


Lagged Population Growth in a Termite Host Colony: Cause or Consequence of Inquilinism?

VB RODRIGUES¹, DA COSTA^{1,2}, PF CRISTALDO³ , O DESOUSA¹

¹Lab de Termitologia, Depto de Entomologia, Univ Federal de Viçosa, Viçosa, MG, Brasil

²Depto de Zoologia, Univ do Estado do Mato Grosso, Tangará da Serra, MT, Brasil

³Programa de Pós-Graduação em Agricultura e Biodiversidade, Univ Federal de Sergipe, São Cristóvão, SE, Brasil

Keywords

Constrictotermes cyphergaster, ecological interaction, inquilinism, *Inquilinitermes microcerus*, population dynamic

Correspondence

PF Cristaldo, Programa de Pós-Graduação em Agricultura e Biodiversidade, Univ Federal de Sergipe, São Cristóvão, SE, Brasil; pfellipec@gmail.com

Edited by Heraldo Vasconcelos – UFU

Received 6 July 2018 and accepted 11 September 2018

© Sociedade Entomológica do Brasil 2018

Abstract

The presence of foreign organisms in the colonies of social insects could affect energy allocation to growth and reproduction of these hosts. Highly specialized invaders of such long-lived hosts, however, can be selected to be less harmful. After all, it pays for these symbionts to keep their host's good health thereby prolonging cohabitation in the homeostatic environment of the termite colony. Here, we investigated such a hypothesis, focusing on populational parameters of a termite host sharing its nest with an obligatory termite inquiline. To this end, 19 natural colonies of *Constrictotermes cyphergaster* (Silvestri, 1901) (Termitidae: Nasutitermitinae) were sampled and the (i) number of individuals, (ii) proportion of soldier/workers in the colonies, and (iii) presence/absence of obligatory inquiline *Inquilinitermes microcerus* (Silvestri, 1901) (Termitidae: Termitinae) were measured. Results revealed a negative correlation between the number of individuals and the proportion of soldier/workers in the host colonies with the presence of *I. microcerus* colonies. In search of causal mechanisms for such a correlation, we inspected life history traits of both, inquilines and hosts, hypothesizing that such a result could indicate either (i) a dampening effect of the inquiline upon its host population or (ii) the coincidence of the moment of inquiline infiltration with the natural reduction of *C. cyphergaster* populational growth at the onset of its reproductive phase.

Introduction

The evolution and maintenance of societies are driven by the benefits of intragroup cooperation (Nash & Boomsma 2008) which arise in the form of efficient obtention and conversion of energy into growth and reproduction. The allocation of energy to growth and reproductive efforts, in turn, is affected by the ecological context. After all, energy availability is modulated not only by resource offer but also by the presence of enemies. It follows that these latter two variables are the major factors affecting life history traits and this is particularly true for social insects (Oster & Wilson 1978, Stearns 1989).

In termite colonies, for instance, resource offer has been shown to affect the total number of individuals as well as the

investment in workers and immatures (Cristaldo *et al* 2018). As for the effects of enemies, particularly those infiltrated into insect societies, not much is known for the case of termites. In ants, the effects of intruders in the host colony performance can be variable. *Maculinea teleius* Verity, 1943 (Lepidoptera, Lycaenidae), for instance, has a strong negative effect on its host *Myrmica* Latreille, 1804 (Hymenoptera, Formicidae) given that it feeds on host brood and sexual forms (Witek *et al* 2016). Positive effects of guests on hosts have also been reported: infested colonies of *Formica lemami* Bondroit, 1917 (Hymenoptera, Formicidae) by the “ultra-specialist” hoverfly *Microdon mutabilis* Linnaeus, 1758 (Diptera, Syrphidae) double their production of new queens, due to the biased predatory behavior exhibited by the parasite. By

feeding selectively on ant eggs and small larvae, *M. mutabilis* reduces intranest resource competition, allowing surviving larvae to switch development into queens (Schönrogge et al 2006).

