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RESEARCH ARTICLE

Quantitative variations of *Constrictotermes cyphergaster* (Isoptera) instars over time in a Neotropical semiarid ecosystem

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Abstract

The presence and relative proportion of termite castes can vary according to both intrinsic characteristics of the colony and in response to external stimuli. *Constrictotermes cyphergaster* is a Neotropical termite that demonstrates high densities of arboreal nests in open vegetation ecosystems in Brazil. Numerical variations of the instars in 30 nests of this specie were analyzed over 1 year in the semiarid Caatinga vegetation of northeastern Brazil. The number of individuals per instar was estimated from five subsamples (5 ml) taken from each colony. The abundance of most instars varied significantly among the nests sampled within the same month. Between months, there was significant numerical variation in the numbers of second instar larvae, workers, presoldiers, soldiers and fifth instar nymphs. In the nymphal line, only the fourth instar was found in all months, whereas alates were only found in February, the month with the highest recorded rainfall. With increasing proximity of the swarming event, there was an increase in the differentiation of last two nymphal instars, with subsequent investment in the differentiation of apterous instars and the emergence of early nymphal instars. These results indicate that differentiation of the instars of *C. cyphergaster* is synchronized with the regional climatic cycle and the annual production of alates. However, there was substantial numerical variation between the instars of the colonies sampled at the same time points, suggesting that factors intrinsic to the colony can generate heterogeneous feedback along with responses to environmental factors.

Keywords Population structure · Castes · Swarming · Annual cycle · Neotropical region

Introduction

Termite colonies are composed of individuals from different phenotypes or castes, which have specialized morphologies and behaviors and conduct specific activities within the colony (Noirot 1969). The presence of castes and their proportions in the colonies are the result of genotypic determinations and environmental influences during postembryonic development, and are regulated by feedback systems (Roisin 2000; Miura 2005). Several factors can lead to variations in population composition among nests, such as colony age, colony life history, external climatic conditions, instar development time, resource availability and quality, intra- and interspecific competition, susceptibility to predation, presence and population size of inquilines, and the reproductive capacity of the queen (Noirot 1969; Thorne 1985; Darlington 1986, 1990; Forschler and Towsend 1996; Lepage and Darlington 2000; Miura 2004; Tong et al. 2017; Cristaldo et al. 2018; Rodrigues et al. 2018).

Apterous castes are usually produced continuously by colonies throughout the year, whereas the production of nymphs and alates is more temporally limited (Thorne 1983; Nutting 1969; Torales et al. 1999), a pattern that has been observed in several species of Termitidae (Noirot 1969). This pattern is related to swarming events, the

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main means of dispersal of termites, which are highly seasonal and occur annually in many species (Nutting 1969). The reproductive cycle of colonies can influence mechanisms of population structure regulation, and there may be greater energy allocation devoted towards alate production to maximize the reproductive event; this may have numerical consequences for the other colony members (Banerjee 1966; Lepage and Darlington 2000).

Constrictotermes cyphergaster (Silvestri, 1901) (Termitidae, Nasutitermitinae) is a Neotropical termite known for constructing nests on trees or rocks (Mathews 1977; Constantino 1999) and for foraging at night in exposed columns (Moura et al. 2006a). Its geographic distribution covers areas with open vegetation in Brazil (Caatinga and Cerrado), Bolivia, Paraguay and northern Argentina (Godinho et al. 1989; Constantino 1998). In the Caatinga, *C. cyphergaster* shows a particularly high nest density with approximately 59 active nests/ha and a consumption rate of 44.5 kg of plant organic matter/ha/year, indicating that this species plays an important role in environmental nutrient cycling (Vasconcellos et al. 2007; Moura et al. 2008). Its nests are usually cohabited by other species, such as *Inquilinitermes fur* (Silvestri, 1901) and *I. microcerus* (Silvestri, 1901) (Termitidae, Termitinae), obligatory inquilines of nests of *Constrictotermes* spp. (Mathews 1977; Cunha et al. 2003; Cristaldo et al. 2012; Rodrigues et al. 2018).

