RESEARCH ARTICLE

Termitarium volume as a determinant of invasion by obligatory termitophiles and inquilines in the nests of *Constrictotermes cyphergaster* (Termitidae, Nasutitermitinae)

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Abstract A range of organisms can be found inside termite nests where the degree of association can vary from facultative to obligatory dependence. Studies of the dynamics of nest invasion are still unresolved, so how and when cohabitants enter termite nests remain open questions. This study analyzed one specific aspect of the dynamics of termite nest invasion by obligatory termitophiles and inquilines, i.e., whether cohabitants were more likely to invade a nest when it reached a critical nest size. We collected 36 *Constrictotermes cyphergaster* nests of different sizes and sampled their cohabitant fauna. Our results indicated that the invasion of *C. cyphergaster* nests by obligatory termitophiles and inquilines was dependent on nest size. There appeared to be a critical nest size above which nests were more prone to invasion. Above this size, there was a significantly higher likelihood of finding obligatory cohabitants. Termitophile species were observed in nests ≥2.2 L, whereas inquiline species were only occur in nests ≥13.6 L. This may indicate that the obligatory cohabitants studied here did not occupy *C. cyphergaster* nests at random and that they were dependent on features that made these nests suitable for cohabitation, which are linked to colony development.

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Introduction

Nesting is a characteristic behavior of many invertebrate and vertebrate animals. Nest structures can provide organisms and their offspring a suitable (thermoregulated) and protected environment (Turner, 2000; Jones and Oldroyd, 2007; Hansell, 2007), while in some cases they also provide a place for food storage (Noirot and Darlington, 2000). However, organisms that live in nests for long periods may by troubled by cohabitation or nest usurpation. Examples include, but are not restricted to, birds (Kronland, 2007), salamanders (Harris et al., 1995), fishes (Mills and Reynolds, 2002), and social insects (Ortolani et al., 2008; Tsuneoka, 2008). Nest invaders have been reported to be parasites, commensals, mutualists, or a combination of these (Hughes et al., 2008).

In the case of social hymenopterans, the mechanisms and dynamics of nest invasion, as well as the interactions between host species and cohabitants, have been well investigated (e.g., Rettenmeyer et al., 2011). In termites, there have been plenty of reports on the identity of nest invaders, but studies on the mechanisms, dynamics, and interactions of nest invasion are still ongoing (but see Redford, 1984; Cunha et al., 2003; Costa, 2005; Carrijo et al., 2012).

Organisms that have been found inside termite nests include birds (Brightsmith, 2000), bats (Dechmann et al., 2004), and a range of arthropods (Cunha and Brandão, 2000; Haddad and Dippenaar-Schoeman, 2002; de Visser et al., 2008; Costa et al., 2009; Carrijo et al., 2012), but especially beetles (Costa and Vanin, 2010), ants (Holt and Greenslade, 1979; Diehl et al., 2005), and other termite species (Redford,

1984; Cunha et al., 2003; Cunha and Morais, 2010; Darlington, 2012).

In general, termite species that are found in other termite nests are known as inquilines and they can be categorized into two types: (1) obligatory inquilines: species that closely interact with the host and that have lost their nest-building ability; (2) facultative inquilines: species that retain their nest-building abilities but that can also inhabit nests built by other termite species (Mathews, 1977). Other animals, mainly insects, which are associated with termite nests are known as termitophiles (Kistner, 1990). Some of these species can also be categorized as "obligatory" provided they spend at least part of their developmental cycle exclusively within termite nests, e.g., some species of Staphylinidae. Others are not restricted to termite nests, so they fall into the "facultative" category.

