



RESEARCH ARTICLE - TERMITES

Survivorship and Walking Behavior of *Inquilinitermes microcerus* (Termitidae: Termitinae) in contact with host workers and walls from host nest

JS CRUZ¹, PF CRISTALDO^{1,2}, JJM SACRAMENTO¹, MLR CRUZ^{1,3}, DV FERREIRA^{1,3}, APA ARAÚJO¹

1 - Laboratório de Interações Ecológicas, Departamento de Ecologia, Centro de Ciências Biológicas e da Saúde, Universidade Federal de Sergipe, São Cristóvão-SE, Brazil

2 - Programa de Pós-Graduação em Agricultura e Biodiversidade, Universidade Federal de Sergipe, São Cristóvão-SE, Brazil

3 - Programa de Pós-Graduação em Ecologia e Conservação, Universidade Federal de Sergipe, São Cristóvão-SE, Brazil

Article History

Edited by

Og DeSouza, UFV, Brazil

Received	31 May 2017
Initial acceptance	31 May 2017
Final acceptance	09 July 2017
Publication date	30 March 2018

Keywords

Inquilines, Isoptera, symbiosis, behavior.

Corresponding author

Ana Paula A. Araújo
 Laboratório de Interações Ecológicas
 Departamento de Ecologia
 Centro de Ciências Biológicas e da Saúde
 Universidade Federal de Sergipe (UFS)
 Avenida Marechal Rondon, s/n - Rosa Elze
 CEP 49100-000, São Cristóvão-SE, Brasil.
 E-Mail: anatermes@gmail.com

Abstract

Constrictotermes sp. nests are frequently inhabited by colonies of *Inquilinitermes microcerus*. In this association, *I. microcerus* colonies usually establish their colonies spatially isolated from *Constrictotermes* colonies. Here, we investigated whether the apparent spatial isolation of *I. microcerus* colonies in *Constrictotermes* nests should be related to their needs (e.g. feeding) in relation to the central part of the nest or to a possible stress provoked by the presence of the host. For this, survival and walking behavior bioassays were performed to test the hypothesis that the survivorship of inquilines is: (i) reduced in the presence of host, mainly of those from different nests, (ii) increased in contact with inner walls compared with external walls; and that the distance walked and walking velocity of inquiline is: (iii) increased in the presence of the host and (iv) reduced in contact with the internal walls compared with external walls of host nest. The mean time to death of inquiline workers is lower in contact with host (independently from the same or different nest) compared with control and the mean time to death of inquiline workers is lower in contact with external walls of host nest compared with control group and the inner walls. The distance walked and walking velocity of inquiline workers in contact with their hosts (from the same or different nest) did not differ from control, however, these parameters were reduced when workers were in contact with inner and external walls compared with control. In general, our results showed that *I. microcerus* adopt behavioral strategies to avoid perception by its host.

Introduction

A range of species lives in close associations (*i.e.* symbiosis) (Dimijian, 2000; Redman et al., 2001; Duarte et al., 2014). The maintenance of these associations should require characteristics that allow involved species to deal with each other. Nests of social insects (*e.g.* wasps, bees, ants and termites) allow the maintenance of homeostasis (Noirot & Darlington, 2000) and show a space free of enemies, which provides greater longevity to their colonies. On the other hand, these same characteristics also favor the use of such structures

by symbionts species (see Hughes et al., 2008). Colonies of social insects, stand out in relation to the great diversity of symbionts that cohabit their nests, including parasites, mutualists and commensal species (Hughes et al., 2008).

Termite nests, for example, can house a range of species, such as vertebrates (Brightsmith, 2000; Dechmann et al., 2009) and invertebrates (Cunha & Brandão, 2001; Costa et al., 2009), called as termitophilous. Among these cohabitants, other termite species than that building the nest are included, which are called inquilines (Redford, 1984). Some inquiline species are obligatory, since they do not have the ability to



build their own nests and depend intrinsically of the host nest for its survivorship. These examples are found in species of the genus *Inquilinitermes* Mathews, 1977 (Termitidae: Termitinae) (e.g. *I. fur*, *I. inquilinus* and *I. microcerus*), which inhabit nests of *Constrictotermes* sp. (Mathews, 1977) and in *Serritermes serrifer* (Hagen & Bates, 1858) (Serritermitidae), which is obligatory inquiline of *Cornitermes cumulans* (Emerson & Krishna, 1975) (Termitidae: Syntermitinae). Differently from observed in Hymenoptera, the high incidence of cohabitation in termite nests is intriguing (Campbell et al., 2016; Marins et al., 2016). Like other social insects, in termites, colonies are able to recognize nestmate from non-nestmates, and also invest energy in the production of a specific caste to nest defense (Šobotník et al., 2008).

