

Foraging and Spatial Ecology of a Polydomous Carpenter Ant, *Camponotus leydigi* (Hymenoptera: Formicidae), in Tropical Cerrado Savanna: A Natural History Account

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Abstract

Carpenter ants (genus *Camponotus*) are considered to be predominantly omnivorous, mixing several feeding habits that include predation, scavenging of animal matter, and plant-derived resources. Nitrogen acquisition is crucial for the nutritional ecology of ant colonies because growing larvae require sustainable protein provisioning. Here, we investigate the foraging ecology and the spatial nesting structure of the carpenter ant, *Camponotus leydigi* Forel, in Brazilian cerrado savanna. By marking workers from different nests with distinct colors, we revealed that *C. leydigi* occupies physically separated but socially connected nests (up to 30 m apart), a phenomenon known as polydomy. Observational data on aboveground internest movements in *C. leydigi* corroborate cooperative exchanges between nest units and confirm several types of social connections, including internest transfer of liquid and solid food, transport of colony members (brood, workers), movement of solitary workers, and internest recruitment. Polydomous *C. leydigi* allocate foragers throughout 1,700 m², feeding mostly on termites and plant-derived exudates. Influx of exudates is threefold higher compared with solid food. Uric acid pellets excreted by lizards comprise 20% of the solid diet in *C. leydigi*, a rare quantitative assessment of this peculiar type of nitrogen complementation in ants. Based on video recordings, we hypothesize that nest decentralization in *C. leydigi* may reduce foraging constraints caused by overt interference by the aggressive ant, *Ectatomma brunneum* Smith, F. (Hymenoptera: Formicidae), which regularly blocks nest entrances. Our field study enhances the importance of natural history data to clarify selective pressures underlying the evolution of particular behavioral patterns (nutritional and nesting habits) in ants.

Key words: ant diet, *Ectatomma*, interference behavior, internest movement, uric acid pellet

Ants have existed on Earth for over 100 Myr (LaPolla et al. 2013) and comprise a highly diversified social insect group (Bolton 2020). Their ecological dominance is particularly remarkable in tropical terrestrial ecosystems, where they prevail numerically on soil and vegetation, and consume a wide array of diets (Hölldobler and Wilson 1990). Most ants are viewed as omnivorous and mix several feeding habits, including predation, scavenging of animal matter, and consumption of plant-derived resources such as fleshy fruits and seeds, nectar, and honeydew from plant-sucking hemipterans (Carroll and Janzen 1973, Stradling 1978). Because ants are holometabolous, nitrogen (N) acquisition plays a key role in the nutritional ecology of ant colonies: although workers forage for food to fuel their costly activities, larvae require sustainable protein provisioning their development (Blüthgen and Feldhaar 2010).

Due to morphological modifications in their digestive system (Eisner and Wilson 1952), many ant species (especially in the subfamilies Formicinae and Dolichoderinae) can process large quantities of carbohydrate-rich exudates, such as nectar and honeydew, from which they obtain nitrogen (Blüthgen et al. 2003, Davidson et al. 2003). Although quantities of nitrogenous compounds in such exudates are limited (Davidson 1997), association with endosymbionts can play a crucial role in helping the ants upgrade their nitrogen nutrition (Sauer et al. 2000, Stoll et al. 2007), and likely account for their high abundance in tropical forests (Blüthgen et al. 2003, Davidson et al. 2003). Nitrogen upgrading by endosymbiotic bacteria has been reported for a number of carpenter ants (genus *Camponotus*; Formicinae) harboring obligate intracellular *Blochmannia*, which provide them essential amino acids made from recycled N (Sauer et al. 2000, Feldhaar et al. 2007).

Vertebrate excreta contain large amounts of N-rich waste (Stevens and Hume 2004), and many ants in different groups are known to collect fecal material (e.g., Carroll and Janzen 1973, Stradling 1978, Curtis 1985, Pizo and Oliveira 1999, Blüthgen and Feldhaar 2010), from which some species can obtain usable N (see Feldhaar et al. 2007, Hu et al. 2018). Most studies on ant foraging and nutrition, however, are either conducted in the laboratory or use baits of synthetic food in the field (see Csata and Dussutour 2019 and included references). Among omnivorous ants, the fraction of food influx derived from live arthropod prey, dead animal matter, plant and insect exudates, and animal excreta remains largely undetermined in the field (but see Curtis 1985). In fact, for many ant species, it may be difficult to quantify in the field the influx of liquid versus solid food into ant colonies, as well as to clearly identify the income of animal excreta within the ants' mandibles. Among carpenter ants, this is further complicated by the fact that many *Camponotus* species inhabit physically separated nests (polydomy), making colony boundaries difficult to assess (Debout et al. 2007).

Carpenter Ants in Neotropical Cerrado Savanna

Wilson (1976) recognized *Camponotus* as one of the most prevalent ant genera in the world, occupying wide adaptive zones and occurring in large numbers of species in most zoogeographical regions, and with high local abundances. The so-called Brazilian *cerrados* cover ≈ 2 million km² and comprise a continuum of savanna formations ranging from open grassland to forest woodland (Fig. 1; see Oliveira-Filho and Ratter 2002). *Camponotus* ants are widespread across the cerrado domain, comprising 38 species among a total of 455 ant species recorded in 29 well-preserved sites in Central Brazil (Vasconcelos et al. 2018). These carpenter ants occupy a variety of nest types (on ground and plants) in cerrado (Ronque et al. 2016, 2018), and the most common species have been reported to consume a range of food resources, including plant and insect exudates, arthropod prey, fleshy fruits and seeds, and vertebrate excreta (Oliveira and Freitas 2004, Christianini et al. 2007, Sendoya et al. 2009, Kaminski et al. 2010, Koch et al. 2016, Lange et al. 2019).