These diversified and surprising outcomes (see also Kistner 1979, 1982, Hovestadt et al 2012) tell us that much is yet to be learned from host-guest interactions in social insects, particularly considering the degree of guest specialization on a given host. It starts from the prediction by Bronstein (1994) that the outcomes of facultative relations should be more variable than outcomes of obligate ones. The obligate (and hence, “specialized”) symbionts of social insects will tend to be less damaging than parasites of solitary hosts, due to the characteristics of their host’s life histories. Large size, internal homeostasis, low mortality at maturity, and sessile lifestyle of a social insect colony would impose selective pressure on symbionts towards reduced virulence because it pays for the symbiont to preserve the good health of such a reliable environment (Hughes et al 2008). This is in contrast with the negative correlation between virulence and host specialization that is observed in endoparasites of mammals, such as *Plasmodium* spp. in primates (Garamszegi 2006).

In this regard, interspecific termite cohabitation in a single nest built by one of them, the so-called inquilinism, may provide a useful system to study the above issues. Termite inquiline species colonize host nests, where they coexist with host colonies apparently without contact between them (Cunha et al 2003, Jirošová et al 2016). In its most extreme form, inquilinism in termites involves species which have lost the ability to build their own nest and live obligatorily in nests built by other termite species (Shellman-Reeve 1997). This form of termite inquilinism occurs in the Neotropics in *Inquilinitermes* spp. Mathews, 1977 (Termitidae: Termitinae) and *Serritermes serrifer* (Hagen & Bates, 1858) (Serritermitidae), for example. A handful of similar obligate termite inquilines can be found elsewhere (Shellman-Reeve 1997: pag 66).

Strategies used by termite inquilines to coexist along with their host have been intensely studied in the last years (Cristaldo et al 2012, Florencio et al 2013, Cristaldo et al 2014, Wen et al 2015, Campbell et al 2016, DeSouza et al 2016, Jirošová et al 2016, Marins et al 2016, Cristaldo et al 2016, Cruz et al 2018). By contrast, the effects of obligatory inquilines on the growth and the reproductive success of their hosts are still lacking attention.

In the present study, we investigated the effect of an obligatory inquiline species upon its host colonies, focusing as a model system on the host-guest pair composed by *Constrictotermes cyphergaster* (Silvestri, 1901) (Termitidae: Nasutitermitinae) and its inquiline *Inquilinitermes microcerus* (Silvestri, 1901). *Constrictotermes cyphergaster* species can be found in Brazil, Paraguay, Bolivia, and Northern Argentina (Mathews 1977). The nests are founded in the soil and the colony migrates to the trees when they reach a

suitable size (Vasconcellos et al 2007, DeSouza et al 2016). The *C. cyphergaster* nests can harbor many invertebrates (Cunha & Brandão 2000), including one of two obligate inquilines, i.e., *Inquilinitermes microcerus* and *I. fur* (Silvestri, 1901). In the Brazilian Cerrado, *I. microcerus* colonies have been recorded in 70% of all *C. cyphergaster* nests as long as they are bigger than 13.6 L (Cristaldo et al 2012). Specifically, we investigated whether the presence of *I. microcerus* colonies affects the number of individuals and the soldier/worker proportion of their termite host *C. cyphergaster*. Based on the degree of specialization of this interaction and following the arguments by Hughes et al (2008), we predict that such an inquiline should not affect the number of its host individuals as well as soldier/worker proportion.

Material and Methods

Arboreal nests of *C. cyphergaster* ($N = 19$) were collected near the municipality of Divinópolis, Minas Gerais state, Southeast Brazil (20°10'16"S, 44°49'32.7"W). The study site belongs to “Brazilian Cerrado” biome, being subjected to an equatorial climate with dry winter (*Aw*) (Kottek et al 2006). Samplings were performed in January, July, and November 2015. The current study complied with relevant regulations of Brazil. This includes collecting and transportation permits from The Brazilian Institute for the Environment and Renewable Natural Resources (no. 10014-1), and permission from the land owners to conduct the study on their site. Tacit approval from the Brazilian Government is implied by hiring the authors as Scientific Researchers. No protected species was sampled. No genetic information has been accessed.