Studies of termite cohabitation have revealed a positive relationship between nest size and the number of inquiline species (Domingos, 1983; Redford, 1984; Costa, 2005; Cunha and Morais, 2010) and termitophile species (Carvalho, 2005). To the best of our knowledge, no previous studies have addressed the key aspects of the dynamics of nest invasion. Thus, how and when inquilines and termitophiles enter termite nests are questions that remain open to investigation. In this paper, we focus on one specific aspect of the dynamics of a termite nest invasion by obligatory inquilines and termitophiles, i.e., whether there is a critical nest size above which cohabitants are more likely to invade nests. We addressed this question because it is crucial to future research on the biology of termite cohabitants. If invasion occurs after the nest achieves a specific size, cohabitation must be linked to the host colony's development, and this would allow a large range of hypotheses to be tested. In contrast, the absence of a critical nest size for the establishment of cohabitants must indicate that nest invasion can occur irrespective of colony development, which would lead to completely different research questions. As a model for cohabitation, we used the termite builder *Constrictotermes cyphergaster* Silvestri, 1901 (Termitidae: Nasutitermitinae), its obligatory inquiline *Inquilinitermes microcerus* Silvestri, 1901 (Termitidae: Termitinae), and four species of Coleoptera: Staphylinidae obligatory termitophiles, i.e., *Corotoca melantho* Schiødte, 1853, *Termitocola silvestrii* (Wasmann, 1902), *Spirachtha eurymedusa* Schiødte, 1853, and *Termitoiceus* sp. nov.

Materials and methods

Terms definition

The term "colony" will be used to refer to the biological structure of termite individuals living together, which includes the reproductive pair, workers, soldiers, nymphs (semi-mature young), larvae (termitological jargon for recently hatched young), and eggs. This is intended to be distinct from the "nest", which refers to the physical structure built by termites. "Inquiline" refers to a termite species that establishes its colonies within a nest previously built by other termite species. Here, "termitophile" will refer to four staphylinid species found inside the study nests. The inquiline and termitophile species investigated in this study are considered to be "obligatory" cohabitants because they are not found outside termite nests.

Builder species

Constrictotermes cyphergaster is a common termite species in Brazil, Paraguay, Bolivia, and Northern Argentina (Mathews, 1977; Godinho and Lins, 1989; Moura et al., 2006a). The nest volume and population size or biomass have a linear positive correlation (Vasconcellos et al., 2007). *Constrictotermes cyphergaster* forages at night in exposed columns (Moura et al., 2006a) and feeds mainly on wood in different stages of decomposition, on the surface of the bark of live trees (Moura et al., 2006b), and on lichens (Bourguignon et al., 2011); their consumption per nests has been estimated to be 44.5 kg of plant organic material/ha-year, corresponding to 13 % of the annual production of wood litter (Moura et al., 2008). The nymphal line comprises one larval instar, followed by five nymphal instars, and alates. The apterous line includes two larval instars, followed by workers, presoldiers and soldiers. Both workers and soldiers were shown to be monomorphic, having only one instar each and consisting of only male specimens (Moura et al., 2011). An average of 4.5 workers per soldier has been recorded by Cunha et al. (2003) in *C. cyphergaster* nests.

In the study site, this species builds fragile nests with weak walls made from a thin layer of soil. However, this species has been observed to build nests with hard clay walls in other Brazilian regions (DeSouza, pers. obs.). Nests are often built on trees, although rocks are also used as nest attachments (Moura et al., 2006b; Vasconcellos et al., 2007). In some Brazilian regions, incipient nests of this species are epigeous whereas mature nests are arboreal (Vasconcellos et al., 2007; Cristaldo and DeSouza, pers. obs.). Bezerra-Gusmão et al. (2009) observed that in "Caatinga" (dry shrubland) biome, this species builds polycalic nests. According to Mathews (1977), the interior of the nest consists of fairly thin-walled irregular cells with a gray/buff-colored lining of fecal origin; these cells are large near the outside of the nest but smaller towards the center; they interconnect by small termite-sized holes and do not lead into each other like the much more convoluted galleries of *Nasutitermes* nests. The nest population can be

found all over the nest (Cunha et al., 2003), but the major part is concentrated in the nest core (Cristaldo, pers. obs.). There is no distinct royal cell inside the nest. The royal pair and the eggs are found close together, in the inner part of the nest, near the stem of the support tree, where the walls are thicker and compacted but they also can found hiding in the depression of the bark of the tree (Cunha and Brandão, 2002). Active nests can harbor many cohabitants, including one of two obligatory inquilines, i.e., *Inquilinitermes microcerus* and *Inquilinitermes fur* Silvestri, 1901, and a large number of termitophiles, mainly Staphylinidae (Coleoptera) (Mathews, 1977; Godinho and Lins, 1989; Cunha and Brandão, 2000; Cunha et al., 2003; Vasconcellos et al., 2007). The parts of the nests occupied by cohabitants contain a mass of dark organic material (Mathews, 1977); however, the Staphylinidae species are also found in the middle parts of the nest in close association with the colony (Cristaldo and Rosa, pers. obs.).

