

# 1 **Peaceful behaviour: a strategy employed by an obligate nest invader** 2 **to avoid conflict with its host species**

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13

## 14 **Abstract**

15 In addition to its builders, termite nests are known to house a variety of secondary,  
16 opportunistic termite species, but little is known about the mechanisms governing the  
17 maintenance of such associations. In a single nest, host and intruder are likely to engage in  
18 intense conflict, due to their nestmate discrimination system. An intriguing question is how  
19 individuals cope with such a burden in the long term. Evasive behaviour has been previously  
20 suggested as a mechanism that reduces the frequency of encounters between non-nestmates.  
21 However, due to confinement imposed by the nests' physical boundaries, it is likely that hosts  
22 and inquilines would eventually come across each other. Under these circumstances, it is  
23 plausible that inquilines would be required to behave accordingly to secure their housing. Here,  
24 we tested this hypothesis predicting that, once inevitably exposed to hosts, inquiline individuals  
25 would modulate their behaviour to circumvent conflict. While exploring the behavioural  
26 dynamics of the encounter between both cohabitants, we find evidence for an unusual lack of  
27 aggressiveness by inquilines towards hosts. Such a non-aggressive behaviour is characterised  
28 by evasive manoeuvres that include reversing direction, bypassing and a defensive mechanism  
29 using defecation to repel hosts. The behavioural adaptations we describe may play an intrinsic  
30 role in the stability of cohabitations between termite species: by reducing the costs of conflicts  
31 to both cohabitants, it may improve the chances for stable nest-sharing considerably.

32

33 **Keywords:** Cohabitation, Conflict, Inquilinism, Isoptera, *Inquilinitermes microcerus*,  
34 *Constrictotermes cyphergaster*.

## 35 Introduction

36

37 Nature provides innumerable opportunities to observe animals coexisting (Tokeshi,  
38 2009; Gravel et al. 2011), from migratory species temporarily interacting with local  
39 communities (Kays et al., 2015) to organisms establishing long-term, interspecific relationships  
40 (Wilson, 1988). Of particular interest, the latter group includes species that cohabit a single  
41 place and may, therefore, interact several times throughout their lifespan. These associations, or  
42 *symbioses* (*sensu* De Bary, 1878; see Oulhen et al., 2016), often represent excellent opportunities  
43 to investigate how organisms with independent life-histories end up sharing precisely the same  
44 place. For instance, while making decisions about permanent housing, some organisms opt for  
45 nests already built by a different species, avoiding costs with construction. In addition to  
46 providing shelter, nests may contain resources continuously renewed over time (e.g. food and  
47 water) and attract a variety of opportunistic organisms on the way. That seems to be the case of  
48 termite nests (termitaria), in which is possible to find an impressive richness and abundance of  
49 non-nestmates cohabiting with the original termite builders (Costa et al., 2009; Monteiro et al.,  
50 2017).

51 Although a wide variety of species have been found inside termitaria (Kistner, 1969,  
52 1979, 1990; De Visser et al., 2008), in this paper we focus on a remarkably distinct case of nest  
53 cohabitation between builder and invader, that is, a host termite and a secondary, opportunistic  
54 termite species so-called *inquilines* (*sensu* Araujo, 1970). It is worthwhile mentioning, however,  
55 that inquilinism among termites should not be mistaken with that occurring in Hymenoptera.  
56 Commonly referred as *social parasites* (Nash & Boomsma, 2008), inquiline bees, wasps and ants  
57 tend to establish a close relationship with hosts and exploit their social behaviour intensively  
58 (Hölldobler & Wilson, 1990). In termites, though, inquilines are thought to be primarily  
59 associated with the nest's physical structure itself, regardless of their association with host  
60 species (Shellman-Reeve, 1997; Marins et al., 2016). With proportionally smaller colonies and  
61 relatively low brood care (Korb et al., 2012) it is unlikely, although possible, that inquiline  
62 termites would deplete nest resources intensively, or exploit the host's social structure, as  
63 reported in different inquiline ant species (Buschinger, 2009).

64 Framing precisely inquilinism among termites into the spectrum of symbiotic  
65 interactions (e.g. parasitism, commensalism) can be challenging. For instance, although a  
66 number of studies have provided relevant information on different host-inquiline systems (e.g.  
67 Collins 1980; Redford, 1984; Eggleton & Bignell 1997; Cunha et al. 2003; Costa et al. 2009;  
68 Darlington, 2011; Cristaldo et al. 2012, 2014; Florencio et al. 2013; Campbell et al., 2016;  
69 DeSouza et al. 2016; Rodrigues et al. 2018), it remains unclear which costs (if any) inquiline  
70 termite colonies impose to host species. Even so, it seems plausible that a community of termite

71 species within a single nest would be an ideal scenario for the emergence of conflict. Because  
72 host termite species are known to respond aggressively towards a variety of nest intruders  
73 (Emerson, 1938; Shellman-Reeve, 1997), the confrontation would arise predominantly from  
74 encounters with non-nestmates. Aggressive behaviour seems to be, in fact, a default response of  
75 the soldier caste of termites towards non-nestmates (Noirot, 1970), with individuals engaging  
76 in endless fights while protecting their colonies (Binder 1987). Moreover, in addition to the  
77 typical agonism of soldiers, hidden aggression among termite workers has been reported for  
78 some species (Ishikawa & Miura 2012).