Before removing nests from their supporting tree, nest volume was measured by summing up the volumes of superimposed cylindrical cross-sections into which the nest was visually dissected, and the volumes of the hemispherical caps at both ends of the nest, as described and sketched by Cristaldo et al (2012). At the lab, a population census was performed, breaking the nests into pieces to remove all individuals. Numeric estimation was done manually counting the number of individuals in a 10% aliquot of the volume comprised of all individuals from a given caste in the nest. The total number of individuals in each caste of each nest was estimated extrapolating from the numbers counted in this aliquot (see methodological details in DeSouza et al 2016).

Data were analyzed using generalized linear modeling (GLM) in R statistical software (R Development Core Team 2016). Error distribution was chosen according to the nature of the response variable, as described below. Residual analyses were performed to verify error distribution and model suitability, including tests for overdispersion. At first, we tested for the effect of nest volume on the total number of individuals of both host and inquiline colonies, with

separated models under Gaussian error distribution. Such procedure was conducted to check the possible effect of nest volume per se in nest populations. To check the effect of obligatory inquiline on the colony growth and soldier/workers proportion of host colony, data were submitted to analysis of deviance (ANODEV) under negative binomial and Gaussian error distribution. Models aimed to test the effects of “*presence/absence of inquilines*” (*x-var*) on total host population/nest volume (ind/L) (*y-var*) and soldier/worker proportion/nest volume (proportion S:W/L) (*y-var*). In all analysis, there is no effect of sampling period on the variable tested.

Results

The volume of *C. cyphergaster* nests ranged from 0.09 to 33.00 L, with average of 11.55 ± 2.12 L (mean \pm SE). Inquiline colonies tended to be present in larger nests, as already shown in previous studies (Cristaldo *et al* 2012, DeSouza *et al* 2016); in average, nests with inquilines had 15.63 ± 3.02 L and nests without inquilines had 7.00 ± 0.0 L.

The number of individuals in *C. cyphergaster* colonies was significantly affected by nest volume ($F_{(1,18)} = 4.88$, $P = 0.04$; Fig 1), confirming the pattern already shown by Vasconcellos *et al* (2007). However, no effect of host nest volume was observed in the number of individuals in *I. microcerus* colonies ($F_{(1,9)} = 1.88$, $P = 0.20$). The number of individuals in *C. cyphergaster* colonies ranged from 105 to 30,027, with average of 9570 ± 1994 individuals (workers = 7243 ± 1523 ; soldiers = 2326 ± 458 ; S:W = 0.49 ± 0.08). Inquiline colonies were present in 10 out of 19 *C. cyphergaster* nests; the

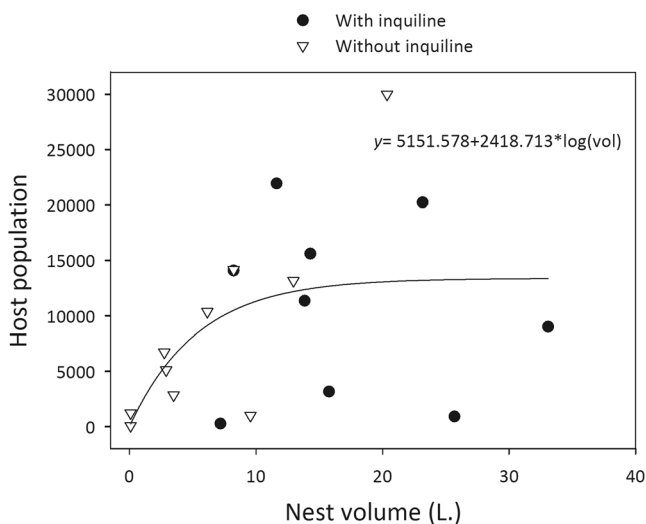


Fig 1 Effect of nest volume in the total number of host individuals composing colonies of *Constrictotermes cyphergaster* (Blattodea: Isoptera) with and without inquiline colonies (*Inquilinitermes microcerus*, Blattodea: Isoptera). Divinópolis, MG, Brazil, 2015. Linear regression with generalized linear models under Gaussian error distribution. Each dot refers to a single nest.

number of *I. microcerus* individuals ranged from 89 to 2969, with average of 1301 ± 212 individuals (workers = 1218 ± 205 ; soldiers = 85 ± 24 ; S:W = 0.07 ± 0.12).