The pattern of differentiation of *C. cyphergaster* castes, as in other Termitidae, is bifurcated. An irreversible division into two lines, apterous and nymphal, occurs at the beginning of development (Noirot and Pasteels 1987; Moura et al. 2011). In this species, the apterous line has two larval instars, followed by workers, presoldiers and soldiers, whereas the nymphal line consists of five nymphal instars and alates. This pattern is considered to be simple, as workers and soldiers do not display sexual dimorphism, are monomorphic and belong to a single instar (Moura et al. 2011).

For population dynamics studies, whole-colony analyses are generally considered the most reliable; however, these are relatively scarce due to the high effort necessarily expended on field work (Thorne 1983). Additionally, studies focusing on termite population quantifications generally do not analyze all of the castes and/or instars in a colony. As such, we investigated whether there were numerical and proportional variations among the instars of *C. cyphergaster* during the year, and if there was quantitative synchrony among the instars of the colonies collected in the same area at the same time. We predicted that there would be numerical variations between the instar over time, in light of the marked climatic oscillations in arid and semiarid ecosystem and their influence on foraging dynamics (Ohiagu 1979; Moura et al. 2006a) and reproduction (Nutting and Haverty 1976). We expected, however, to observe homogeneity in the proportions of instars among the different colonies sampled in the same area at the same moment.

Materials and methods

Study area

The colonies of *C. cyphergaster* used in this study were collected at Fazenda Moreiras (499 hectares), a farm located in an area with typical Caatinga vegetation, in the municipality of São João do Cariri, Paraíba state, Brazil (7°23′51″S; 36°24′49″W). The annual mean temperature in the region is 26 °C, and the annual mean rainfall varies between 250 and 900 mm, with rainfall usually concentrated between February and May (Governo do Estado da Paraíba 1985). During the sampling period, the monthly precipitation in the region was higher in February (86 mm) and June (80 mm), whereas water deficit was higher in December (− 160 mm) and April (− 137 mm) (PROCLIMA 2018).

Termite sampling

Five colonies of *C. cyphergaster* were collected every 60 days between October 2011 and August 2012, for a total of 30 colonies, in order to sample and evaluate any possible temporal variation in the production of all instars. Nests with volumes greater than 35 L were sampled to reduce the possibility of collecting colonies that had not yet reached reproductive maturity. Because *C. cyphergaster* forages at night and all individuals return to the nest early in the morning (Vasconcellos et al. 2007; Moura et al. 2006a), there was no influence of the movement of individuals in the sampling performed. On the other hand, sampling based on different nests can naturally cause biases in population estimates, considering the individual histories of those colonies and local stochastic factors.

The volume of the nests was estimated using the hemiellipsoid formula: $V = 2/3\ \pi\ \mathrm{h.D.d}$ (where h = nest height, D = ½ of the largest diameter, and d = ½ of the smallest diameter) (Vasconcellos et al. 2007), considering that nest volume would influence the numbers of individuals in *C. cyphergaster* colonies (Rodrigues et al. 2018). Termites were extracted manually, and the specimens that remained in the nest fragments were extracted by floating (Bandeira and Vasconcellos 2002). Individuals collected were fixed in FAA solution (37% formalin:acetic acid:ethanol = 1:1:3) for 24 h and later transferred to 75% ethanol for storage.

Population quantification

In the present study, the term “population” corresponds to the estimated number of individuals (total or per instar) of

C. cyphergaster inhabiting a nest. For population estimates per nest, five 5 ml subsamples were randomly removed from each colony after homogenization of the material. During the process of homogenization, colony individuals were randomized during flotation and homogeneously deposited on a surface to separate the subsamples. Those subsamples were weighed (wet weight, after excess liquid was removed), and the individuals were counted. The following instars were quantified: two larval instars (L1 and L2), workers (W), soldiers (S), presoldiers (PS), five nymphal instars (N1–N5) and alates (A). The individuals of *C. cyphergaster* and of their inquilines (*I. microcerus* and *I. fur*) were distinguished based on the number of hairs on the dorsal region of the head (approximately 6 × more abundant in inquilines) and on the mandible morphology (Moura et al. 2011).