Since obligatory inquilines have a closer relationship with their hosts, they are expected to exhibit strategies that allow the temporal stability of this interaction. Although inquilines benefit from the nest of host colony, with no costs to constructing this structure (Jirošová et al., 2016), a series of evidences suggest that the inquiline seems to avoid (physically and chemically) its host. Studies have shown that the colonies of *Inquilinitermes* sp. are small in size relative to their host and they are usually found in the central parts of the host nest where individuals of host colony are rarely observed (Cunha et al., 2003). The aggregation of the inquilines in the central part of host nest may be related to the fact that they use this structure as a food resource (Mathews, 1977; Bourguignon et al., 2011; Cristaldo et al., 2012; Florencio et al., 2013; Barbosa-Silva et al., 2016). In addition, recent studies have shown evidence that individuals of *I. microcerus* can use chemical cues as a strategy to avoid conflicts, since they avoid chemical cues of the whole body, as well as the trail and alarm signals emitted by its host, *C. cyphergaster* (Cristaldo et al., 2014; 2016). However, in spite of such advances in the understanding this interaction, the final balance for both partners still need to be unraveled.

In the present study, we investigated whether the apparent spatial isolation of *I. microcerus* colonies in *Constrictotermes* sp. nests should be related to their needs (e.g. feeding) in relation to the central part of the nest or to a possible stress caused by the presence of host colony. For this, survival and walking behavior bioassays were performed to test the hypothesis that the survivorship of inquilines is: (i) reduced in the presence of host, mainly of those from different nests, (ii) increased in contact with inner walls compared with external walls; and that the distance walked and walking speed of inquiline is: (iii) increased in the presence of the host, mainly of those from different nests and (iv) reduced when in contact with the internal walls of nest compared with external walls.

Material and Methods

Study site and termite collection

Nests of *Constrictotermes* sp. ($N=9$) were collected in June 2016 at Campus Rural of Federal University of Sergipe,

in São Cristóvão (11° 01'S e 37° 12'O), Northeast, Brazil. The mean monthly precipitation and temperature in the region are 1.200 mm and 25 °C, respectively. According to Köppen classification, the climate is As' type (tropical with rainy winter and dry summer) (Pidwirny, 2011).

Collection consisted in the complete removal of nests from the field using spades and picks. The nests were taken to the laboratory and fragmented to verify the presence of inquiline colonies, which were found in three of the nests sampled. The identification of species was conducted in comparison with samples from the Isoptera Collection of University of Brasília (UnB), in which samples were deposited. The host was identified as *Constrictotermes* sp. (#10745 and 10747) and the inquiline as *Inquilinitermes microcerus* (#10746 and 10748).

Bioassays

Bioassays were conducted to check whether the survivorship and walking behavior of *I. microcerus* workers are affected by the presence of its host (from the same or different nest) and by the contact of inquilines with its host nest walls (inner and external walls).

Survival bioassays

To check whether the presence of host affects the survivorship of inquiline workers, the following treatments were established: (i) 20 inquiline workers alone (control), (ii) 10 inquiline workers with 10 host workers from the same nest (SH) and (iii) 10 inquiline workers with 10 host from different nest (DH). Bioassays were conducted in a Petri dish (Ø 9 cm x 1.5 cm [height]) covered with a filter paper.

To check whether the contact with host nest wall affects the survivorship of inquiline workers, the following groups were established: (i) 10 inquiline workers alone (control), (ii) 10 inquiline workers with 7 g of substrate from inner wall of host nest (IW) and (iii) 10 inquiline workers with 7 g of substrate from external wall of host nest (EW). Fragments from inner (easily recognized by its dark coloration) and external walls of host nest were ground with a mortar and pestle and sieved through a 6-mesh sieve. Then, the material was weighed in a precision balance and distributed at the bottom of the Petri dish on the filter paper. In control group, Petri dishes were covered only with filter paper.

For both survival bioassays, three replicates were performed per nest for each treatment, totalizing 27 replicates. The mean value of three replicates/nest were then used in the statistical analyses. Petri dishes were kept in a biochemical oxygen demand (BOD) incubator (25°C, without light) and the quantification of dead individuals was performed at one-hour intervals in the first day and then two-hours intervals until the death of all individuals.

Walking behavior bioassays

Walking behavior bioassays were conducted in a Petri dish (Ø 9 cm x 1.5 cm) covered with a black paper with the

same treatments described above. However, in this bioassay, only one individual was placed in the control group and nest wall treatments and two individuals in the host treatments. Three replicates were performed per nest and treatment, totalizing 27 replicates. The mean value of three replicates/nest were then used in the statistical analyses.

To allow the visualization and recorded of walking behavior of inquiline workers, individuals placed in the Petri dish were previously marked with a mixture of white gouache and glue (2:1) following the procedure described in Marins et al. (*in press*). The movement of individuals was video-recorded for 10 min using a camera (Panasonic SD5 Superdynamic - model WV-CP504), equipped with Spacecom lens (1/3 "3-8 mm) coupled to a computer. The distance walked and walking velocity were captured by EthoVision XT® software (version 8.5, Noldus Integration System, Sterling, VA) and the data were analyzed using the Studio 9 software (Pinnacle Systems, Mountain View, CA).