79 Curiously enough, as opposed to hosts, inquiline colonies may be found in the wild  
80 severely depleted in their contingent of soldiers (Cunha et al. 2003). The proportion of soldiers  
81 in some cases may account for less than one per cent of the colony (HH, pers. obs.). Relying on  
82 nest invasions to persist may, hence, represent a considerable risk for inquiline colonies, and an  
83 intriguing question is how cohabitation in such terms is even possible. Not surprisingly,  
84 previous works have tackled such an issue, suggesting proximate mechanisms that would allow  
85 inquilines and hosts to meet less frequently within the nest. In this regard, immediately after  
86 successful invasions, inquilines would establish themselves in the nest by decreasing chances of  
87 being noticed by hosts in the first place. Inquiline termites could achieve such an effect through  
88 various behaviours, including: (i) avoiding walking in galleries crowded by hosts (Grassé, 1986;  
89 Mathews, 1977); (ii) not conflicting with dietary requirements of the host (Miura & Matsumoto,  
90 1997; Florencio et al., 2013); (iii) intercepting hosts' chemical signals and using the information  
91 acquired to preclude encounters with hosts (Cristaldo et al., 2014, 2016a); and (iv) keeping the  
92 colony isolated from hosts by changing the nest structure (e.g. building their own galleries and  
93 sealing chambers: HH, pers. obs.). Although functioning through independent mechanisms,  
94 these behavioural strategies seem to coincide in a single outcome: by preventing direct contact,  
95 inquilines reduce the frequency of encounter with hosts.

96 As efficient as it may seem, however, while such strategies could potentially attenuate  
97 conflictual events, they would not entirely prevent encounters from happening. For most  
98 inquiline species (including the one studied here), there is no evidence yet of colonies exiting  
99 nests after they break in, neither for nest defence nor for foraging. The only known exception is  
100 the winged reproductive caste that leaves the nest during swarming (Matsuura, 2010). These  
101 facts together suggest that there is an associated probability of interspecific encounter to be  
102 considered. Besides, the confinement imposed by the nest's physical boundaries would keep  
103 individuals locally restricted and bound to meet in the long-term. Under these circumstances  
104 inquilines would be required to behave accordingly, for instance, mitigating detrimental  
105 consequences of aggressive encounters with nest owners.

106           Although hinted in the past, this intuitive, theoretical prediction was never directly  
107 tested, and little is known about host-inquiline dynamics within the nest, or to what extent  
108 inquiline strategies are sufficient to cope with the menace of imminent confrontation with hosts.  
109 This information could provide important clues about how these cohabitations hold in nature. A  
110 conservative approach to this issue would sustain that inquilines should replicate, at the  
111 individual level, the evasive behaviour they exhibit as a group. In this context, one would expect  
112 the strategies to avoid conflict (highlighted above) to be mere consequences of a non-  
113 threatening posture exhibited by inquiline individuals. Here, we tested this hypothesis  
114 predicting that, once inevitably exposed to hosts, inquiline individuals would adopt a non-  
115 aggressive posture and modulate their behaviour to a less threatening profile. As a result, the  
116 colony would be able to reduce conflict with nest owners collectively. Such an assumption  
117 would imply that inquiline individuals should weaken conflict escalation by (i) being lethargic  
118 and minimising encounters with hosts and (ii) exhibiting low aggressiveness by avoiding either  
119 initiating or retaliating attacks.

120           To test these assumptions, we observed in detail the behaviour of an obligate inquiline  
121 termite, *Inquilinitermes microcerus* Silvestri (1901) (Termitidae: Termitinae), in the presence of  
122 its host termite, *Constrictotermes cyphergaster* Silvestri 1901 (Termitidae: Nasutitermitidae).  
123 We exposed species to each other under two different experimental scenarios: (i) in closed  
124 arenas, as to keep individuals locally restricted and favour host-inquiline encounters; and (ii) in  
125 open arenas, where inquilines had a chance to flee from hosts. By compiling full ethograms for  
126 the encounter between *I. microcerus* and *C. cyphergaster*, we add new information to the current  
127 knowledge on nest-sharing termite species. These descriptions highlight relevant aspects to  
128 consider while studying the underlying mechanisms of coexistence between species living in  
129 environments circumscribed by discrete physical barriers. Furthermore, we argue that the  
130 behavioural profiles here described lend support to the notion of inquilines as peaceful guests,  
131 contributing to the growing view of conflict-avoidance as an effective strategy to coexist in  
132 harsh environments.