Statistical analysis

To estimate the populations of *C. cyphergaster*, the weight of the subsamples was standardized to 5 g. The intramonthly variations in the populations of each instar refer to evaluations among the five nests sampled in the same month, without the interference of a time parameter. For intermonthly variations, were analyzed 30 nests to evaluate instars variations over time (during six different months). Both, intra- and intermonthly variations were analyzed using one-way ANOVA with Tukey's a posteriori test. The relationship between instars was assessed using Pearson's correlation, as well as the relationships between the populations (total, per instar, and per lineage) and nest volumes. The ratio and proportion between individuals in the same nest and between nests were calculated using the monthly means of the population estimates per 5 g of each instar. The caste and instar ratios were calculated to evaluate if there were alterations over time in colony investments in certain instars. The analyses and graphics were performed using Statistica 7.0 software (StatSoft, Inc. 2004).

Results

Constrictotermes cyphergaster nests had an average volume of 72.6 ± 22.5 L (mean ± standard deviation). Among the 30 nests sampled, 93% (28 nests) had *Inquilinitermes* spp., 21 nests contained *I. fur* (75%) and seven *I. microcerus* (25%). Queens were found in 27 nests, with three queens being found in one of them (nest 11); no kings were observed (Online Resource 1).

The total population ranged from 26,052 to 129,548 individuals/nest. The apterous population (L1, L2, W, S, PS) ranged from 25,980 to 129,032 individuals/nest, whereas the nymphal population (N1–N5, A) ranged from 0 to 5.822 individuals/nest. Only worker ($r = 0.37$, $N = 3$, $P < 0.05$) and N4 ($r = 0.41$, $N = 30$, $P < 0.05$) populations were significantly related to nest volume. The mean population estimates per liter of each instar for each nest are presented in Online Resource 1.

Intramonthly variation in colony composition

Most populations of instars varied significantly among the nests sampled in the same month. Only the L2 populations did not vary significantly among nests in December ($F_{4;20} = 2.34$; $P = 0.09$); the N5 populations in February ($F_{4;20} = 1.45$; $P = 0.25$); the N3 populations in April ($F_{4;20} = 1.61$; $P = 0.21$); and the N2 and N3 populations in August ($F_{4;20} = 0.25$; $P = 0.90$, $F_{4;20} = 2.46$; $P = 0.08$) (Online Resource 2).

Intermonthly variation in colony composition

The L2, W, PS, S and N5 populations varied significantly between the months (Fig. 1, Online Resource 3). L2, W and PS were most abundant in February, whereas soldiers were most abundant in April. The populations of workers were lowest in October and December, whereas the L2, PS and S populations were lowest in June. The N5 population was most abundant in December.

Instars of the apterous line were found in all nests and months of collection (Fig. 1, Online Resource 1). Among the instars of the nymphal line, only N4 was present in all months, although it was not found in all nests. Early-stage nymphs (N1, N2 and N3) were found in February and April; N5 was found in December and February, and alates were only present in one nest in the month of February. Four colonies (3, 5, 7 and 12) did not have nymphal or alate instars in subsamples.

Relationship and proportion between instars

There was a significant, positive relationship between several instars, including L1 × PS ($r = 0.69$; $N = 30$; $P < 0.05$); L2 × PS ($r = 0.75$; $N = 30$; $P < 0.05$); L1 × L2 ($r = 0.76$; $N = 30$; $P < 0.05$); and N1 × N2 ($r = 0.49$; $N = 30$; $P < 0.05$) (Online Resource 4). The mean proportions of individuals in the sampled colonies were workers (67.1%), soldiers (18.2%), larvae 2 (8.1%), larvae 1 (4.7%), presoldiers (1.0%) and nymphs (0.9%) (Fig. 2). Table 1 presents the ratios between the different instars in terms of the total population, as well as between the instars and the numbers of workers per colony. The lowest ratios relative to the total population were seen with workers and soldiers, while the first nymphal instars demonstrated the greatest ratios in relation to the total population and to the number of workers.