Inquiline species

Inquilinitermes spp. are medium to small termite species occurring in South America where they are obligate inquilines in the arboreal nests of *Constrictotermes* spp., probably deriving their food from the nest material (Mathews, 1977). *Inquilinitermes microcerus* is only found in *C. cyphergaster* nests, where their galleries are of dark grey material, distinct from the *C. cyphergaster* nests (Mathews, 1977). The size of *I. microcerus* colonies are smaller than the builder termite, varying from 160 to 10,840 individuals (Cunha et al., 2003). The colonies are restricted to certain portions of the nest, usually close to its core (Cunha et al., 2003).

Termitophile species

Coleoptera, mainly Staphylinidae, have more termitophiles forms than any other group, perhaps more than all other groups put together (Seevers, 1957; Kistner, 1969, 1982, 1990; Grassé, 1986; Jacobson et al., 1986). Despite the large number of reports, there is surprisingly little in the literature about their biology and how they are collected (Kistner, 1969, 1990). The Aleocharine subfamily is by far the most successful group of cohabitant in nests of social insects, especially in ant and termite nests (Seevers, 1957, 1965 and references). One of the most extraordinary features of termitophile Staphilynidae is the ability of many species to achieve physogastry. Sometimes, this physogastry is followed by subsequent secondary sclerotization of some or all of the expanded membrane. This is a feature of the Corotocini tribe (Jacobson et al., 1986), here represented by *Corotoca melantho*, *Spirachtha eurymedusa* and *Termitoiceus* sp. nov. (Seevers, 1957; Kistner, 1982; Jacobson et al., 1986; Kistner, 1990). The abdomen of some Coro-

tocini can be further modified to include the presence of several pairs of membranous lobes that look like legs (*S. eurymedusa*) and according to Kistner (1979) this feature is used by beetles to integrate themselves into the termite society. Another interesting feature is the viviparity in *Corotoca*, and perhaps in *Spirachtha* (Seevers, 1957). All these features allow these species to engage close relationships with their termites hosts, enough to be classified as "True Guests" (Kistner, 1979). These three Corotocini species were found only in *Constrictotermes* spp. nests, so far (Seevers, 1957; Fontes, 1977; Jacobson et al., 1986). Although all Corotocini termitophiles exhibit some degree of physogastry, the members of the tribe Termitonannini (here represented by *Termitocola silvestrii* (Wasmann 1902)) in the majority of cases are limuloid (Seevers, 1957; Kistner, 1969). *Termitocola silvestrii* have been found associated exclusively with *C. cyphergaster* (Seevers, 1957; Kistner, 1979; Cunha and Brandão, 2000).

Study site

The study was conducted in the "Cerrado" (an environment that is ecologically but not floristically similar to savanna) near Sete Lagoas town (19°27′S, 44°14′W), in the state of Minas Gerais, southeastern Brazil. The altitude varies from 800 to 900 m above sea level at the study site. According to Köppen's classification, the study area lies in Aw (equatorial with dry winter) climate (Kottek et al., 2006). The total accumulated rainfall during 2008 was 1,469 mm while the mean monthly temperature varied from 16.4 to 29.1 °C (Agritempo, 2009). In 2011, the rainfall was 695.3 mm while the mean monthly temperature varied from 16.9 to 29.3 °C (Agritempo, 2012). Natural fire is recurrent in the entire Cerrado and at this particular site. The native biota is considered fire-dependent or at least fire-tolerant (Coutinho, 1990; DeSouza et al., 2003).

Sampling

To test the effect of nest size on the presence of obligatory cohabitants in *C. cyphergaster* nests, we removed 36 nests of different sizes from trees, which were measured and dissected thoroughly to search for cohabitants. The choice of nests was made arbitrarily, in an attempt to sample nests in a continuous range of volume that was manageable for our aim. All cohabitants found in the nest (including the resident builders) were collected with entomological forceps, placed in 80 % alcohol, labeled, and taken to the laboratory for identification. Termites were identified to species level, following Mathews (1977) and specific literature referred to by Constantino (2002). Identifications were confirmed by comparison with the collection of the Isoptera Section of the Entomological Museum of the Federal

University of Viçosa (MEUV), where voucher specimens were deposited. Termitophiles were sent to specialists for identification to the lowest taxonomic level possible.