Camponotus leydigi Forel is a widespread ground-nesting species in the cerrado savanna (Vasconcelos et al. 2018) for which there

are only brief reports of its occurrence on foliage harvesting plant and insect exudates (Fig. 2a and b; Schoereder et al. 2010, Bächtold et al. 2012). In this field study, we provide a first account of the foraging and nutritional ecology of *C. leydigi*, in connection with its nesting habit in an area of open savanna (Fig. 1). By marking workers from different nests with distinct color codes and following their aboveground movements, we disclosed a polydomous nesting structure in this species (nest units up to ≈ 30 m apart). We document internest transfer of food, workers and brood, and internest recruitment. Polydomous *C. leydigi* can exploit a large foraging terrain by allocating foragers among spatially dispersed nests to nearby sources of solid (termite mounds) and liquid food (on foliage), avoiding long round trips. We record a peculiar harvesting of scattered N-rich pellets of uric acid from lizard excretion and provide a quantitative assessment of this type of dietary complementation in ants. Video recordings suggest that nest decentralization in *C. leydigi* may be related to overt interference by the aggressive ant *Ectatomma brunneum* Smith, F. (Ectatomminae), which regularly blocks nest entrances.

Materials and Methods

Study Site

Fieldwork was undertaken in a reserve of cerrado savanna near Itirapina (22°15'S, 47°49'W), state of São Paulo, southeast Brazil. The study was carried out in an area of open savanna (*campo cerrado*) consisting of scattered trees and shrubs and a large proportion of grassland (Fig. 1). The climate of the region is characterized by a rainy season from October to March and a dry season from April to September. Mean annual rainfall is 1,360 mm, concentrated mostly in the rainy season. Mean annual temperature is 21.8°C (data from 1994 to 2004, from the reserve's climatological station).

Ant Activity Rhythm

Nests of *C. leydigi* were tagged between September 2015 and March 2017 by active searching and baiting within ≈ 1.5 ha of



Fig. 1. General view of the open cerrado savanna at Itirapina, southeast Brazil. Photograph by H. Soares Jr.

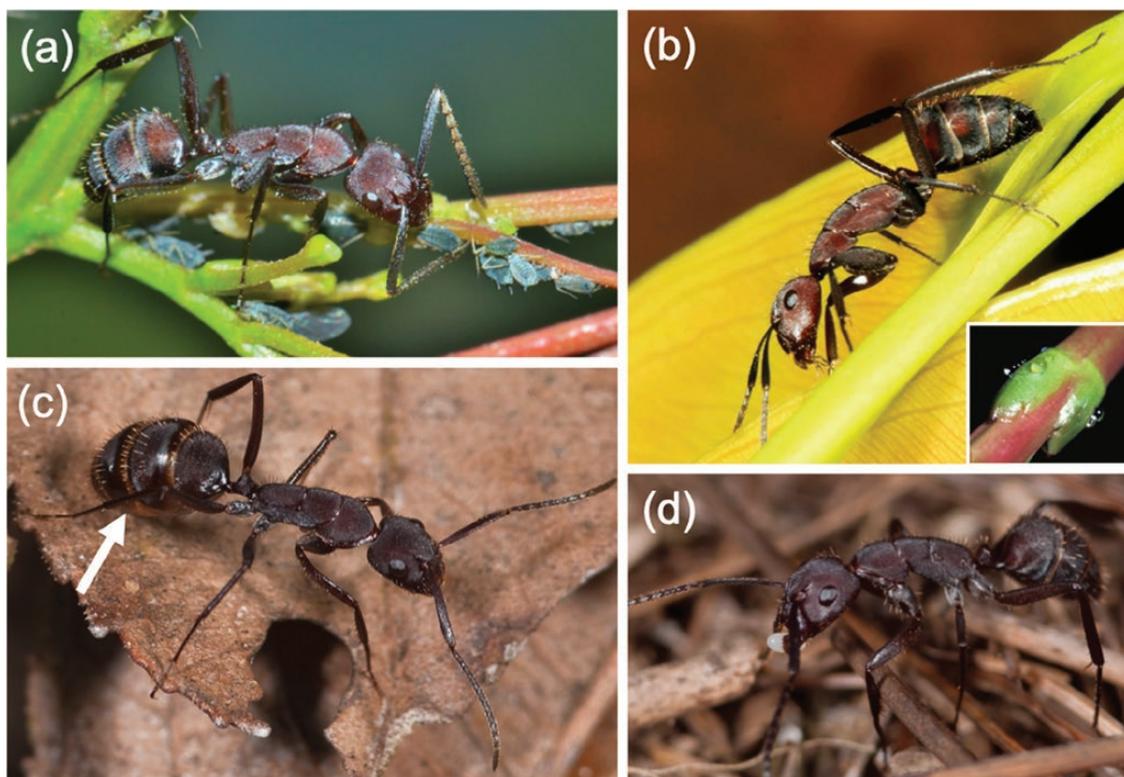


Fig. 2. Behavior of the carpenter ant, *Camponotus leydigi*, in open cerrado savanna of southeast Brazil. (a) *Camponotus leydigi* harvesting honeydew from aphids (photograph by L. Mota) and (b) extrafloral nectar from glands on the stipules (inset) of *Ouratea spectabilis* (Ochnaceae) (photograph by S. F. Sendoya; inset photograph by P. S. Oliveira). (c) Replete worker, with swollen gaster filled with liquid food (arrow), returning to the nest. (d) Internest brood transport (see [Supp Video S5 \[online only\]](#)). Photographs (c) and (d) by H. Soares Jr.