Statistical Analyses

To check whether survivorship of *I. microcerus* workers (*y-axis*) is affected by the presence of their hosts (from the same or different nests) or by the contact of host nest wall (inner or external wall), data were submitted to Survival Analysis using Weibull distribution. The mean time to death of all individuals in the Petri dish was calculated in each treatment \times nest and then, data were submitted to Analysis of Deviance (ANODEV).

To check whether the distance walked (mm) and the walking velocity (mm/s) of inquiline workers (*y-axis*) is affected by the presence of their hosts (from the same or different nests) or by the contact of host nest wall (inner or external wall), data were submitted to Analysis of Deviance (ANODEV).

All analyses were performed in the R statistical software (R Development Core Team 2015) using Generalized Linear Modelling (GLM) followed by residual analyses to check the suitability of distribution choice. Statistical simplification among treatments was performed via *t* test using *multcomp* package.

Results

Survival bioassays

The survivorship of *I. microcerus* workers was significantly lower in the treatments with presence of host than in the control ($F_{2,6} = 6.905$, $P = 0.027$; Fig 1A). However, no significant differences in the mean time to death of inquilines was observed in the treatments with host from same or different nests ($P = 0.65$).

Inquiline workers in contact with external wall of host nest (EW) showed a lower mean time to death compared with inquiline workers in contact with the inner wall of host nest (IW) and with control (inquiline workers alone) ($F_{2,6} = 28.070$; $P < 0,001$; Fig 1B). Control and inquiline workers in contact with the inner wall of host nest (IW) did not show significant differences between them ($P = 0.83$).

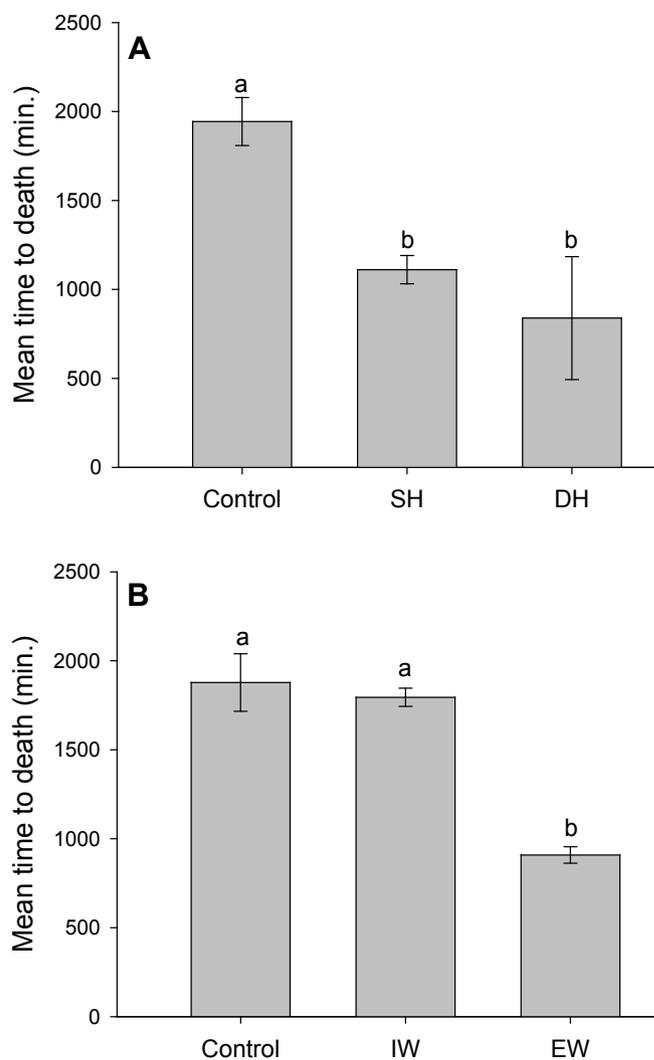


Fig 1. Survival of *Inquilinitermes microcerus* workers in different treatments. A) Control (inquilines workers alone), SH (inquiline workers with host workers from the same nest), DH (inquiline workers with host workers from different nest; B) control (inquiline workers alone), IW (inquiline workers in contact with inner wall of host nest), EW (inquiline workers in contact with external wall of host nest). Different letters in each graphic indicates significant difference among treatments.

Walking behavior bioassays

Most representative trails of *I. microcerus* workers in all treatments are showed in Fig 2.

The presence of host (from same or different nest) did not affect significantly the distance walked ($F_{2,6} = 1.13$, $P = 0.32$) and the walking velocity ($F_{2,6} = 0.19$, $P = 0.82$) of *I. microcerus* workers.

The distance walked ($F_{2,6} = 7.31$, $P < 0.001$) and the walking velocity ($F_{2,6} = 0.654$, $P = 0.02$) of inquiline workers were significantly reduced when in contact with host nest walls (inner or external) compared with the control group (Fig 3A-B). However, there were no significant differences in the distance walked and the walking velocity of inquiline workers in contact with the inner or external walls of host nest ($P = 0.10$).