Sampling was conducted in July 2008 and May 2011, during daylight from 7:30 a.m. to 2:00 p.m. Only undamaged arboreal nests were inspected.

Nest volumes were recorded as suitable descriptors of size. Volumes of termite nests are usually calculated with a formula for the most approximate geometric form (see Coles, 1980; Domingos, 1983; Cunha et al., 2003). However, the wide geometric diversity of termite nest forms (Negret and Redford, 1982), coupled with frequent irregularities in shapes, suggest that this type of approximation will always be prone to significant errors. To minimize this error, nests volumes were calculated based on the Cavalieri principle, by summing up the volumes of several superimposed cylindrical cross sections into which the nest was visually decomposed and the volumes of the hemispherical caps at both ends of the nest (see Fig. 1) in a manner similar to that described in Rodrigues et al. (2004). To improve accuracy, in cases where the nest encompassed its supporting tree trunk, the volume of the trunk was also estimated and subtracted from total estimated nest volume.

Data analysis

The data were analyzed by logistic regression, a form of generalized linear modeling (GLM) under binomial errors, which is suitable for modeling the effects of one or more continuous or categorical explanatory variables on a binary response variable (Logan, 2010). We aimed to determine the effects of the continuous explanatory variable "nest volume" (x-var) on the binary response variable "presence/absence of cohabitants" (y-var).

Logistic models differ from traditional linear regression models because they do not describe the rate of change in the response variable with change in the explanatory variable. Our logistic model describes the likelihood that a given cohabitant would be present in a termitarium of a given size, thereby establishing the likelihood of a relationship between the response and the predictor. A linear model would be inappropriate in this case because it is not bounded by logical probability limits of 0 and 1.

We used a GLM to test whether a sigmoid curve with an asymptote towards 0 and 1 at the y-axis (i.e., a logistic model) fitted the data better than a horizontal line parallel to the x-axis, which intercepted the y-axis at 0.5 (i.e., equal chances of presence and absence). The choice of this sigmoid function (H_1) over a horizontal line (H_0) would establish a relationship between nest volume and cohabitation and also show that there is a critical nest volume above which cohabitants are more likely to be found in the nest (i.e., likelihood >50 %). This critical size would correspond to the inflection point of the sigmoid curve. The likelihood of housing termitophiles/inquilines is related to the nest volume according to the logistic equations:
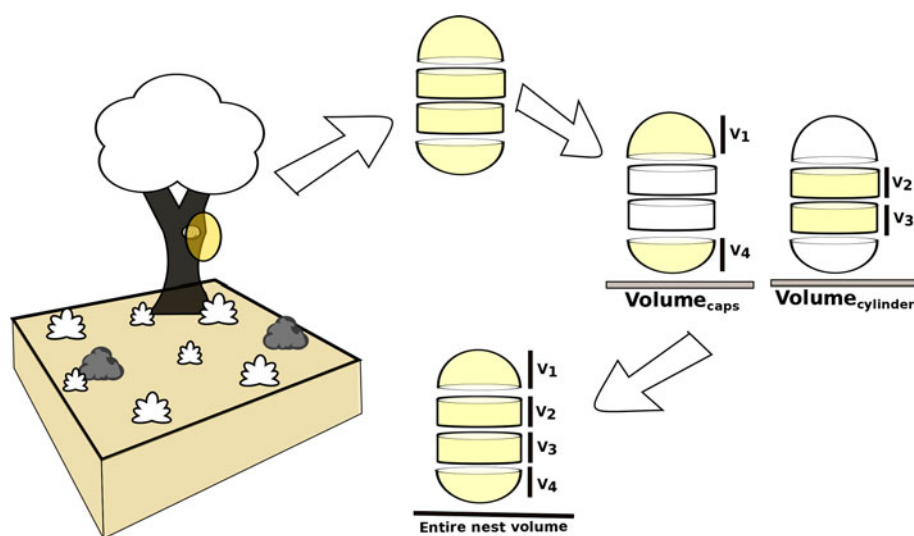
(a) termitophiles
$$\log(p/q) = -0.4608 + 0.2106v$$

(b) inquilines
$$\log(p/q) = -3.1265 + 0.2296v$$

where (p/q) is the odds ratio of housing/not housing a guest and v is the nest volume, given in liters (L).