open savanna. Nest entrances ($n = 42$) were located by placing baits of diluted honey on the ground and on leaves and by following attracted workers on their way back to their nests. No tagged nests were destroyed or relocated throughout the study. Data on ant activity were taken during the rainy season (March) and the dry season (September). Eight different nests (four per season) were sampled (11–81 m apart from one another), as follows: N_{13} , N_{15} , N_{19} , N_{25} (rainy season); N_{16} , N_{18} , N_{28} , N_{31} (dry season). We recorded the number of workers exiting or entering the nests within a 24-h period, every 2 h in sessions of 20 min. In each sampling session, we used a thermo hygrometer to record the air temperature and humidity near nest entrances (5 cm above ground surface). We used red lights during nocturnal samplings to avoid disturbing ant foragers. Six nests were excavated to obtain demographic data (N_{20} , N_{22} , N_{35} , N_{38} , N_{40} , N_{41}).

Diet

We used two methods to survey the food items retrieved by foragers of *C. leydigi*. Solid food items were sampled near the nest entrance by removing items from the mandibles of returning foragers from any of nine tagged nests (N_1 , N_2 , N_3 , N_4 , N_7 , N_8 , N_9 , N_{10} , N_{11}). Samplings were carried out intermittently in the morning (0800–1100 h) and in the afternoon (1600–1830 h), in the rainy and dry season (different nests were sampled in each season). This procedure allowed the collection of a large number of food items ($n = 128$), over a total of 72 h for the nine monitored nests altogether. Except for pellets of uric acids and fecal material that were kept dry, all food items were preserved in 70% alcohol and brought to the laboratory for more detailed identification.

Additionally, to investigate the proportion of solid versus liquid food in the diet of *C. leydigi*, we recorded videos (Sony Handycam DCR-SR85) of returning workers at the entrance of seven nests (N_2 , N_3 , N_4 , N_5 , N_6 , N_8 , N_{11}), totaling 47 h of sampling (intermittent sessions from 0900 to 1900 h). Video screenings allowed us to distinguish and count returning workers carrying solid or liquid food (repletes, i.e., worker with inflated gaster due to liquid storage; see [Fig. 2c](#)), as well as unladen ants.

Foraging Range and the Polydomous Nesting Structure

To determine the foraging ranges of *C. leydigi* colonies, we monitored individually marked foragers from three nests (N_2 , N_3 , N_9) in the rainy and dry season. We used baits of diluted honey placed in the immediate vicinity of tagged nests to induce ant foraging activity. Individuals exiting the nests were then individually marked with dots of enamel paint (Testors Co., Rockford, IL) on the thorax and/or gaster, using a distinct color for each of the three tagged nests (white, green, and yellow; total of 215 marked workers altogether). The paint lasted several weeks, but occasionally, some ants had to be re-marked due to color fading. The paint is nontoxic and has proven an effective marking method for several insect taxa, including ants ([Cooley et al. 1998](#), [Holbrook 2009](#)). Foraging ranges were assessed by following marked ants as they exited their nests, and by recording the maximal distance they had traveled before returning to the nest. Foraging trails were measured and mapped using flags, and their geographical directions were determined with a compass. Foraging activity by marked workers was recorded on nonconsecutive days during

the rainy and dry season, totaling 96 h. Observations were carried out mainly at the peak hours of ant activity (see below). We also made video recordings to assess the agonistic interactions between *C. leydigii* and *E. brunneum*, an aggressive ant species commonly seen at our study site. The following interspecific interactions were documented, totaling 31 h of intermittent behavioral recordings: 1) blocking of nest entrance by *E. brunneum*; 2) overt physical aggression between workers (opened mandibles); and 3) defensive behavior by *C. leydigii* at nest entrance (phragmosis) against approaching *E. brunneum*. After terminating the recording and mapping of the foraging and internest trails used by the ants, we replaced the flags marking the ant foraging trails for white plates that could be clearly seen from above. We then used a DJI Phantom 4 drone to obtain an aerial view (80 m high) of the complex spatial structure of nesting by *C. leydigii* and of its whole foraging range.

We used the orthodontal plaster casting method (Williams and Lofgren 1988) to describe the nest architecture of 8 nests of *C. leydigii* (N_{25} , N_3 , N_{10} , N_{11} , N_{17} , N_{21} , N_{25} , N_{30}). We poured a thin slurry of this plaster (Yamayai) into the nest entrance until the nest was filled. After 3 d, the hardened casts were excavated and taken to the laboratory. Because the casts always broke during excavation, their dried pieces were photographed and reconstructed using Adobe Photoshop (version CS5). Ant voucher specimens are deposited at the Museu de Zoologia da Universidade Estadual de Campinas (ZUEC, Campinas, Brazil).

Results

Ant Activity and Foraging Ecology

Colonies of *C. leydigii* were active all day long throughout the year, with a slight bimodal pattern in the dry period when ant activity increased a little at dawn and dusk hours (Fig. 3). Individual foragers left their underground nests and searched for food above and beneath the leaf litter, and on foliage of herbs and shrubs (Fig. 2a and b). Foraging trails extended for up to ≈ 15 m (Fig. 4); food items were retrieved singly, and no cooperation during prey retrieval was ever observed.