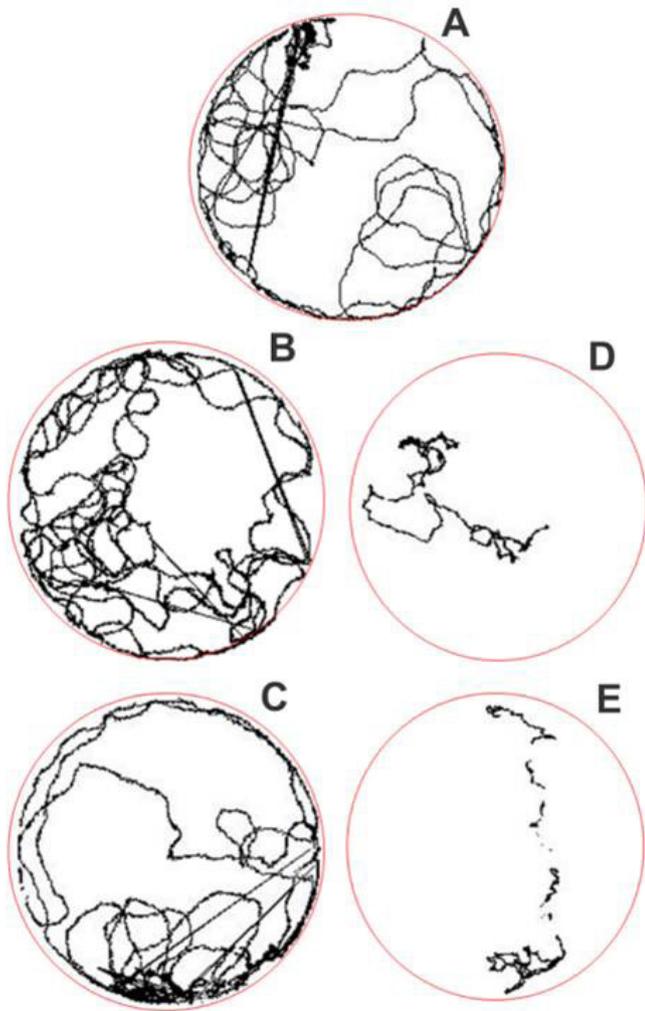


Fig 2. Most representative trails of *Inquilinitermes microcerus* workers in the following treatments: A) inquiline workers alone, B) inquiline workers with host workers from the same nest, C) inquiline workers with host workers from different nest, D) inquiline workers in contact with substrate from the inner wall of host nest and E) inquiline workers in contact with substrate from the external wall of host nest.

Discussion

In the present study, we investigated how the presence of the host species (*Constrictotermes* sp.) as well as the contact with host nest wall can modulate the survivorship and the walking behavior of its obligatory inquiline *I. microcerus*. In general, our results suggest that *I. microcerus* adopt strategies to avoid perception by its host, as already showed by previous studies.

The mean time to death of *I. microcerus* workers was lower in the presence of host than in the absence of it (Fig 1A). Interestingly, the mean time to death of inquiline workers was not dependent of host origin (*i.e.* from same or different nest). Such result can indicate that inquilines do not acquire the odor of the host colony, which could minimize the stress with its host colonies. In fact, *C. cyphergaster* and its obligatory inquiline *I. microcerus* do not share the

same profile of cuticular hydrocarbons (Cristaldo, *unpublished data*), a strategy usually used by inquilines of social insects. In Hymenoptera, for example, the integration of social inquiline in the host nests is facilitated by the acquisition of host colony odor by inquilines [e.g. bees (Dronnet et al., 2005), wasps (Sledge et al., 2001), and ants (Lenoir et al., 2001)]. Thus, it is expected that the relationship of obligatory inquilinism observed here is mediated by other evolutionary stable strategies, allowing a faster establishment of *I. microcerus* in nests of *Constrictotermes* sp.

The fact that inquilines apparently did not acquire the odor of its host colony suggests that they should use strategies to avoid meeting the host. However, here we found that the distance walked and the walking velocity of inquiline workers have not been changed in contact with host workers. This lack of changes in the walking behavior of inquiline workers in the presence of host can be a strategy to not becoming apparent, which would reduce possible conflicts. Thus, inquiline workers seem to minimize any reaction of perception and aggressiveness on the part of its host. Our results are in agreement with recent studies that showed that *I. microcerus* is able to recognize the trail pheromone of its host *C. cyphergaster*. By doing so, the inquiline can avoid galleries occupied by its host, facilitating the coexistence between them (Cristaldo et al., 2014). Inquilines are also able to recognize the alarm pheromone of its hosts, using it for their own benefit, either to avoid spaces inhabited by hosts or to escape from predators (Cristaldo et al., 2016). Recently, Jirošová et al. (2016) showed that soldiers of *I. inquilinus*, an obligatory inquiline of *C. cavifrons*, produce chemical substances that are repellent to its host, suggesting that spatial separation of colonies is chemically mediated, which allow the coexistence by reduction of direct conflicts. To avoid the host, inquiline individuals could also contribute to reduce the chances of selection of strategies of counterattack by the host. In addition, reports in the literature suggest that inquiline colonies are usually found spatially isolated in the host nest and that they use galleries that do not overlap with those used by its host colonies (Mathews, 1977; Cunha et al., 2003; Cristaldo et al., 2012). This apparently spatial segregation could occur to avoid direct contact with the host (see Mathews, 1977; Florencio et al., 2013).

