WW. 1988. Recolonização de vegetação de Cerrado após queimada por formigas arborícolas. *Rev Bras Biol.* 48:459–466.
- Oliveira PS. 1997. The ecological function of extrafloral nectaries: herbivore deterrence by visiting ants and reproductive output in *Caryocar brasiliense* (Caryocaraceae). *Funct Ecol.* 11:323–330.
- Oliveira PS, Brandão CRF. 1991. The ant community associated with extrafloral nectaries in the Brazilian Cerrados. In: Cutler DF, Huxley CR, editors. Ant-plant interactions. Oxford: Oxford University Press; p. 198–212.
- Oliveira PS, Del-Claro K. 2005. Multitrophic interactions in a neotropical savanna: ant-hemipteran systems, associated insect herbivores, and a host plant. In: Burslem DFRP, Pinard MA, Hartley SE, editors. Biotic Interactions in the Tropics. Cambridge (UK): Cambridge University Press; p. 414–438.
- Oliveira PS, Freitas AVL. 2004. Ant-plant-herbivore interactions in the neotropical cerrado savanna. *Naturwissenschaften.* 91:557–570.
- Oliveira PS, Rico-Gray V, Díaz-Castelazo C, Castillo-Guevara C. 1999. Interaction between ants, extrafloral nectaries and insect herbivores in Neotropical coastal sand dunes: herbivore deterrence by visiting ants increases fruit set in *Opuntia stricta* (Cactaceae). *Funct Ecol.* 13:623–631.
- Oliveira-Filho AT, Ratter JA. 2002. Vegetation physiognomies and the woody flora of the Cerrado biome. In: Oliveira PS, Marquis RJ, editors. The Cerrados of Brazil: ecology and natural history of a neotropical savanna. New York: Columbia University Press; p. 91–120.
- Orr AG, Charles JK. 2007. Foraging in the giant forest ant, *Camponotus gigas* (Smith) (Hymenoptera: formicidae): evidence for temporal and spatial specialization in foraging activity. *J Nat His.* 28:861–872.
- Pfeiffer M, Lisenmair KE. 2000. Contributions to the life history of the Malaysian giant ant *Camponotus gigas* (Hymenoptera, Formicidae). *Insect Soc.* 47:123–132.
- Porter SD, Tschinkel WR. 1993. Fire ant thermal preferences: behavioral control of growth and metabolism. *Behav Ecol Sociobiol.* 32:321–329.
- R Core Team. 2015. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. [accessed 2016 Sep 12]. <http://www.R-project.org/>.
- Raimundo RLG, Freitas AVL, Oliveira PS. 2009. Seasonal patterns in activity rhythm and foraging ecology in the Neotropical forest-dwelling ant, *Odontomachus chelifer* (Formicidae: ponerinae). *Ann Entomol Soc Am.* 102:1151–1157.
- Ronque MUV, Azevedo-Silva M, Mori GM, Souza AP, Oliveira PS. 2016. Three ways to distinguish species: using behavioural, ecological, and molecular data to tell apart two closely related ants, *Camponotus renggeri* and *Camponotus rufipes* (Hymenoptera: formicidae). *Zool J Linn Soc.* 176:170–181.
- Rosengren R. 1977. Foraging strategy of wood ants (*Formica rufa* group), I: age polyethism and topographic traditions. *Acta Zool Fennica.* 149:1–30.
- Santos JC, Del-Claro K. 2009. Ecology and behaviour of the weaver ant *Camponotus (Myrmobrachys) senex*. *J Nat His.* 43:1423–1435.
- Schoederer JH, Sobrinho TG, Madureira MS, Ribas CR, Oliveira PS. 2010. The arboreal ant community visiting extrafloral nectaries in the Neotropical Cerrado savanna. *Terr Arthropod Rev.* 3:3–27.
- Sendoya SF, Freitas AVL, Oliveira PS. 2009. Egg-laying butterflies distinguish predaceous ants by sight. *Am Nat.* 174:134–140.

- Silvestre R, Brandão CRF, Da Silva RR. 2003. Gupo funcionales de hormigas: el caso de los grêmios del Cerrado. In: Fernández F, editor. Introducción a las hormigas de La región Neotropical. Bogotá: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt; p. 113–148.
- Steiner FM, Crozier RH, Schlick-Steiner BC. 2010. Colony Structure. In: Lach L, Parr CL, Abbott KL, editors. Ant ecology. Oxford: Oxford University Press; p. 177–193.
- Talbot M. 1943. Population studies of the ant, *Prenolepis imparis* Say. Ecology. 24:31–44.
- Traniello JFA. 1977. Recruitment behavior, orientation, and the organization of foraging in the carpenter ant *Camponotus pennsylvanicus* DeGeer (Hymenoptera: formicidae). Behav Ecol Sociobiol. 2:61–79.
- Tschinkel WR. 2005. The nest architecture of the ant, *Camponotus socius*. J Insect Sci. 5:1–18.
- Weidenmüller A, Mayr C, Kleineidam CJ, Roces F. 2009. Preimaginal and adult experience modulates the thermal response behavior of ants. Curr Biol. 19:1897–1902.
- Wilson EO. 1959. Some ecological characteristics of ants in New Guinea rain forests. Ecology. 40:437–447.
- Yamamoto M, Del-Claro K. 2008. Natural history and foraging behavior of the carpenter ant *Camponotus sericeiventris* Guérin, 1838 (Formicinae, Campotonini) in the Brazilian tropical savanna. Acta Ethol. 11:55–65.