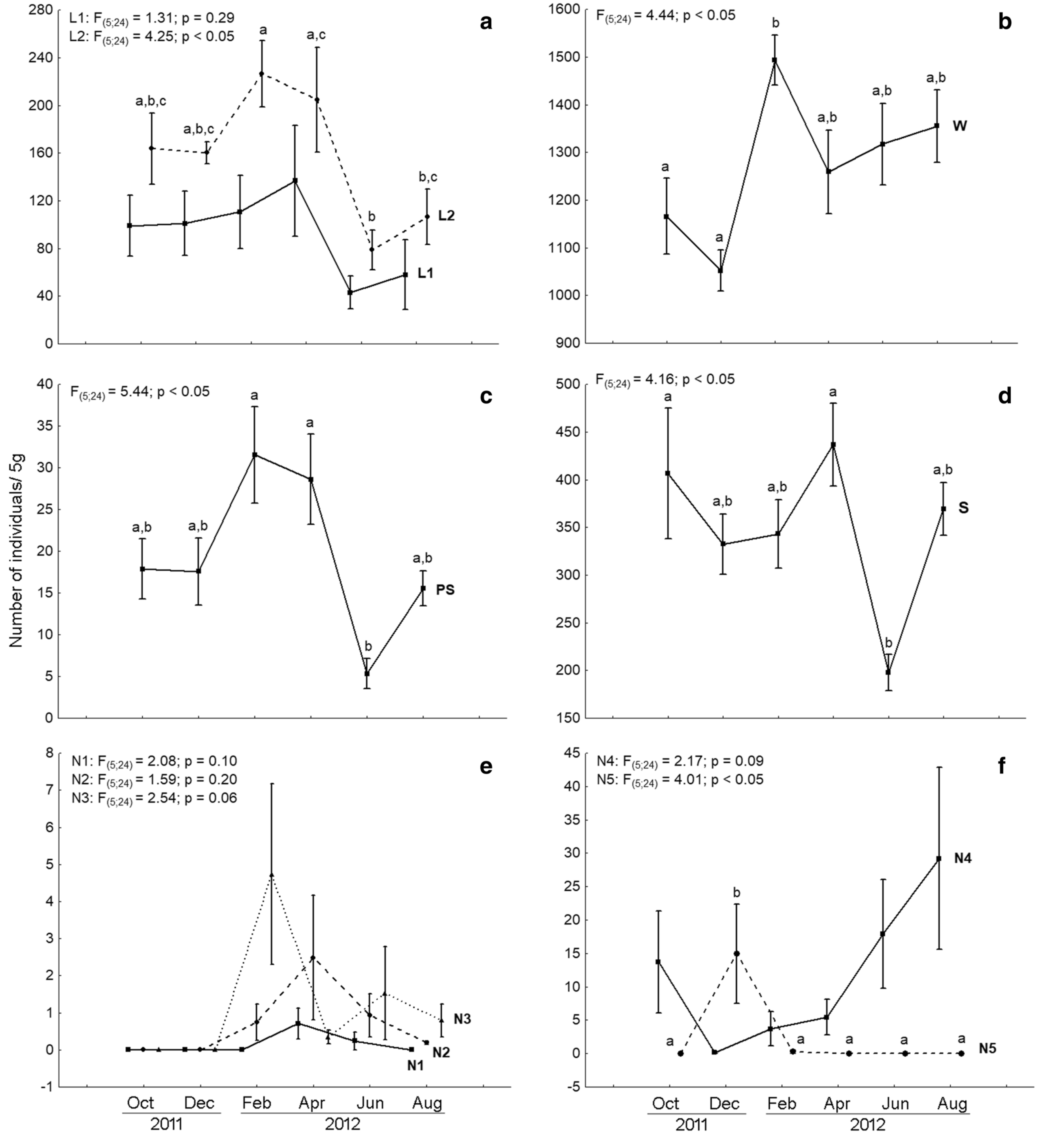

Fig. 1 Intermonthly variation in apterous (**a**–**d**) and nymphal (**e**–**f**) instars of *Constrictotermes cyphergaster* (number of individuals/5 g) in colonies collected between Oct/2011 and Aug/2012 in the municipality of São João do Cariri, Paraíba state, Brazil. *L1*, *L2* larval instars, *W* workers, *PS* presoldiers, *S* soldiers, *N1*–*N5* nymphal instars. Different letters (**a**, **b**) indicate that instar levels varied significantly between months based on the results of one-way ANOVA and Tukey's testing. ■ = mean; I = ± standard error

Discussion

There was no quantitative synchrony among the instars of the different *C. cyphergaster* colonies at any given time. Additionally, quantitative variations were observed between instar numbers during the year, especially in terms of increases in the differentiation of the last two nymphal instars during the months preceding swarming events, with