The presence of inquiline colonies significantly affected the mean number of individuals *per* volume of host nests (deviance = 22.12, $df = 18$, $P = 0.007$); nests with *I. microcerus* colonies presented a smaller number of host individuals *per* liter (777 ± 208 ind/L) as compared with nests without colonies of obligatory inquilines (2843 ± 1431 ind/L). Similarly, the mean proportion of soldiers relative to workers *per* nest volume in the host colonies was significantly affected by the presence of inquiline colonies ($F_{(1,17)} = 6.24$, $P = 0.01$). Host colonies without *I. microcerus* colonies presented a higher proportion of soldiers relative to workers *per* nest volume as compared with host colonies without inquiline colonies (Fig 2).

Discussion

Here, we analyzed the effect of the obligatory inquiline *I. microcerus* on the total nest population of its host *C. cyphergaster*. In general, our results showed that inquiline presence significantly affected the size of its host population *per* nest volume (ind/L) and also the soldier/worker proportion (Fig 2). It is tempting to suppose that such host-guest correlations would reveal causation, so that inquilines would be indeed harmful to their host. There are, however, other lines of reasoning pointing to diverting direction. In the lines to follow, we try to inspect both facets of this issue.

Once established inside a social insect nest, invaders can shift behavioral or physiological traits of their hosts (e.g., Foitzik *et al* 2004, Carvell *et al* 2008). *Myrmica* ant colonies

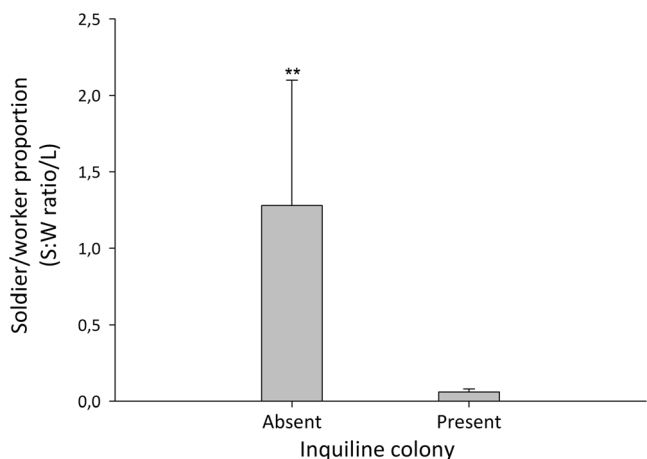


Fig 2 Effect of inquiline colonies (*Inquilinitermes microcerus*, Blattodea: Isoptera) in the mean proportion of soldiers relative to workers of host colonies (*Constrictotermes cyphergaster*, Blattodea: Isoptera) *per* nest volume. Divinópolis, MG, Brazil, 2015. Analysis of deviance with generalized linear models under Gaussian error distribution. Double asterisk symbols indicate significant ($P < 0.01$) differences between treatments.

infected by *Maculinea* larvae, for example, have a higher number of foragers when compared to uninfected nests (Witek *et al* 2016). *Formica lemni* (colonies infiltrated by the hoverfly *Microdon mutabilis* (Linnaeus)) produce more new queens than unaffected ones (Schönrogge *et al* 2006). In both cases, the effect in the host is explained by the predation strategies of the invader larvae upon their host brood, but this would not apply to our system. After all, *I. microcerus* individuals are not predators but detritivores (the same trophic level of their host) and seem to feed on organic materials, such as hosts' feces or nest walls (Mathews 1977, Florencio *et al* 2013).