The inner wall of host nest is formed not only by excrement of host but also by excrement of inquilines. Contrary to our hypothesis, inquiline workers in contact with inner wall of host nest did not survival more than those in the control group (Fig 1B). This absence of significant variation can be related with two factors: *i)* the inability of inquiline workers to ingest the substrate of inner wall, as it was used in our bioassay and *ii)* the obstacle represented by the substrate. Once the wall substrate has been macerated, it can be assumed that the inquiline workers were unable to ingest such particles, thereby reducing a possible effect of food on the increment in the survival of them. In addition, the presence

of this substrate may have been an obstacle to walking, increasing the energy expenditure of these individuals, thus masking a possible positive effect of this treatment. This last explanation is supported by the fact that the walking behavior was reduced when in contact with the inner and external walls in the same way when compared to the control group (Fig 2 and 3A-B). On the other hand, the contact with the external wall (EW) of host nest significantly reduced the survivorship of inquiline workers compared to IW and the control group (Fig 1B). The external wall of host nest should present less signs that indicate to the inquiline workers the presence of a known environment and it should limit the contact among the individuals of its colonies, which would explain the greater mortality of this treatment when compared to the control. This suggests that the reduction of walking behavior may be more related to some obstacle to any behavioral change due to chemical signals in these structures. On the other hand, survival seems to have been more influenced by the presence of chemical signals of the colony.

A series of hypothesis have been proposed to explain the cohabitation in termite nests: (i) inquilines become imperceptible in the nest (e.g. perceiving the chemical cues of its host or using different spaces in the host nest) (Cristaldo et al., 2012; 2014; 2016), (ii) inquilines have ability to repel their hosts (Jirošová et al., 2016) or (iii) inquilines do not overlap diet with their host (diet segregation; Florencio et al., 2013). The present study supports the idea that avoidance strategies used by inquilines can be the primary factor of coexistence between the obligatory inquiline *I. microcerus* and its host *Constrictotermes* sp. Previous studies have already indicated that avoidance strategy seems to occur by perception of chemical cues from host, here we showed that *I. microcerus* also have behavioral mechanisms that can avoid possible conflict easing the cohabitation in its host nests.

Acknowledgements

We are grateful to Prof. Reginaldo Constantino (UnB) for species identification. P.F.C. thanks CNPq/FAPITEC-SE (#302246/2014-6) and PNPd-CAPES. JSC is supported by PIBIC/FAPITEC-SE (#019.203.01192/2016-1). The other co-authors were supported by CAPES or CNPq grants.

Authors contribution

APA Araújo and PF Cristaldo conceived and design the experiments. JS Cruz, PF Cristaldo, JJ Marques, DV Ferreira and APA Araújo carried out the fieldwork. JS Cruz, PF Cristaldo, JJ Marques, ML Cruz, DV Ferreira and APA Araújo performed the bioassays. APA Araújo and PF Cristaldo performed the data analyses. JS Cruz, PF Cristaldo and APA Araújo wrote the manuscript.

References

- Ackerman, I.L., Teixeira W.G., Riha S.J., Lehmann J. & Fernandes E.C.M. (2007). The impact of mound-building termites on surface soil properties in a secondary forest of Central Amazonia. *Applied Soil Ecology*, 37: 267–276.
- Almeida, C.S., Cristaldo P.F., Florencio D.F., Cruz N.G., Santos A.A., Oliveira A.P., Santana A.S., Ribeiro E.J.M., Lima A.P.S., Bacci L. & Araújo A.P.A. (2016). Combined foraging strategies and soldier behaviour in *Nasutitermes* aff. *coxipoensis* (Blattodea: Termitoidea: Termitidae). *Behavioural Processes*, 126: 76–81.
- Andara, C., Issa S. & Jaffé K. (2004). Decision-making systems in recruitment to food for two *Nasutitermitinae* (Isoptera: Termitidae). *Sociobiology*, 44: 139–151.