Of a total of 128 solid food items recorded as part of the diet of *C. leydigii* in the open savanna, arthropods (entire or in parts) comprised 66% of the food items retrieved by foragers (Fig. 5a). Termite mounds are abundant in the study area (Fig. 4), with workers (mostly) and soldiers of *Silvestritermes euamignathus* (Silvestri) (Termitidae) accounting for nearly half of the solid diet of *C. leydigii* (Fig. 5a). They were hunted at broken sections of their superficial ground tunnels, where exposed termites were captured by the ants and brought straight to the nest. Pellets of uric acid attached to feces of common cerrado lizards, such as *Micrablepharus atticolus* Rodrigues (Fig. 6; Supp Video S1 [online only]), accounted for nearly 20% of the solid food retrieved by foraging ants, whereas pieces of fecal material made up 10% (Fig. 5a).

Videos at nest entrances revealed that 66% of the *C. leydigii* foragers return to their nests without a food item (308/470), whereas 34% bring liquid or solid food in their mandibles (162/470; Fig. 5b). Food influx into the nests in the form of exudates (Fig. 2a–c) was nearly threefold higher than solid items, as expressed by the quantity of returning foragers bringing each type of food (121 vs 41 ants; Fig. 5b). Termites and uric acid pellets comprised together about half of the solid items retrieved by foragers (Fig. 5b).

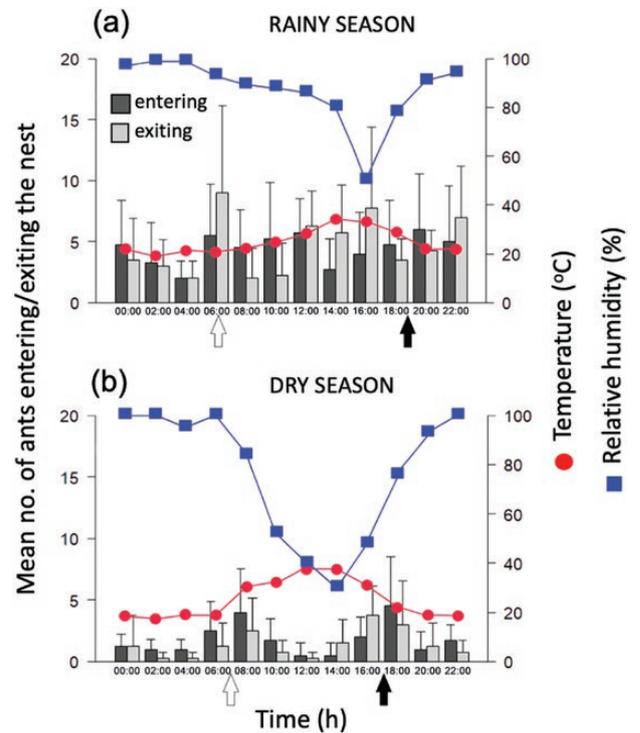


Fig. 3. Daily foraging activity of *Camponotus leydigii* colonies ($n = 4$ nests in each season) during the rainy (a) and dry (b) seasons in open cerrado savanna, southeast Brazil. Foraging activity is expressed for inbound and outbound workers (data are means \pm SD). Air temperature and humidity were recorded simultaneously during each sampling of ant activity (data are means). The arrows indicate sunrise (white) and sunset (black).

Behavioral Interactions

In addition to desiccation risk in the hot open savanna, the main enemy of *C. leydigii* during foraging was the ant *E. brunneum*, an aggressive competitor and predator. Although we witnessed eight predation events by *C. leydigii* on *E. brunneum*, on five occasions the latter species was seen preying on *C. leydigii* as well. Moreover, *E. brunneum* workers often used sticks, dry leaves, and stones to block the entrances of *C. leydigii* nests (Supp Video S2 [online only]). This behavior prevented foraging activity by *C. leydigii* for at least 2 h, until complete removal of the blocking material. On many occasions, we witnessed *C. leydigii* fleeing after attacks by a sentinel *E. brunneum* at the nest entrance, and eventually falling prey (Supp Video S3 [online only]). Major workers of *C. leydigii* were observed to block the nest entrance with their heads against intrusion by *E. brunneum*, a defensive behavior known as phragmosis (Supp Video S4 [online only]). Notwithstanding, *E. brunneum* workers were seen intruding into *C. leydigii* nests several times to deposit blocking material at the entrance tunnel (Supp Video S2 [online only]). On 13 occasions, *E. brunneum* aggressively expelled *C. leydigii* from liquid food sources such as extrafloral nectaries and hemipteran trophobionts. Other enemies of *C. leydigii* foragers included spiders, antlions, and parasitic wasps.