133 **Methods**

134

135 ***Biological model***

136 The termite *C. cyphergaster* (hereafter, host) is a Neotropical species widely distributed  
137 in South America (Mathews, 1977; Krishna et al., 2013) known to forage at night in exposed  
138 columns and without the protection of covered galleries (Moura et al., 2006). In this species,  
139 nest foundation starts on the ground with a royal couple, and after reaching a certain size,  
140 colonies migrate to the trees, where they establish typical arboreal nests (Vasconcellos et al.,  
141 2007). At this phase, it is usual to find colonies of *I. microcerus*, a secondary opportunistic  
142 termite species that inhabit the nests (hereafter, inquilines). Such a suggestive name as  
143 *Inquilinitermes* has its reasons: inquilines seem to be unable to build nests by their own  
144 (Emerson, 1938; Mathews, 1977), being found so far exclusively within host nests. Although it  
145 remains unclear how exactly nest invasion occurs, there seems to be a critical nest volume  
146 above which inquiline colonies are more likely to be found within host nests (13.6 L, see  
147 Cristaldo et al., 2012). The nest's size seems to indirectly affect inquilinism in termites, being  
148 negatively related to defence rates (DeSouza et al., 2016). Besides, while evaluating populational  
149 parameters of nests containing inquiline colonies, Rodrigues et al. (2018) reported a negative  
150 correlation between the number of individuals and the proportion of soldier/workers.  
151 Compared to hosts, inquiline colonies are much smaller in size, but still easily detectable due to  
152 a characteristic dark lining covering their galleries (Cunha et al., 2003; Cristaldo et al., 2012;  
153 Florencio et al., 2013). Inside the nest, inquiline colonies are often associated with chambers  
154 filled with a black material, hypothesised in the past as waste dumped by hosts (Emerson,  
155 1938), but still of unknown origin.