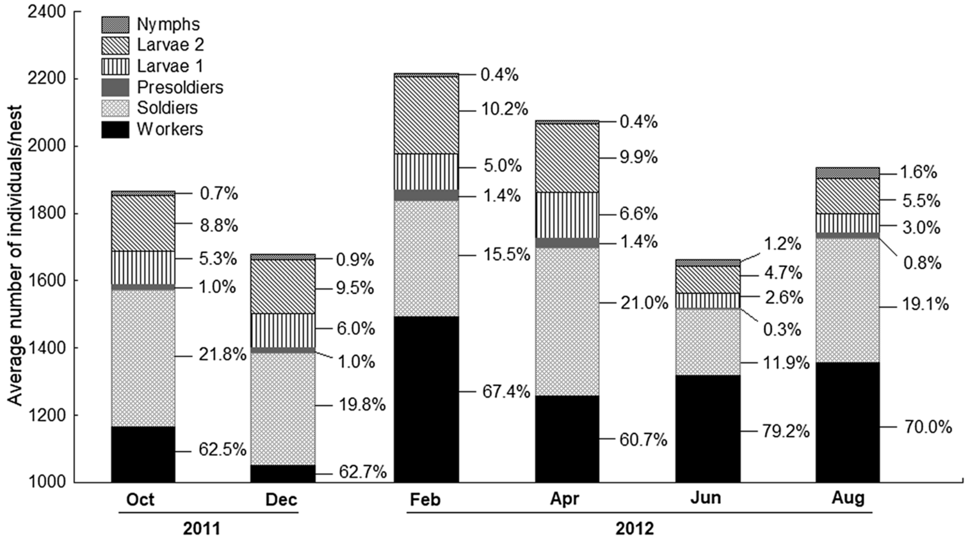

Fig. 2 Mean numbers and proportions of individuals per instar of *Constrictotermes cyphergaster* from colonies collected between Oct. 2011 and Aug. 2012 in the municipality of São João do Cariri, Paraíba state, Brazil. The y-axis initiates at 1000, to avoid flattening the bars of the less numerous instars

Table 1 Mean ratios of the total population and worker populations and the numbers of individuals per instar (estimated per 5 g) from *Constrictotermes cyphergaster* colonies collected between Oct. 2011 and Aug. 2012 in the municipality of São João do Cariri, Paraíba state, Brazil

Month	Ratio instar (1):total population (*x*)									
	W:P	S:P	PS:P	L1:P	L2:P	N1:P	N2:P	N3:P	N4:P	N5:P
Oct	1.6	5.0	123.7	23.6	13.3	–	–	–	105.3	–
Dez	1.6	5.1	111.7	22.2	10.6	–	–	–	418.7	132.6
Feb	1.5	6.7	79.7	36.4	10.6	–	519.5	201.1	487.7	2415.8
Apr	1.7	4.9	82.2	27.3	12.6	2173.7	2490.9	3093.2	1097.4	–
Jun	1.3	8.5	471.3	68.9	25.3	240.1	3183.9	1696.7	241.5	–
Aug	1.4	5.3	137.2	127.6	21.8	–	6459.5	1182.7	109.7	–

Month	Ratio instar (1):worker population (*x*)								
	S:W	PS:W	L1:W	L2:W	N1:W	N2:W	N3:W	N4:W	N5:W
Oct	3.2	80.4	15.6	8.7	–	–	–	72.5	–
Dez	3.3	71.4	14.5	6.7	–	–	–	248.8	86.5
Feb	4.5	54.7	25.2	7.3	–	321.3	134.3	319.6	1468.9
Apr	2.9	51.5	17.6	8.0	1258.4	1589.5	1971.3	710.7	–
Jun	6.8	376.0	55.5	20.2	196.4	2540.0	1373.5	189.8	–
Aug	3.7	96.5	92.1	15.5	–	4471.9	848.3	78.4	–

Those ratios were calculated by dividing the total population or the worker population by the numbers of individuals of each instar. In October, for example, the S:W ratio signifies that for each (1) soldier there are approximately 3 (3.2) workers in the colony

P total population, *W* workers, *S* soldiers, *PS* presoldiers, *L1*, *L2* larval instars, *N1–N5* nymphal instars

subsequent investments in the differentiation of apterous instars and the emergence of early nymphal instars. Those variations are assuredly influenced by multiple biological and environmental factors. Such variations may indicate that colonies collected at the same time nevertheless demonstrate heterogeneous intrinsic situations and, consequently, different responses to external factors, such as resource availability and climatic variations. Similar results were observed in *Odontotermes stercorivorus* (Truckenbrodt 1978) and *Cornitermes cumulans* (Torales et al. 1999).