In this context, factors modified by the presence of *I. microcerus* could affect the population of their host, including the nest populational density and internal nest temperature. Another colony growing inside the host nest would inflate the number of individuals therein and this could change its density which, in turn, impacts interindividual connectivity (DeSouza & Miramontes 2004) and the transmission of information and resources among conspecifics. More individuals can also change the nest temperature, affecting the transmission of nutrients and hormones (Liu *et al* 2005, Scharf *et al* 2007). These hypothetical effects of the inquiline are not mutually exclusive and can act together to interfere the host population.

The soldier/worker proportion of the host also shifted in the presence of inquiline colonies (Fig 2). The detection of invaders is determinant to elicit defensive behaviors or to trigger defensive immune responses in the hosts, as seen in ants and beetles. The presence of phorids (Diptera: Phoridae) in the nest of their ant hosts (Formicidae: Attini) caused the host to present defensive behaviors (Elizalde & Folgarait 2012). *Phoracantha* beetles (Coleoptera: Cerambycidae) increase their immune response against the parasitoid wasp *Avetianella longoi* Siscaro, 1992 (Hymenoptera: Encyrtidae). Thus, if the inquiline colony was detected by the host, it seems plausible to expect an increase in defensive traits, such as a differential investment in soldiers, in an attempt to expel the invader from the nest. However, colonies of *I. microcerus* seem to use chemical insignificance to avoid detection by their host inside the nest (Cristaldo *et al* 2014, 2016). Additionally, it is been also shown that *C. cyphergaster* host individuals are not able to perceive alarm signals emitted by their inquiline *I. microcerus*, indicating that such host colonies are not able to detect these inquiline colonies (Cristaldo *et al* 2016). Thus, decrements in soldier/worker proportion in the presence of inquiline colonies here observed are not likely to arise from the host perceiving the invader but would possibly reflect more indirect effects (e.g., populational density or nest temperature) as hypothesized above.

Although our results point to a negative effect of this inquiline upon its host colony, current termitological literature seems to point to a different direction. Authors such as

Florencio *et al* (2013), Cristaldo *et al* (2014, 2016), and Cruz *et al* (2018) demonstrated that these inquilines tend to use strategies to avoid direct conflict and this has been always interpreted as evidence in favor of the absence of such negative effects. Here, we observed that the inquiline population remains small and constant inside the host nest, a result that, by all means, does not conflict with findings by these earlier authors. The novelty brought about by our results would challenge the *interpretation* that the consequence of avoiding conflict would be to totally prevent negative effects upon the host. That is, it seems that such non-fluctuating small colonies of the inquiline might minimize rather than prevent problems to their host. In other words, such inquilines would be exerting lower virulence upon their hosts, hence securing a long-term symbiosis. This is entirely in line with these inquilines life history: these termite colonies are long-lived, infecting a definitive host colony (there are no records of guest emigration after infiltrating the host colony). It is plausible to suspect of a mechanism of density-dependent regulation to limit the guest colony size thereby avoiding over-exploitation of some limited resource (Poulin 2007). Such a dampened growth would still inflict some damage to the host (as we have observed here) but such a damage would not be severe enough to compromise their symbiotic relationship.

An alternative hypothesis would sustain that the observed effect on host population would be related to a factor other than the inquilines themselves. It is well known (Cristaldo *et al* 2012, DeSouza *et al* 2016), and also confirmed by our data, that *I. microcerus* tend to be found in bigger and probably older nests. These are precisely the nests that would be aged enough to hold host colonies which are apt to enter reproduction. Being energetically costly, efforts on reproduction would compromise colony growth and defense (Oster & Wilson 1978, de Jong & van Noordwijk 1992, Cox *et al* 2010) so that bigger nests would stop investing in populational increments of both workers and soldiers (in this regard, it is interesting to observe in Fig 1 that smaller nests were the ones which grew faster). If inquilines simply use this as a window of opportunity to infiltrate the nest, the negative correlation here observed between host population and inquiline presence would arise from ontogenetic reasons totally independent of inquilinism.