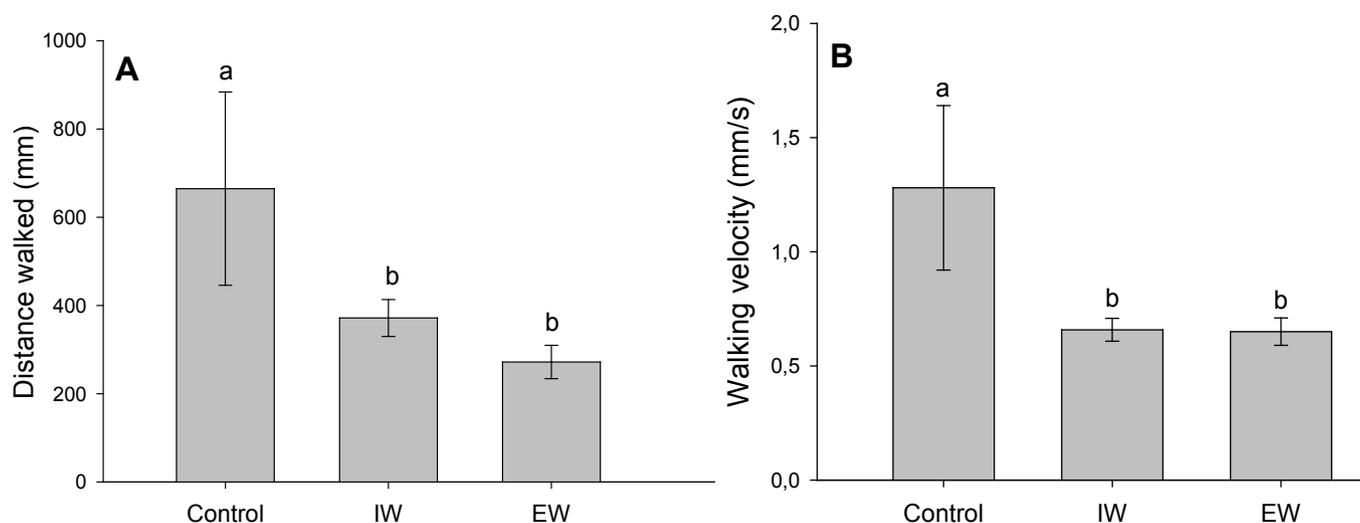


Fig 3. Distance walked (A) and walking velocity (B) of *Inquilinitermes microcerus* workers in the following treatments: control (inquiline workers alone), IW (inquiline workers in contact with substrate from the inner wall of host nest) and EW (inquiline workers in contact with substrate from the external wall of host nest). Different letters in each graphic indicates significant difference among treatments.