According to Truckenbrodt (1978), variations in nymphal production between nests of similar sizes sampled over the same period may be more closely related to internal colony factors than to environmental conditions. Those factors can be related to colony age and include, for example, the maintenance of healthy reproductive royal couples and feedback mechanisms in the colony. Variations in the quality of microhabitats where nests are built should also be considered (Vasconcellos et al. 2015), as well as the fact that that larval production can compete with nymphal production (Soki and

Josens 1996); and mature colonies may temporarily interrupt the production of nymphs because of their high energy cost (Thorne 1983) or because of internal problems in the colony.

Intramonthly variations in the populations of most apterous and nymphal instars of *C. cyphergaster* occurred even among colonies with similar volumes. Considering the use of different colonies in the study, and the procedures applied in laboratory, certain levels of variation among populations are to be expected. Only worker and N4 populations were found to be significantly related to nest volume, demonstrating small differences from the results reported by Vasconcellos et al. (2007) and Rodrigues et al. (2018). Different from the present study, however, those authors evaluated only soldier and worker instars, and examined nests showing large variations in their volumes (0.09–56.8 L). In addition, some colonies did not have individuals of the nymphal line, even in months when a high production of fourth and/or fifth instar nymphs was recorded.

Despite these intramonthly variations, our results indicate that the differentiation of the nymphal line of *C. cyphergaster* is related to regional climatic cycles. Previous studies have found that *C. cyphergaster* swarmings are related to precipitation events, occurring during or at the end of the rains (Mill 1983; Moura et al. 2006a, 2011). In the present study, fifth instar nymphs were found in December and February, whereas alates were recorded only in February. Knowing that February was the month with the highest rainfall index in the region, this record coincides with the previously described pattern in which the differentiation of the fifth nymphal instar began approximately 2 months before the increase in the level of precipitation, during which alate differentiation and subsequent swarming occurred (Moura et al. 2011). The reduced number of alates, restricted to only one nest, indicates that the swarming peak was missed during the sampling of the present study.

The temporally limited production of the nymphal line was reaffirmed by the absence of early nymphal instars (N1, N2 and N3) in the months prior to the peak of precipitation (October and December), which should be related to a greater investment on last nymphal instars differentiation during this period. Moura et al. (2011) reported that only the fifth instar nymphs and alates varied in terms of presence/absence in the colonies of this species over 1 year. Although there was no significant difference, it was possible to observe a lower abundance of N4 in December, the same period when N5 differentiation occurred. In the present study, only the fourth instar of the nymphal line was recorded in all sampling months. This finding may indicate that this instar lingers for longer in the colonies, accumulating energy and awaiting the proper climatic moment to differentiate into fifth instar nymphs. Accurate data regarding the duration of nymphal instars of termites are still scarce; however, Kaiser (1956) noted that each nymphal stage in *Anoplotermes pacificus* lasts 14 days, except for the penultimate stage when development is arrested during the entire dry season. Thus, the continuous presence of N4 in colonies of *C. cyphergaster* can lead to reproductive security in the colony—if the queen dies or loses her ability to lay eggs, these nymphs can potentially replace the queen. Several studies have recorded nymphoid neotenics originating mainly from fourth or fifth nymphal instars in some species (Myles 1999; Barbosa et al. 2012; Haifig and Costa-Leonardo 2016).

Instars of the apterous line of *C. cyphergaster* were produced continuously throughout the year, but the populations of most instars varied between months. Continuous production of the apterous line and temporally limited production of the nymphal line have previously been observed in several Termitidae (Noirot 1961, 1969). The apterous population ranged from 25,980 to 129,032 individuals/nest, with workers being the most abundant individuals in the colonies—more than 60% of the population—highlighting the importance of this caste, which performs most functions in termite nests (Banerjee 1966). There was also substantial investment in the production of soldiers; because this species forages in exposed columns, so colony defense is a priority (Cunha et al. 2003). The mean ratio between these two instars (soldiers:workers) was 1:4.1, an intermediate result relative to that previously recorded for the species, e.g., 1:2.7 (Vasconcellos et al. 2007) and 1:4.5 (Cunha et al. 2003). According to Rodrigues et al. (2018), the presence of *I. microcerus* colonies can negatively affect the numbers of individuals and the soldier/worker proportions in *C. cyphergaster* colonies.