In summary, our study shows a negative correlation between the presence of *I. microcerus* inquilines and the populational growth and soldier/worker proportion of their host colonies, *C. cyphergaster*. Such a result could indicate either (i) a dampening effect of the inquiline upon its host population or (ii) the coincidence of the moment of inquiline infiltration with the natural reduction of *C. cyphergaster* populational growth at the onset of its reproductive phase. These results open unexplored avenues for research on termite inquilinism.

Acknowledgments We thank Ângelo Fonseca and Iara Rabelo Fonseca for logistic support during the fieldwork in Divinópolis, MG, Helder Hugo dos Santos for help during the field work, Yuri Carvalho de Carvalho, Livia Fonseca Nunes, and Renan Marinho for help during the lab work. We extensively used free software, especially but not restricted to, R + RStudio, LaTeX + Kyle, Ubuntu, Inkscape, LibreOffice, JabRef, Firefox, latex2rtf, custom-bib, yEd, as well as the free searching site Google Scholar, to whose authors we are profoundly thankful. This is contribution #77 from the Lab of Termitology at Federal Univ. of Viçosa, Brazil (<http://www.isoptera.ufv.br>), deriving from VBR's PhD thesis.

Authors' Contribution VBR, PFC, and ODS conceived and design the experiments; VBR and DAC performed the experiments; VBR, PFC, and ODS analyzed the data; and VBR, PFC, and ODS wrote the paper.

Funding Information VBR holds a PhD grant from CAPES and CAPES/PDSE (88881.132021/2016-01). ODS holds a CNPq research fellowship (no. 307990/2017-6). PC holds a post-doctoral grant from CAPES/PNPD (no. 1680248). This work has been partially supported by FAPEMIG, CNPq, CAPES.

Compliance with Ethical Standards The current study complied with relevant regulations of Brazil. This includes collecting and transportation permits from The Brazilian Institute for the Environment and Renewable Natural Resources (no. 10014-1), and permission from the land owners to conduct the study on their site. Tacit approval from the Brazilian Government is implied by hiring the authors as Scientific Researchers. No protected species was sampled. No genetic information has been accessed.