- Barbosa-Silva, A.M., Farias M.A.A., Mello A.P., Souza A.E.F., Garcia H.H.M. & Bezerra-Gusmão M.A. (2016). Lignocellulosic fungi in nests and food content of *Constrictotermes cyphergaster* and *Inquilinitermes fur* (Isoptera, Termitidae) from the semi-arid region of Brazil. *Fungal Ecology*, 20: 75–78.
- Bourguignon, T. & Roisin Y. (2006). A new genus and three new species of termitophilous *Staphylinids* (Coleoptera: Staphylinidae) associated with *Schedorhinotermes* (Isoptera: Rhinotermitidae) in New Guinea. *Sociobiology*, 48: 1–13.
- Bourguignon, T., Šobotník J., Lepoint G., Martin J.M., Hardy O.J., Dejean A. & Roisin Y. (2011). Feeding ecology and phylogenetic structure of a complex neotropical termite assemblage, revealed by nitrogen stable isotope ratios. *Ecological Entomology*, 36: 261–269.
- Brightsmith, D. (2000). Use of arboreal termitaria by nesting birds in the Peruvian Amazon. *The Condor*, 102: 529–538.
- Campbell, C., Russo L., Marins A., Desouza O., Schönrogge K., Mortensen D., Tooker J., Albert R. & Shea K. (2016). Top-down network analysis characterizes hidden termite-termite interactions. *Ecology and Evolution*, 6: 6178–6188.
- Constantino, R. (1999). Chave ilustrada para identificação dos gêneros de cupins (Insecta: Isoptera) que ocorrem no Brasil. *Papéis Avulsos de Zoologia*, 40: 387–448.
- Constantino, R. (2005). Padrões de diversidade e endemismo de térmitas no bioma Cerrado. In A.O. Scariot, J.C.S. Silva & J.M. Felfili (Eds.), *Cerrado: ecologia, biodiversidade e conservação* (pp. 319–333). *Biodiversidade, Ecologia e Conservação do Cerrado*. Ministério do Meio Ambiente, Brasília.
- Constantino, R. & Costa-Leonardo A.M. (1997). A new species of *Constrictotermes* from central Brazil with on mandibular glands of workers (Isoptera: Termitidae: Nasutitermitinae). *Sociobiology*, 30: 213–223.
- Costa-Leonardo, A.M. (2002). *Cupins-praga: Morfologia, Biologia e Controle*. Rio Claro: Divisa Editora, 128pp.
- Costa-Leonardo, A.M., Casarin F.E. & Lima J.T. (2009). Chemical communication in Isoptera. *Neotropical Entomology*, 38: 1–6.
- Costa, D.A., Carvalho R.A., Lima Filho G.F. & Brandão D. (2009). Inquilines and invertebrate fauna associated with termite nests of *Cornitermes cumulans* (Isoptera, Termitidae) in the Emas National Park, Mineiros, Goiás, Brazil. *Sociobiology*, 53: 443–453.
- Cristaldo, P.F., DeSouza O., Krasulová J., Jirošová A., Kotalová K., Lima E.R., Šobotník J. & Sillam-Dussès D. (2014). Mutual use of trail-following chemical cues by a termite host and its inquiline. *PLoS ONE*, 9: 1–9.
- Cristaldo, P.F., Rodrigues V.B., Elliot S.L., Araújo A.P.A. & DeSouza O. (2016). Heterospecific detection of host alarm cues by an inquiline termite species (Blattodea: Isoptera: Termitidae). *Animal Behaviour*, 120: 43–49.
- Cristaldo, P.F., Rosa C.S., Florencio D.F., Marins A. & DeSouza O. (2012). Termitarium volume as a determinant of invasion by obligatory termitophiles and inquilines in the nests of *Constrictotermes cyphergaster* (Termitidae, Nasutitermitinae). *Insectes Sociaux*, 59: 541–548.
- Cunha, H.F., Costa D.A., Filho E.K., Silva L.O., Brandão D. & Espírito-Santo Filho K. (2003). Relationship between *Constrictotermes cyphergaster* and inquiline termites in the Cerrado (Isoptera: Termitidae). *Sociobiology*, 42: 1–10.
- Cunha, H.F. & Brandão D. (2000). Invertebrates associated with the neotropical termite *Constrictotermes cyphergaster* (Isoptera: Termitidae, Nasutitermitinae). *Sociobiology*, 37: 593–599.
- Dangerfield, J.M., McCarthy T.S. & Ellery W.N. (1998). The mound-building termite *Macrotermes michaelseni* as an ecosystem engineer. *Journal of Tropical Ecology*, 14: 507–520.
- Davies, A.B., Levick S.R., Robertson M.P., van Rensburg B.J., Asner G.P. & Parr C.L. (2015). Termite mounds differ in their importance for herbivores across Savanna types, seasons and spatial scales. *Oikos*, 1–9.
- Dechmann, D.K.N., Santana S.E. & Dumont E.R. (2009). Roost making in bats - adaptations for excavating active termite nests. *Journal of Mammalogy*, 90: 1461–1468.
- Dimijian, G.G. (2000). Evolving together: the biology of symbiosis, part 1. *BUMC Proceedings*, 13: 217–26.
- Dronnet, S., Simon X., Verhaeghe J., Rasmont P. & Errard C. (2005). Bumblebee inquiline in *Bombus (Fernalda epsithyrus) sylvestris* (Hymenoptera, Apidae): behavioural and chemical analyses of host-parasite interactions. *Apidologie*, 36: 59–70.
- Duarte, S., Silva F.C.P., Zauli D.A.G., Nicoli J.R. & Araújo F.G. (2014). Gram-negative intestinal indigenous microbiota from two siluriform fishes in a tropical reservoir. *Brazilian Journal of Microbiology*, 45: 1283–1292.
- Emerson, A.E. & Krishna K. (1975). The termite family Serritermitidae (Isoptera). *Natural History*, 2570: 1–31.
- Engel, M.S., Grimaldi D.A. & Krishna K. (2009). Termites (Isoptera): their phylogeny, classification, and rise to ecological dominance. *American Museum Novitates*, 3650: 1–27.
- Ferreira, E.V.O., Martins V., Junior A.V.I., Giasson E. & Nascimento P.C. (2011). Ação dos térmitas no solo. *Ciência Rural*, 41: 804–811.
- Florencio, D.F., Marins A., Rosa C.S., Cristaldo P.F., Araújo A.P.A., Silva I.R. & DeSouza O. (2013). Diet segregation between cohabiting builder and inquiline termite species. *PLoS ONE*, 8: e66535.
- Hughes, D.P., Pierce N.E. & Boomsma J.J. (2008). Social