Analyses were performed in R (R Development Core Team, 2011), followed by residual analysis to check the suitability of the error distribution and model fitting.

Fig. 1 Nest volumes were calculated by summing the volumes of cylinders and hemispherical caps into which the nest was visually decomposed

Results

Of the 36 termite nests built by *C. cyphergaster*, 21 (70 %) contained inquilines and termitophiles, nine (25 %) contained only termitophiles, while six (16.7 %) contained no cohabitants. There were two species of inquilines, i.e., *I. microcerus* and *Heterotermes longiceps* Snyder, 1924 (Rhinotermitidae: Heterotermitinae). Of these, only the first is known to be an obligatory inquiline. *Heterotermes longiceps* was found in a single nest alongside *I. microcerus* and staphylinid termitophiles. Among the termitophiles, there were four Staphylinidae species, i.e., *Corotoca melantho*, *Termitocola silvestrii*, *Spirachtha eurymedusa*, and *Termitoiceus* sp. nov.. *Corotoca melantho* was the most frequent and it was present in all 30 nests containing termitophiles, while *T. silvestrii* was found in eight nests, *S. eurymedusa* in three nests and *Termitoiceus* sp. nov. in only one nest. Nest volumes ranged from 0.42 to 51.30 L with an average of 19.49 L. The distribution of termitophile and inquiline species along the nest sizes was summarized in the Supplementary Material 1. The nest size was correlated with the presence of termitophile ($\chi^2 = 20.756$, $df = 35$, $p < 0.001$) and inquiline species ($\chi^2 = 21.294$, $df = 35$, $p < 0.001$). The analyses indicated a critical
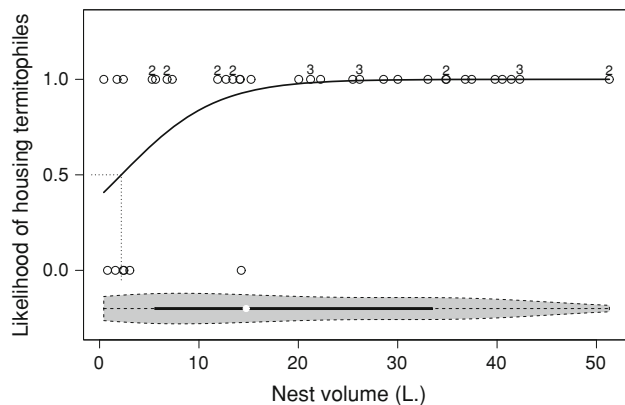

Fig. 2 Effect of nest volume on the presence of four species of staphylinid termitophiles in *Constrictotermes cyphergaster* nests ($\chi^2 = 20.756$, $df = 35$, $p < 0.001$). Sete Lagoas, MG, Brazil, 2008–2011. Logistic regression with Generalized Linear Models under binomial errors and logit link function. On *y*-axis, *0* indicates the absence of termitophiles whereas *1* indicates their presence. Each *dot* refers to a single termitarium. At the *upper set of dots* (i.e., at $y = 1$) *superscript digits* indicate the number of termitophile species inhabiting that given termitarium; absence of digits indicates a single termitophile species. Likelihood of housing termitophile species is related to nest volume according to the logistic equation: Log $(p/q) = -0.4608 + 0.2106v$; where (p/q) is the odds ratio of housing/not housing termitophiles and *v* is the nest volume, given in liters (L). The critical nest volume above which the likelihood of housing termitophiles exceeds 50 % is represented by a *dotted line* (2.2 L). At the *bottom*, a violin plot depicts for all inspected nest volumes, the median (*white dot*) and its associated first and third quartiles (*black bar*) as well as the density trace (*grey area*)
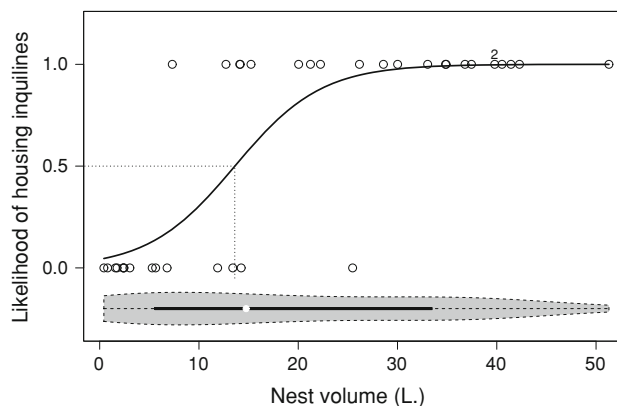