The Polydomous Nesting Structure

By marking foragers of three nests (N_2 , N_3 , N_6) with distinct colors, we discovered a complex polydomous structure consisting of 11 interconnected nests of a major *C. leydigii* colony, with internest trails of up to ≈ 30 m, exploiting an area of approximately 1,700 m² (Fig. 4). In this open savanna, foraging activity was sparsely distributed and

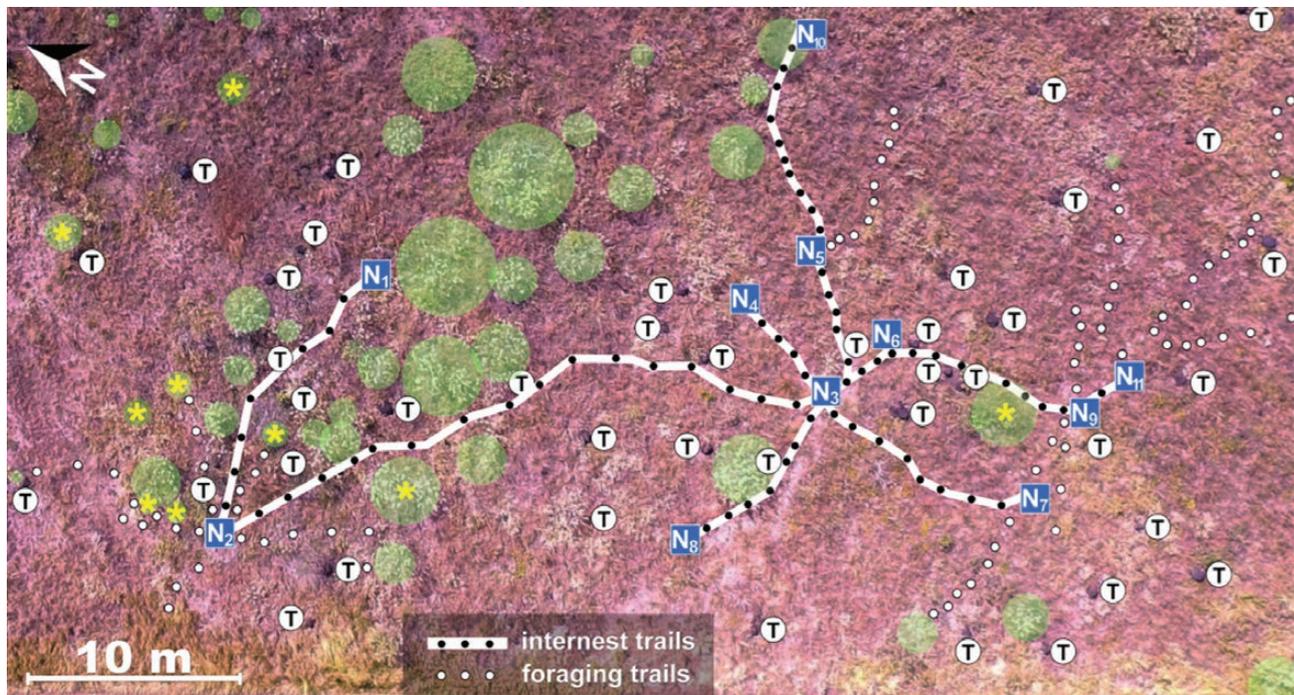


Fig. 4. Aerial photograph (80 m high; DJI Phantom 4 drone) showing the spatial nesting structure of a polydomous colony of *Camponotus leydigi*, in an area of open cerrado savanna in southeast Brazil. Dots along internest and foraging trails indicate the location of individual ants (not necessarily on the same day). Ant locations were marked with white plates to be visible from above. The colony occupies 11 nests, whose identities are indicated by subscript numbers (N_{1-11}). Termite mounds (dark spots on the ground) are indicated by 'T'. Shaded circles designate patches of herbs or shrubs, some of which containing liquid food sources such as extrafloral nectaries or honeydew-producing hemipterans designated by an asterisk (*). See also Fig. 8 for internest social connections between constituent nests. Photograph by D. Conciani.

ants departed from various nests toward different directions in the search for food, targeting mostly patches of plants with liquid resources (sometimes followed by nestmate tandem recruitment), nearby termite mounds, or prey items scattered on the ground (Fig. 4).

We recorded intense aboveground ant traffic among nests, especially through nest N_3 that occupied the center of the colony domain (Fig. 4). We noted that brood transportation between nests consistently departed from nest N_3 (Fig. 2d), whose increased architectural complexity compared with adjacent nests suggests queen presence and reproductive activity (Fig. 7). Nearly all internest social connections recorded in the field were centered around nest N_3 , including transport of brood and adult ants (Supp Video S5 [online only]), exchange of solitary and recruited workers, as well as the sharing of liquid and solid food (Fig. 8). Social connections via regular reciprocal behaviors between individuals from intercommunicating nests, including resource sharing, confirm a single cooperative colonial unit in this polydomous ant species.

Excavations of six *C. leydigi* nests from another site but in the same cerrado reserve revealed that all but one had brood, with 114–432 workers per nest (255.0 ± 127.5 ants; mean \pm SD; $n = 6$ nests). This finding suggests that a major colony of *C. leydigi* occupying 11 nesting units, such as the one described in this study (Fig. 4), may contain over 2,500 workers altogether.

Discussion

Foraging Ecology

Despite the hot weather in the open cerrado savanna, *C. leydigi* is active all day long, even in the hottest hours. In tropical habitats, arthropod prey and liquid food sources are known to be more abundant in the wet season, when ant activity also increases (Levings and

Windsor 1996, Díaz-Castelazo et al. 2004). In the cerrado, extrafloral nectar and honeydew are indeed more available in wet months, when both exudate sources are constantly attended by many ant species (Belchior et al. 2016, Sendoya et al. 2016). Our results show that *C. leydigi* feeds intensively on plant and insect exudates in the open savanna, corroborating previous accounts on this species from other cerrado sites (Costa et al. 1992, Schoederer et al. 2010, Bächtold et al. 2012, Lange et al. 2013). Higher foraging activity by *C. leydigi* in the wet season of cerrado also follows the period of increased availability of termites (Pinheiro et al. 2002), its main prey, and corresponds with greater brood quantity in the colony, which requires augmented protein intake by foragers (see also Yamamoto and Del-Claro 2008, Ronque et al. 2018).