References

- Bronstein JL (1994) Conditional outcomes in mutualistic interactions. *Trends Ecol Evol* 9:214–217. [https://doi.org/10.1016/0169-5347\(94\)90246-1](https://doi.org/10.1016/0169-5347(94)90246-1)
- 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. *Ecol Evol* 6:6178–6188. <https://doi.org/10.1002/ece3.2313>
- Carvell C, Rothery P, Pywell RF, Heard MS (2008) Effects of resource availability and social parasite invasion on field colonies of *Bombus terrestris*. *Ecol Entomol* 33:321–327. <https://doi.org/10.1111/j.1365-2311.2007.00961.x>
- Cox R, Parker E, Cheney D, Liebl AL, Martin LB, Calsbeek R (2010) Experimental evidence for physiological costs underlying the trade-off between reproduction and survival. *Funct Ecol* 24:1262–1269. <https://doi.org/10.1111/j.1365-2435.2010.01756.x>
- Cristaldo P, Rosa C, Florencio D, 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). *Insect Soc* 59:541–548. <https://doi.org/10.1007/s00040-012-0249-3>
- Cristaldo PF, DeSouza O, Krasulová J, Kutalová K, Lima ER, Šobotník S, Sillam-Dussès D (2014) Mutual use of trail-following chemical cues by a termite host and its inquiline. *PLoS One* 9:e85315. <https://doi.org/10.1371/journal.pone.0085315>
- Cristaldo PF, Rodrigues VB, Elliot SL, Araújo APA, DeSouza O (2016) Heterospecific detection of host alarm cues by an inquiline termite species (Blattodea: Isoptera: Termitidae). *Anim Behav* 120:43–49. <https://doi.org/10.1016/j.anbehav.2016.07.025>
- Cristaldo PF, Almeida CS, Cruz NG, Ribeiro EJM, Rocha MLC, Santos AA, Santana AS, Araújo APA (2018) The role of resource density on energy allocation in the neotropical termite *Nasutitermes* aff. *coxiopensis* (Termitidae: Nasutitermitinae). *Neotrop Entomol* 47:329–335. <https://doi.org/10.1007/s13744-017-0525-z>
- Cruz JS, Cristaldo PF, Sacramento JJM, Cruz MLR, Ferreira DV, Araújo APA (2018) Survivorship and walking behavior of *Inquilinitermes microcerus* (Termitidae: Termitinae) in contact with host workers and walls from host nest. *Sociobiology* 65:31–37. <https://doi.org/10.13102/sociobiology.v65i1.1780>
- Cunha HF, Brandão D (2000) Invertebrates associated with the neotropical termite *Constrictotermes cyphergaster* (Isoptera: Termitidae, Nasutitermitinae). *Sociobiology* 37:593–599
- Cunha HF, Costa DA, Espírito-Santo Filho K, Silva LO, Brandão D (2003) Relationship between *Constrictotermes cyphergaster* and inquiline termites in the Cerrado (Isoptera: Termitidae). *Sociobiology* 42:761–770
- de Jong G, van Noordwijk AJ (1992) Acquisition and allocation of resources: genetic (CO) variances, selection, and life histories. *Am Nat* 139:749–770. <https://doi.org/10.1086/285356>
- DeSouza O, Miramontes O (2004) Non-asymptotic trends in the social facilitated survival of termites (Isoptera). *Sociobiology* 44:1–12
- DeSouza O, Araújo AP, Florencio DF, Rosa CS, Marins A, Costa DA, Rodrigues VB, Cristaldo PF (2016) Allometric scaling of patrolling rate and nest volume in *Constrictotermes cyphergaster* termites: hints on the settlement of inquilines. *PLoS One* 11(1):e0147594. <https://doi.org/10.1371/journal.pone.0147594>
- Elizalde L, Folgarait PJ (2012) Behavioral strategies of phorid parasitoids and responses of their hosts, the leaf-cutting ants. *J Insect Sci* 12(135): 1–26. <https://doi.org/10.1673/031.012.13501>
- Florencio DF, Marins A, Rosa CS, Cristaldo PF, Araújo APA, Silva IR, DeSouza O (2013) Diet segregation between cohabiting builder and inquiline termite species. *PLoS One* 8(6):e665. <https://doi.org/10.1371/journal.pone.0066535>
- Foitzik S, Backus VL, Trindl A, Herbers JM (2004) Ecology of *Leptothorax* ants: impact of food, nest sites, and social parasites. *Behav Ecol Sociobiol* 55:484–493. <https://doi.org/10.1007/s00265-003-0718-9>
- Garamszegi Z (2006) The evolution of virulence and host specialization in malaria parasites of primates. *Ecol Lett* 9:933–940. <https://doi.org/10.1111/j.1461-0248.2006.00936.x>
- Hovestadt T, Thomas JA, Mitesser O, Elmes GW, Schönrogge K (2012) Unexpected benefit of a social parasite for a key fitness component of its ant host. *Am Nat* 179:110–123. <https://doi.org/10.1086/663203>
- Hughes D, Pierce N, Boomsma J (2008) Social insect symbionts: evolution in homeostatic fortresses. *Trends Ecol Evol* 23:672–677. <https://doi.org/10.1016/j.tree.2008.07.011>
- Jirošová A, Sillam-Dussès D, Kyjaková P, Kalinová K, Jancarík A, Majer P, Cristaldo PF, Hanus R (2016) Smells like home: chemically mediated co-habitation of two termite species in a single nest. *J Chem Ecol* 42: 1070–1081. <https://doi.org/10.1007/s10886-016-0756-1>
- Kistner D (1979) Social and evolutionary significance of social insect symbionts. In: Hermann H (ed) *Social insects*. Academic, New York, pp 339–413
- Kistner D (1982) The social insect's bestiary. In: Herman L (ed) *Social insects*, vol II. Academic, New York, pp 1–244
- Kottek M, Grieser J, Beck C, Rudolf B, Rubel F (2006) World map of the Köppen-Geiger climate classification updated. *Meteorol Z* 15:259–263. <https://doi.org/10.1127/0941-2948/2006/0130>
- Liu Y, Henderson G, Mao L, Laine RA (2005) Effects of temperature and nutrition on juvenile hormone titers of *Coptotermes formosanus* (Isoptera: Rhinotermitidae). *Ann Entomol Soc Am* 98:732–737. [https://doi.org/10.1603/0013-8746\(2005\)098\[0732:EOTANO\]2.0.CO;2](https://doi.org/10.1603/0013-8746(2005)098[0732:EOTANO]2.0.CO;2)
- Marins A, Costa D, Russo L, Campbell C, DeSouza O, Björnstad ON, Shea K (2016) Termite cohabitation: the relative effect of biotic and abiotic factors on mound biodiversity. *Ecol Entomol* 41:532–541. <https://doi.org/10.1111/een.12323>