Fig. 3 Effect of nest volume on the presence of *Inquilinitermes microcerus* (Isoptera: Termitidae) inquiline in *Constrictotermes cyphergaster* (Isoptera: Termitidae) nests ($\chi^2 = 21.294$, $df = 35$, $p < 0.001$). Sete Lagoas, MG, Brazil, 2008-2011. Logistic regression with Generalized Linear Models under binomial errors and logit link function. On *y*-axis, 0 indicates the absence of inquilines whereas *1* indicates their presence. Each *dot* refers to a single termitarium. At the *upper set of dots* (i.e., at $y = 1$) *superscript* digits indicate the number of inquiline species inhabiting that given termitarium; absence of digits indicates a single inquiline species. Likelihood of housing inquiline species is related to nest volume according to the logistic equation: Log $(p/q) = -3.1265 + 0.229v$; where (p/q) is the odds ratio of housing/ not housing inquilines and *v* is the nest volume, given in liters (L). The critical nest volume above which the likelihood of housing inquiline exceeds 50 % is represented by a *dotted line* (13.6 L.). At the *bottom*, a violin plot depicts for all inspected nest volumes, the median (*white dot*) and its associated first and third quartiles (*black bar*) as well as the density trace (*grey area*)

volume above which cohabitants were more likely to be found in *C. cyphergaster* nests, and this volume was smaller for termitophiles than inquilines. Termitophiles were more likely to be found in nests $\geq 2.2 \pm 0.10$ L (Fig. 2) whereas inquilines were more likely to be found in nests $\geq 13.6 \pm 0.07$ L (Fig. 3).

Discussion

Our results suggest that the invasion of *C. cyphergaster* nests by obligatory termitophiles and inquilines was dependent on nest size (Figs 2, 3). There appeared to be a critical nest size above which nests were more prone to invasion, and above this size there was a significant increase in the likelihood of finding obligatory cohabitants in *C. cyphergaster* nests.

Several reports have shown a positive correlation between nest size and the richness and abundance of cohabitants in termite nests, including nests built by *Armitermes euamignathus* Silvestri, 1901 (Termitidae: Syntermitinae) (Domingos, 1983), *C. cyphergaster* (Cunha et al., 2003), *Cornitermes cumulans* Kollar in Pohl, 1832 (Termitidae: Syntermitinae) (Redford, 1984; Costa, 2005; Carvalho, 2005), *Cornitermes snyderi* Emerson in Snyder, 1949

(Termitidae: Syntermitinae), and *Syntermes grandis* Rambur, 1842 (Termitidae: Syntermitinae) (Cunha and Morais, 2010). The novel finding of our study was that, at least for the cohabitants studied here, this correlation did not hold linearly for all nest sizes, while it dropped to zero cohabitants in nests below a specific size. This may indicate that, rather than randomly invading nests, inquilines and termitophiles can only settle in suitable nests and this suitability is linked to the nest size. Previous studies do not mention this kind of relationship but, rather, report (in some cases only suggest) a linear one, even when dealing with the same termite host species, *C. cyphergaster*. This seems to be more linked to the sampling and analytical procedures than to any biological reason. First, some authors (e.g., Domingos, 1983; Redford, 1984) do not present a formal statistical test of the alleged positive correlation between nest volume and termitophile/inquiline abundance and richness. Rather, they derive this pattern from field observation and accumulated experience. Second, logistic relationships as the one described here need data points referring to "zero values", i.e., termitaria holding only the builder termite and no inquilines or termitophiles, but some authors (e.g. Cunha et al., 2003; Costa, 2005; Carvalho, 2005) focused their work exclusively on guest-bearing termitaria. Third, even when considering these non-invaded termitaria, authors (e.g. Cunha and Morais, 2010) do not explicitly model invader presence as a sigmoidal function of nest volume/size.