As already reported for most *Camponotus* species around the world (Brown 2000, Degnan et al. 2004, and included references), *C. leydigi* presents an omnivorous diet combining predation on live arthropods, scavenging dead animal matter and vertebrate excreta, and harvesting plant and insect exudates. As the first group of predatory social insects to live and forage primarily on the ground, ants are considered the main predators of termites (Hölldobler and Wilson 1990). Indeed, termites comprised almost 50% of the solid prey items of *C. leydigi* in open cerrado. Video recordings at nest entrances, however, revealed that influx of liquids is nearly threefold higher compared with solid food and can be promoted by tandem recruitment to exudate sources on leaves. An even more disproportionate rate was obtained by Holt (1955), with *Formica rufa* Linnaeus (Formicinae), in which influx of honeydew was fourfold greater compared with solid food (81 vs 19%). These findings confirm that omnivorous formicine ants are indeed functional herbivores, obtaining their nitrogen to a large extent from plant-based resources (Blüthgen et al. 2003, Davidson et al. 2003). The capacity

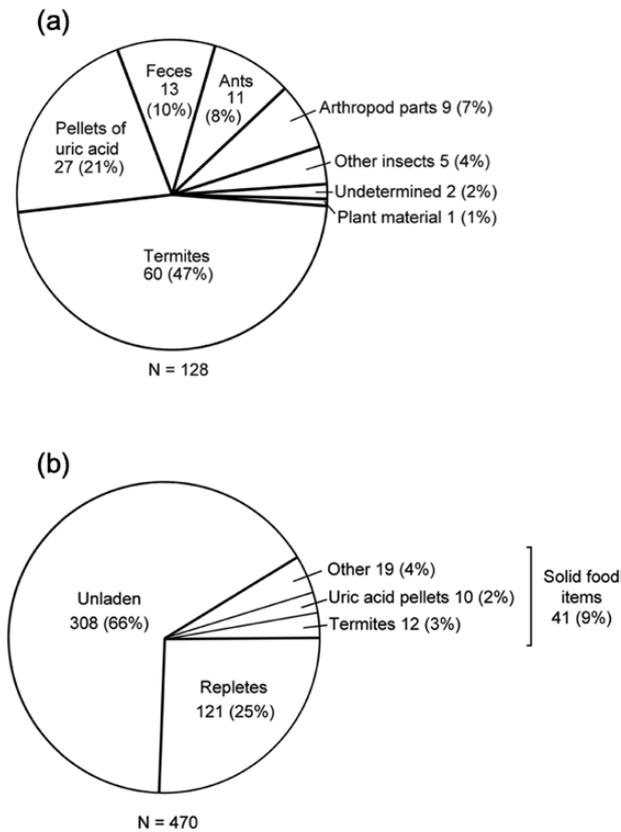


Fig. 5. Diet of *Camponotus leydigi* in an area of open cerrado savanna, southeast Brazil. (a) Solid food items retrieved by ant foragers ($n = 128$ laden ants) during 72 h of intermittent samplings of nine nests (0800–1100 h; 1600–1830 h). (b) Influx of solid and liquid food ($n = 470$ returning ants) based on video recordings of returning workers at nest entrances, totaling 47 h of intermittent samplings (0900–1900 h; 7 nests).

to access plant-derived nitrogen may explain the high abundance of formicine ants in tropical habitats (Davidson 1997), as seen in cerrado savanna among dominant, exudate-harvesting *Camponotus* (Oliveira and Brandão 1991, Schoederer et al. 2010, Lange et al. 2013, Sendoya et al. 2016, Ronque et al. 2018). However, because nectar and honeydew contain limited amounts of nitrogenous compounds, carpenter ants must collect (and store in replete workers) great quantities of exudates to sustain growing larvae and egg-producing queens (Stradling 1978, Davidson 1997).

As functional herbivores, exudate-feeding ants are unable to obtain sufficient N from their N-limited diets, and conversion of dominant nitrogenous waste compounds into usable N requires the aid of microbes (Hu et al. 2018). Omnivorous *Camponotus* face this challenge by selecting food that enhances nutritional upgrade via their endosymbiont *Blochmannia* (Sauer et al. 2000, Stoll et al. 2007), which recycles common nitrogen wastes, including urea and uric acid, and provides essential amino acids to ant hosts (Feldhaar et al. 2007). *Blochmannia* has been found in over 30 *Camponotus* species, including the subgenus *Myrmaphaenus* to which *C. leydigi* belongs (Degnan et al. 2004, Feldhaar et al. 2007, and included references). Our data on the diet of *C. leydigi* show that uric acid pellets from lizard excretion and feces comprise together 30% of the solid food items retrieved by ant foragers. Lizards living in water-limited environments are usually protected from excessive water loss, and N wastes are excreted as dry pellets of uric acid (Stevens and Hume 2004, Pianka and Vitt 2006). In addition to *M. atticolus*, other lizards