- insect symbionts: evolution in homeostatic fortresses. *Trends in Ecology and Evolution*, 23: 672–677.
- Jirošová, A., Sillam-Dussès D., Kyjaková P., Kalinová B., Dolejšová K., Jančařík A., Majer P., Cristaldo P.F. & Hanus R. (2016). Smells like home: chemically mediated co-habitation of two termite species in a single nest. *Journal of Chemical Ecology*, 42: 1070-1081.
- Jones, C.G., Lawton J.H. & Shachak M. (1994). Organism as ecosystem engineers. *Oikos*, 69: 373–386.
- Jones, J.C. & Oldroyd B.P. (2006). Nest thermoregulation in social insects. *Advances in Insect Physiology*, 33: 153–191.
- Jouquet, P., Boulain N., Gignoux J. & Lepage M. (2004). Association between subterranean termites and grasses in a West African savanna: Spatial pattern analysis shows a significant role for *Odontotermes n. pauperans*. *Applied Soil Ecology*, 27: 99–107.
- Jouquet, P., Dauber J., Lagerlöf J., Lavelle P. & Lepage M. (2006). Soil invertebrates as ecosystem engineers: Intended and accidental effects on soil and feedback loops. *Applied Soil Ecology*, 32: 153–164.
- Jouquet, P., Tavernier V., Abbadie L. & Lepage M. (2005). Nests of subterranean fungus-growing termites (Isoptera, Macrotermitinae) as nutrient patches for grasses in savannah ecosystems. *African Journal of Ecology*, 43: 191–196.
- Jouquet, P., Traoré S., Choosai C., Hartmann C. & Bignell D. (2011). Influence of termites on ecosystem functioning. Ecosystem services provided by termites. *European Journal of Soil Biology*, 47: 215–222.
- Lee, K.E. & Wood T.G. (1971). *Termites and soil*. New York: Academic Press London, 251pp.
- Lenoir, A., Hefetz A., Simon T. & Soroker V. (2001). Comparative dynamics of gestalt odour formation in two ant species *Camponotus fellah* and *Aphaenogaster senilis* (Hymenoptera : Formicidae). *Physiological Entomology*, 26: 275–283.
- Léonard, J. & Rajot J.L. (2001). Influence of termites on runoff and infiltration: quantification and analysis. *Geoderma*, 104: 17–40.
- Lima, J.T. & Costa-Leonardo A.M. (2007). Recursos alimentares explorados pelos cupins (Insecta : Isoptera). *Biota Neotropica*, 7: 243–250.
- Marins, A., Costa D., Russo L., Campbell C., Desouza O., Bjørnstad O.N. & Shea K. (2016). Termite cohabitation: The relative effect of biotic and abiotic factors on mound biodiversity. *Ecological Entomology*, 41: 532–541.
- Mathews, A.G.A. (1977). *Studies on termites from the Mato Grosso State, Brazil*. Rio de Janeiro: Academia Brasileira de Ciências, 267pp.
- Noirot, C. & Darlington J.P.E.C. (2000). Termites: evolution, sociality, symbioses, ecology. In T. Abe, D.E. Bignell & M. Higashi (Eds.), *Termite nests: architecture, regulation and defence* (pp. 121–139). Netherlands: Kluwer Academic.
- Pidwirny, M. (2011). Köppen Climate Classification System.
- Prestes, A.C. & Da Cunha H.F. (2012). Interações entre cupins (Isoptera) e formigas (Hymenoptera) co-habitantes em cupinzeiros epigeos. *Revista de Biotecnologia & Ciência*, 1: 50-60.
- Prestwich, G.D. (1984). Defense mechanisms of termites. *Annual Review of Entomology*, 29: 201–232.
- R Development Core Team. (2015). *R: A Language and Environment for Statistical Computing*. The R Foundation for Statistical Computing. ISBN: 3-900051-07-0, Vienna, Austria.
- Redford, K.H. (1984). The termitaria of *Cornitermes cumulans* (Isoptera, Termitidae) and their role in determining a potential keystone species. *Biotropica*, 16: 112–119.
- Redman, R.S., Dunigan D.D. & Rodriguez R.J. (2001). Fungal symbiosis from mutualism to parasitism: Who controls the outcome, host or invader? *New Phytologist*, 151: 705–716.
- Rosa, C.S., Marins A. & DeSouza O. (2008). Interactions between beetle larvae and their termite hosts (Coleoptera; Isoptera, Nasutitermitinae). *Sociobiology*, 51: 1–7.
- Sledge, M.F., Dani F.R., Cervo R., Dapporto L. & Turillazzi S. (2001). Recognition of social parasites as nest-mates: adoption of colony-specific host cuticular odours by the paper wasp parasite *Polistes sulcifer*. *Proceedings Biological Sciences*, 268: 2253–2260.
- Šobotník, J., Hanus R. & Roisin Y. (2008). Agonistic behavior of the termite *Prorhinotermes canalifrons* (Isoptera : Rhinotermitidae). *Journal of Insect Behavior*, 21: 521–534.
- Thompson, G.G. & Thompson S.A. (2015). Termitaria are an important refuge for reptiles in the pilbara of Western Australia. *Pacific Conservation Biology*, 21: 1–8.
- Traniello, J.F. (1981). Enemy deterrence in the recruitment strategy of a termite: Soldier-organized foraging in *Nasutitermes costalis*. *Proceedings of the National Academy of Sciences of the United States of America*, 78: 1976–1979.
- Traniello, J.F. & Leuthold R.H. (1981). Behavior and ecology of foraging termites. In T. Abe, D.E. Bignell & M. Higashi (Eds.), *Termites: evolution, sociality, symbioses, ecology* (pp. 141-168). Dordrecht, Netherlands: Kluwer Academic Publishers.