There was an increase in the proportion of workers in June and August, concomitant with a decrease in the proportion of larvae and a higher proportion of nymphs. This is possibly due to greater investment in the production of N4 in this period, in addition to early nymphal instars. The relative proportions between castes may fluctuate according to the colony's lifetime and seasonality, as has been previously observed in *Cubitermes severus* (Bodot 1969; Lepage and Darlington 2000). Apterous castes can vary in number due to several factors, such as in *Cubitermes speciosus*, which showed an increase in the population density of workers concomitant with increased precipitation (Soki and Josens 1996); in *Microcerotermes strunkii*, in which the proportion of soldiers increased during swarming time (Torales and Coronel 2004); and in *Odontotermes redemanni*, where both workers and soldiers were more abundant when there was an increase in nymph production (Banerjee 1966).

Workers and presoldiers of *C. cyphergaster* were more abundant in February, and soldiers were more abundant in April. In those same months, the early nymphal instars began to differentiate. Termite colonies may invest more in larvae, workers, and soldiers to restart the reproductive cycle (Thorne 1983; Torales and Coronel 2004), a time when the colony requires more immature individuals and greater amounts of food. During the rainy season, foraging events for *C. cyphergaster* occur more frequently, with a larger number of individuals, and mean consumption per event is higher (Moura et al. 2006a, b). Moura et al. (2006a, b) related these results to the need to accumulate energy to be used during the dry season, when alate production generally increases the colony biomass. Increased production of apterous castes, especially of workers, after the swarming time may result in an increased capacity of the colonies to obtain food in light of the energy needs of the colony generated by nymphal differentiation.

Queens were identified in 90% of all nests, but only one nest demonstrated polygyny. In contrast, multiple reproductives and high incidences of secondary reproductives have been reported in *C. cyphergaster* nests in Cerrado vegetation (Cunha and Brandão 2002). The difficulty encountered in finding kings in *C. cyphergaster* nests is related to the absence of a distinct royal chamber, as was indicated in a previous study (Moura et al. 2011). In this species, when the king is not identified at the time of collection, histological analysis of the gonads is necessary for differentiation between kings and dealates. Inquiline species were identified in 93% of the collected nests; *I. fur* was more common than *I. microcerus*, in contrast with the proportion recorded in *C. cyphergaster* nests in the Cerrado region, where *I. microcerus* was predominant (Cunha et al. 2003; Cristaldo et al. 2012). Other studies have reported the presence of *Inquilinitermes* spp. in 70% of *C. cyphergaster* nests in the Cerrado (Cristaldo et al. 2012) and in 75% of nests in the Caatinga region (Vasconcellos et al. 2007).

Constrictotermes cyphergaster actively participates in nutrient cycling and consumption of organic matter in the Caatinga region (Vasconcellos et al. 2007; Moura et al. 2008). This is the first study to quantify all of its instars, contributing to greater understanding of the numerical dynamics within colonies and the ecological importance of the castes of this species. The intramonthly variations in the composition of the colonies of *C. cyphergaster* indicate that, although they are mature colonies exposed to the same regional climatic regime, they may not be synchronous in the production of nymphal instars, possibly due to the influence of several intrinsic and/or environmental factors. Nevertheless, our results suggest that precipitation exerts an important influence on the annual cycle of differentiation of *C. cyphergaster* instars and that the proximity of the swarming event promotes the differentiation of late nymphal instars (N5 and A), with subsequent increases in the differentiation of the apterous instars and emergence of the early nymphal instars. The presence of fourth instar nymphs in all the sampled months may indicate a longer duration of this nymphal stage, representing an energy-related strategy, a strategy of fast production of fifth instar nymphs and alates; or a contribution of nymphoid secondary reproductives. Future studies of the duration of nymphal instar stages and factors influencing differentiation are necessary to improve understanding of the reproductive strategies of Neotropical termites.

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