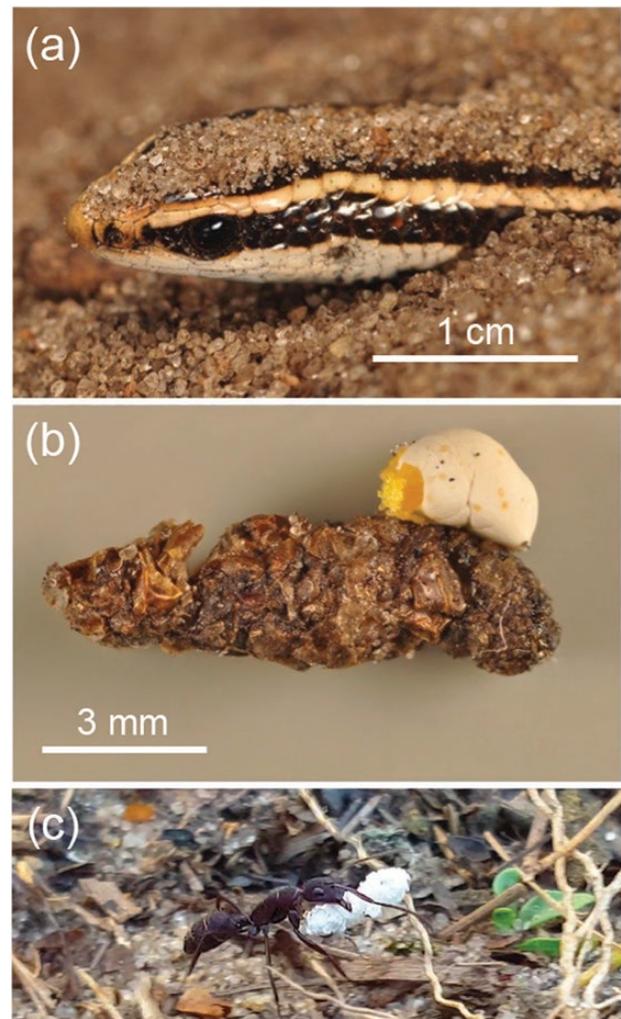


Fig. 6. Harvesting of uric acid pellets from lizard excretion by *Camponotus leydigi* in an area of open cerrado savanna, southeast Brazil. (a) The lizard *Micrablepharus atticolus* and (b) its fecal mass with a dried pellet of uric acid attached. (c) Still photograph from a video showing a forager of *C. leydigi* carrying to its nest a recently collected uric acid pellet (Supp Video S1 [online only]). These N-rich pellets may account for nearly 20% of the solid food items retrieved by this ant species (Fig. 5). Photographs by H. Soares Jr.

in the genera *Tropidurus* and *Ameiva* were also regularly seen in our study area, all of which commonly feed on termites in cerrado (Costa et al. 2008). Collection of bird droppings containing uric acid has also been documented in carpenter ants of the genera *Camponotus* and *Polyrhachis* (Feldhaar et al. 2007, Blüthgen and Feldhaar 2010) and in turtle ants of the genus *Cephalotes* (Myrmicinae; Hu et al. 2018). In the Namib Desert (South Africa), Curtis (1985) found that bird and lizard feces accounted for 22% of the material brought to the nests by the dune ant *Camponotus detritus* Emery.

Resources, Behavioral Interactions, and Polydomy

The dynamics of foraging and nest allocation in ants can be affected by the temporal and spatial distribution of food resources, the quality of the food, the competitive environment, and exposure to natural enemies (Hölldobler and Lumsden 1980, Holway and Case 2000, Csata and Dussutour 2019). In our study site, the main food resources exploited by *C. leydigi* present distinct distribution patterns. Although exudate sources are clumped and predictable through time, termites and (presumably) uric acid pellets are sparsely



Fig. 7. Representative casts of two nests of a polydomous colony of *Camponotus leydigi* inhabiting an area of open cerrado savanna, southeast Brazil. (a) Cast of nest N_3 with increased number of chambers and more complex architecture, from which most events of internest brood transportation departed (Fig. 2d; Supp Video S5 [online only]), suggesting queen presence and reproductive activity (see also Tschinkel 2005). (b) Cast of nest N_{11} , showing decreased architectural complexity. Scale bars = 15 cm. See Fig. 4 for nest identities and locations and Fig. 8 for internest social connections.

distributed in the open cerrado (see Fig. 4). Therefore, nesting decentralization through polydomy may allow *C. leydigi* colonies 1) to alleviate foraging constraints caused by frequent interference (and predation) from superior ant competitors (Hölldobler and Lumsden 1980), 2) to exploit more efficiently nearby exudate sources and reduce travel times (Davidson 1997, Lanan and Bronstein 2013, Stroeymeyt et al. 2017), and 3) to improve discovery of uniformly dispersed food (Kloft et al. 1965, Hölldobler 1971, Traniello and Levings 1986, Pfeiffer and Linsenmair 1998).

Our field observations and videos indicate that regular interference from *E. brunneum* may cause considerable foraging costs to *C. leydigi*, including allocation of workers to defend the nest entrance (phragmosis) and to remove blocking material, loss of workers due to predation (or injury), and exclusion of foragers from exudate sources (see also Hölldobler 1982, Gordon 1988). As reported here for *C. leydigi*, *E. brunneum* also forages day and night and has an omnivorous diet consisting of termites, ants, and other arthropods (Overall 1986, Vieira and Antonialli 2006), and is very aggressive near exudate sources at our study site (Ibarra-Isassi and Oliveira 2018). Such an asymmetric competition has been shown to lead inferior ant competitors to feed on less preferred food (Blüthgen and Fiedler 2004a,b). Therefore, we suggest that a polydomous nesting habit may help *C. leydigi* colonies to reduce some of the constraints imposed by competitively superior *E. brunneum*. By allocating multiple nests over a large foraging area in the open savanna, polydomous *C. leydigi* probably reduces foraging costs of long trips (desiccation, natural enemies), improves competitive ability by exploiting clumped (exudates) and dispersed food resources (including uric acid pellets), and reduces interference contests with *E. brunneum* (see Hölldobler and Lumsden 1980, McIver 1991, Holway and Case 2000, Debout et al. 2007, Stroeymeyt et al. 2017).