Of the various hypotheses that might explain our result, the simplest one is related to the incremental increase in free space as a nest grows. In termite nests, linear and sublinear correlations are known to exist between nest size and its termite builder population (Josens and Soki, 2010). Specifically for *C. cyphergaster* nests, this correlation is linear (Vasconcellos et al., 2007; Josens and Soki, 2010) but their population is bound to fluctuate seasonally (Lepage and Darlington, 2000; Moura et al., 2006b) such that some parts of the nest may remain unoccupied by the resident builders, as it happens with other termite builders (Noirot and Darlington, 2000). It is conceivable that such spaces would be larger and more frequent in bigger nests compared with smaller nests, such that some of these spaces may be largely unpatrolled above a certain nest size. Invaders might therefore more frequently enter in such unoccupied spaces in the case of larger nests, leading to the sigmoid function observed in Figs. 2, 3. This might apply to any free space in nests and also to a mass of dark organic material found in the nests of *C. cyphergaster*, which is known to house inquilines and termitophiles (Mathews, 1977).

A deeper consideration of our results showed that termitophiles and inquilines differed substantially in terms of the critical nest size correlated with their presence in *C. cyphergaster* termitaria. Termitophilous staphylinids were more likely to occupy nests that were on average three times smaller than the nests where *I. microcerus* inquilines also occurred. If nest size correlated with nest age in such a species (as it seems to be), one could safely assume that staphylinids were able to invade *C. cyphergaster* nests earlier than *I. microcerus*. This might lead to hypotheses that link the degree of colony maturation to invasion by cohabitants. Termitophile staphylinids here reported seem not to need to be hosted by a fully mature termite colony, but appear to only require that the colony is established and functional. Among them, *C. melantho* and *S. eurymedusa* present mimetic physogastry and are well accepted by their hosts, being licked and fed by termite workers (Costa and Vanin, 2010; Grassé, 1986). It seems therefore that, as long as a colony holds enough workers, such staphylinids would be able to establish themselves as termitophiles. On the other hand, the limuloid body of *T. silvestrii* seems to obstruct interactions, as it would ease hiding and offer a few contact points a termite could grab if trying to attack the beetle. It appears that, unlike the previous two termitophiles which possess morphogical features enabling interactions with their host, *T. silvestrii* traits help to minimize such contacts. This could mean that *T. silvestrii* does not actually need the termite colony itself but it is linked to some (unknown) feature of the termitarium. If this is so, *T. silvestrii* would be able to invade a nest as soon as it attains some minimal set of typical traits. Associations of organisms with termitaria rather than termites are not a novelty, and are known as "termitariophily", a term coined by K. Berg as early as 1900 (Araújo 1970, p. 536). In short, a termite nest would be suitable to these staphylinids as soon as it attains a size enough to hold (1) a minimum critical amount of workers to keep interactions stable or (2) a minimal set of features which characterizes it as a proper termite nest. As these conditions are not necessarily linked to full colony maturation, small young nests may be suitable to invasion by such beetles, and this would explain the differences in patterns recorded in Figs. 2, 3.

Inquilinitermes microcerus seemed to be much more dependent on the maturity of the host colony, because they were found in larger (and possibly older) nests than those occupied by staphylinids. One particular feature of *C. cyphergaster* nests suggested a link between their maturity and the likelihood of their invasion by *I. microcerus*. These nests originate in the soil, where they first develop an epigeous structure that houses the colony while an arboreal unit is built. When an arboreal unit reaches around 7 L in size, the royal couple moves in after migrating from the epigeous unit, which is then abandoned (Vasconcellos et al., 2007). Thus, if *I. microcerus* preferably occupies *C. cyphergaster* arboreal nests measuring ≥13.6 L, as depicted in Fig. 3, they will necessarily invade nests that have been housing a royal couple for a long period and such nests might possibly

be fully mature. This hypothetical interdependence between nest maturity and invasion by *I. microcerus* remains open to investigation. However, some evidence seems to support this hypothesis, because *Inquilinitermes* sp. have been seen entering *C. cyphergaster* nests through structures built to release their alates (M.A. Bezerra-Gusmão, pers. comm.) and alates are only released from mature nests.

Clearly, all these hypotheses require further testing and we present them as possible explanations to highlight research pathways that might lead to a better understanding of the phenomenon of cohabitation in termite nests. These hypotheses appear to follow naturally from the study reported here, because our focal inquilines and termitophiles did not occupy *C. cyphergaster* nests at random. Instead, nest invasion was apparently dependent on features that make these nests suitable for cohabitation, which may be linked to colony development.

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