- Mathews AGA (1977) Studies on termites from the Mato Grosso state, Brazil. *Academia Brasileira de Ciências*, Rio de Janeiro, p 267
- Nash D, Boomsma J (2008) Communication between hosts and social parasites. In: D'Ettoire P, Hughes D (eds) *Sociobiology of communication: an interdisciplinary perspective*. Oxford University Press, Oxford, pp 55–79
- Oster G, Wilson E (1978) *Caste and ecology in the social insects*. Princeton University Press, Princeton, p 352
- Poulin R (2007) *Evolutionary ecology of parasites*. Princeton University Press, Princeton, p 332
- R Development Core Team (2016) R: a language and environment for statistical computing. The R foundation for statistical computing. ISBN: 3-900051-07-0, Vienna, Austria
- Scharf ME, Buckspan CE, Grzymala TL, Zhou X (2007) Regulation of polyphenic caste differentiation in the termite *Reticulitermes flavipes* by interaction of intrinsic and extrinsic factors. *J Exp Biol* 210:4390–4398. <https://doi.org/10.1242/jeb.010876>
- Schönrogge K, Gardner GM, Elmes GW, Napper EK, Simcox DJ, Wardlaw JC, Breen J, Barr B, Knapp JJ, Pickett JA, Thomas JA (2006) Host propagation permits extreme local adaptation in a social parasite of ants. *Ecol Lett* 9:1032–1040. <https://doi.org/10.1111/j.1461-0248.2006.00957.x>
- Shellman-Reeve J (1997) The spectrum of eusociality in termites. In: The evolution of social behavior in insects and arachnids, pp 52–93
- Stearns S (1989) Trade-offs in life-history evolution. *Funct Ecol* 3:259–268. <https://doi.org/10.2307/2389364>
- Vasconcellos A, Araújo V, Moura F, Bandeira A (2007) Biomass and population structure of *Constrictotermes cyphergaster* (Silvestri) (Isoptera: Termitidae) in the dry forest of Caatinga, Northeastern Brazil. *Neotrop Entomol* 36:693–698. <https://doi.org/10.1590/S1519-566X2007000500009>
- Wen P, Mo J, Lu C, Tan K, Šobotník J, Sillam-Dussès D (2015) Sex-pairing pheromone of *Ancistrotermes dimorphus* (Isoptera: Macrotermitinae). *J Insect Physiol* 83:8–14. <https://doi.org/10.1016/j.jinsphys.2015.11.006>
- Witek M, Ślipński P, Naumiec K, Krupski A, Babik H, Walter B, Symonowicz B, Dubiec A (2016) Performance of *Myrmica* ant colonies is correlated with the presence of social parasites. *Ecol Entomol* 41: 284–291. <https://doi.org/10.1111/een.12299>