The Social Attributes of Polydomy

A correct assessment of colony boundaries is crucial to understand the various levels of organization within social insect colonies and to

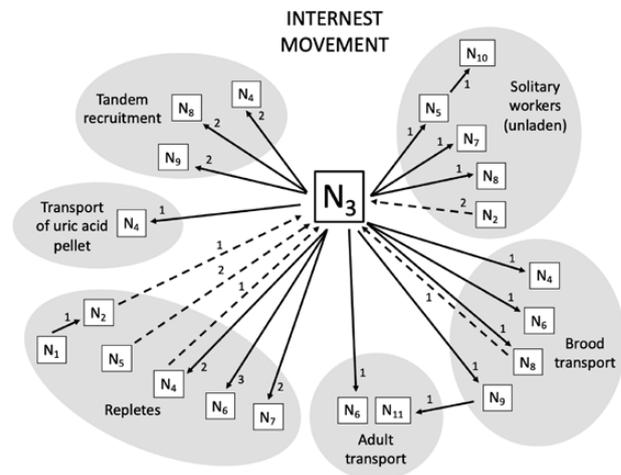


Fig. 8. Flow diagram summarizing all types of internest social connections observed in the field within a polydomous colony of *Camponotus leydigi* occupying 11 spatially separated nests, in an area of open cerrado savanna, southeast Brazil. All but three internest movements involved nest N_3 , located at the center of the colony domain and in which reproductive activity most likely occurred (Fig. 7). Internest movements toward nest N_3 are represented by dashed arrows. Numbers in each arrow indicate quantity of workers seen performing the action. See Fig. 4 for nest identities and locations.

identify the functioning of a single cooperative and ecological unit (Debout et al. 2007, Ellis et al. 2017). Because polydomous colonies occupy multiple, spatially separated nests, it is frequently difficult to establish which nests belong to same colony, making it necessary to demonstrate social connections between constituent nests to confirm a colonial unit. Polydomy has been recorded in over 160 ant species and appears to be a common nesting habit in the genus *Camponotus* (Debout et al. 2007). Our field data on internest movements in *C. leydigi* unequivocally corroborate cooperative exchanges between nest units (sometimes reciprocal) and confirm several types of social connections (Fig. 8): 1) sharing of resources (liquid and solid food), 2) movement of solitary workers, 3) recruitment of workers, and 4) transport of colony members (brood, workers). Some behaviors may represent more than one type of social connection. For instance, sharing of liquid food also includes internest movement of replete workers, and exchange of workers (including majors) can also be considered sharing of resources (see Robinson 2014, Ellis et al. 2017). As also suggested for other ant species, the polydomous nesting structure in *C. leydigi* may generate among-nest division of labor, in which some nests may specialize on producing or rearing brood, whereas others may engage in the collection of nearby exudates (see also Hölldobler and Lumsden 1980, Holway and Case 2000, Ellis and Robinson 2014, Stroeymeyt et al. 2017). Molecular analyses are currently underway to determine the degree of relatedness among workers from constituent nests of polydomous *C. leydigi*.

Our study provides a detailed field account of the foraging and spatial ecology of *Camponotus leydigi*, a conspicuous ant species of tropical cerrado savanna. We show that polydomous *C. leydigi* disperse its multiple nests over nearly 1,700 m² of open cerrado. Influx of liquid food is nearly threefold higher compared to solid food items. We provide a rare quantitative assessment of uric acid pellets excreted by lizards as a dietary complementation in ants, comprising about 20% of the solid diet of *C. leydigi*. Nest decentralization in polydomous *C. leydigi* may additionally reduce foraging constraints caused by aggressive interference from *E. brunneum* at nest entrances. Although

ants are abundant and dominant in most terrestrial ecosystems, there is a general lack of ecological data for most species, especially in tropical habitats (Wilson 2017). This study helps fill this gap by showing that field data on ant biology and natural history are crucial to clarify the selective pressures underlying the evolution of particular behavioral patterns (nutritional and nesting habits) in the environment. In the future, solid advances in community ecology will depend increasingly on a detailed knowledge of species and their natural history, which feeds and drives theory' (Wilson 2000, 1).

Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

Video S1. Foragers of *Camponotus leydigi* bringing pellets of uric acid to the nest.

Video S2. Part 1: Worker of *Ectatomma brunneum* blocking the nest entrance of *Camponotus leydigi*. Part 2: *Camponotus leydigi* removing stick from the nest interior.

Video S3. Predation of *Camponotus leydigi* worker at the nest entrance, by sentinel *Ectatomma brunneum*.

Video S4. Phragmosis by major worker of *Camponotus leydigi* against approaching *Ectatomma brunneum*.

Video S5. Internest transport of colony members (larva and worker) by *Camponotus leydigi*.

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Data Availability

Data from this study are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.x3ffb7gb> (Soares and Oliveira 2020).

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