156

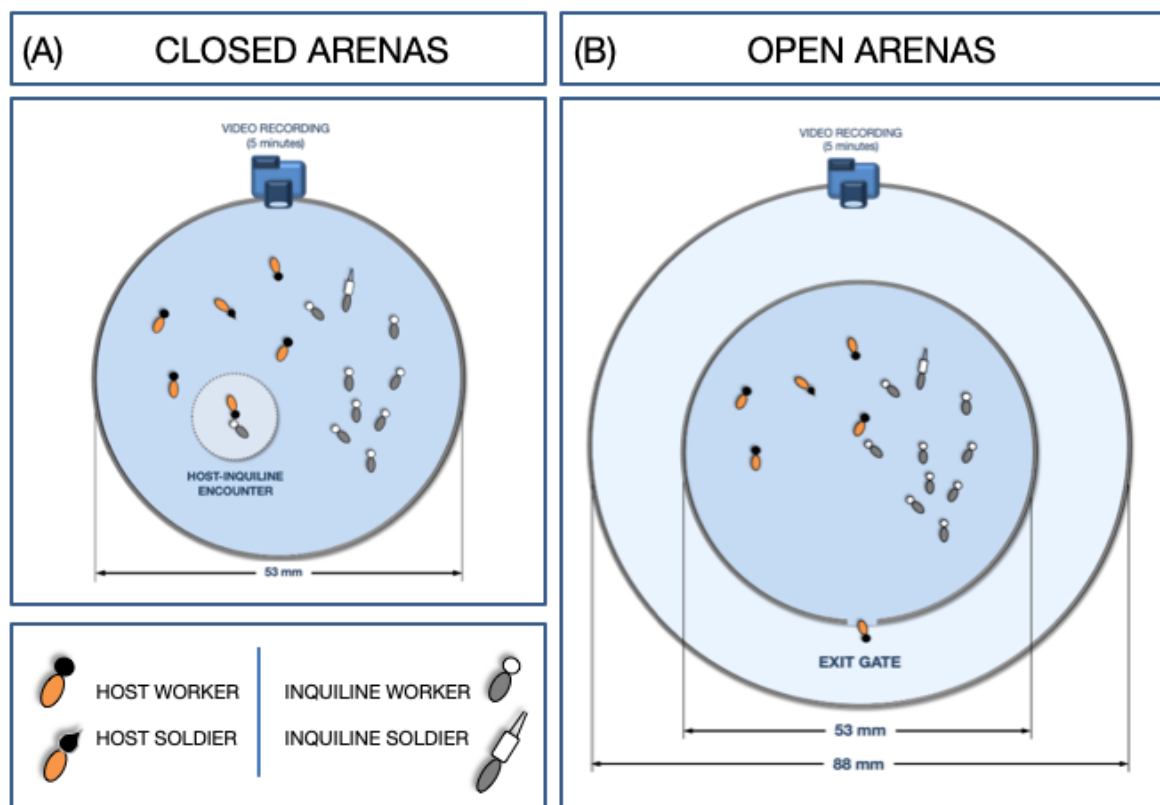
157 ***Study site and collection***

158 To carry out experiments, 27 host nests with inquiline colonies were collected from two  
159 locations in the Brazilian Cerrado (Ratter, Ribeiro, & Bridgewater, 1997): 15 nests collected  
160 near the municipality of Sete Lagoas (19°27'57"S, 44°14'48"W) in July 2012; and 12 nests  
161 collected near the municipality of Divinópolis (20°08'20"S, 44°53'02"W) in January 2015. Both  
162 sites, located in Southeastern Brazil (State of Minas Gerais), have climate resembling savannas  
163 (Aw, in Köppen-Geiger classification), and are subjected to an equatorial climate with dry  
164 winters (Aw) (Kottek et al., 2006).

165

166 **Experimental design**

167 In order to access behavioural profiles at host-inquiline encounters, cohabitants were  
168 taken from their nests, acclimatised for 30 minutes in separate containers, and then gathered in  
169 arenas for video recording (**Fig. 1**). Experimental arenas consisted of plastic Petri dishes ( $\emptyset$   
170 53mm) lined with paper (Whatman N° 1), and video-samples were taken with a digital camera  
171 (Nikon D300S, 720p, 25fps). All videos were recorded under visible light, and the room  
172 temperature was controlled between 23°C and 25°C.  
173



174

175 **Figure 1.** Arena settings for video recording: (A) Closed arenas, (B) Open arenas. We recorded video-  
176 samples of five minutes (300 seconds) for focal animal observation, which was carried out by observers  
177 using a 14" LED-LCD 1080p screen; an example of a heterospecific encounter is highlighted by a lighter  
178 circle within the closed arena (A). The internal area had a diameter of 53mm. The external area had a  
179 diameter of 88mm. A gate consisted of a single opening with diameter of 3.5mm on the arena wall  
180 connecting internal and external areas.  
181

181

182 We designed two experiments to test our predictions. In the first experiment (**Fig. 1A**),  
183 host and inquiline individuals were mutually confined in closed arenas, a locally restricted  
184 condition intentionally designed to improve the chances of an encounter between the species. In  
185 the second experiment, hosts and inquilines were gathered in arenas mostly identical to those  
186 used in the first setup, except for the presence of an exit gate. This gate consisted basically of a  
187 single opening ( $\emptyset$  3.5mm) on the arena wall, giving access to an external circular area ( $\emptyset$  88mm)



188 encompassing the inner one ( $\emptyset$  53mm). This second experiment was conducted to inspect  
189 whether inquilines would (i) remain idle or (ii) move away when given a chance to flee from  
190 host aggressions (**Fig. 1B**). The latter response could potentially lead to spatial segregation  
191 between species, a result that would be in line in field observations.

192 We defined two treatments using open arenas to test whether the presence of inquilines  
193 would affect how hosts explore the space available: (i) open arenas containing host and  
194 inquilines; and (ii) open arenas containing only hosts, as a control. Experiments were conducted  
195 with individuals kept under optimal density (0.12; for details, see Miramontes & DeSouza, 2008)  
196 and in a worker-to-soldier ratio similar to that found in natural conditions (Cunha et al., 2003).  
197 Experimental groups, therefore, contained: (i) one soldier and four workers for hosts and (ii)  
198 one soldier and nine workers, for inquilines. Individuals composing a given experimental group  
199 were never present in a second trial, as to avoid interference from prior contact with non-  
200 nestmates.

201

## 202 ***Behaviour annotation and observational protocol***

203 To determine observable behaviours of relevance to our scope, we performed the  
204 following procedure: before the main experiments, preliminary observations were taken as to  
205 detect behaviours possibly performed by individuals. Video-samples used to perform these  
206 observations were never reused in the main experiments. At this phase, we spent efforts to  
207 describe as many behaviours as possible. Because extensive behavioural descriptions may  
208 contribute to misleading observation (Lehner, 1998), we created a flowchart with simple,  
209 straightforward labels hierarchically organised (**Fig. 2**). Observers used this diagram and a list  
210 of short behavioural descriptions (**Table 1**) as a reference for annotation.

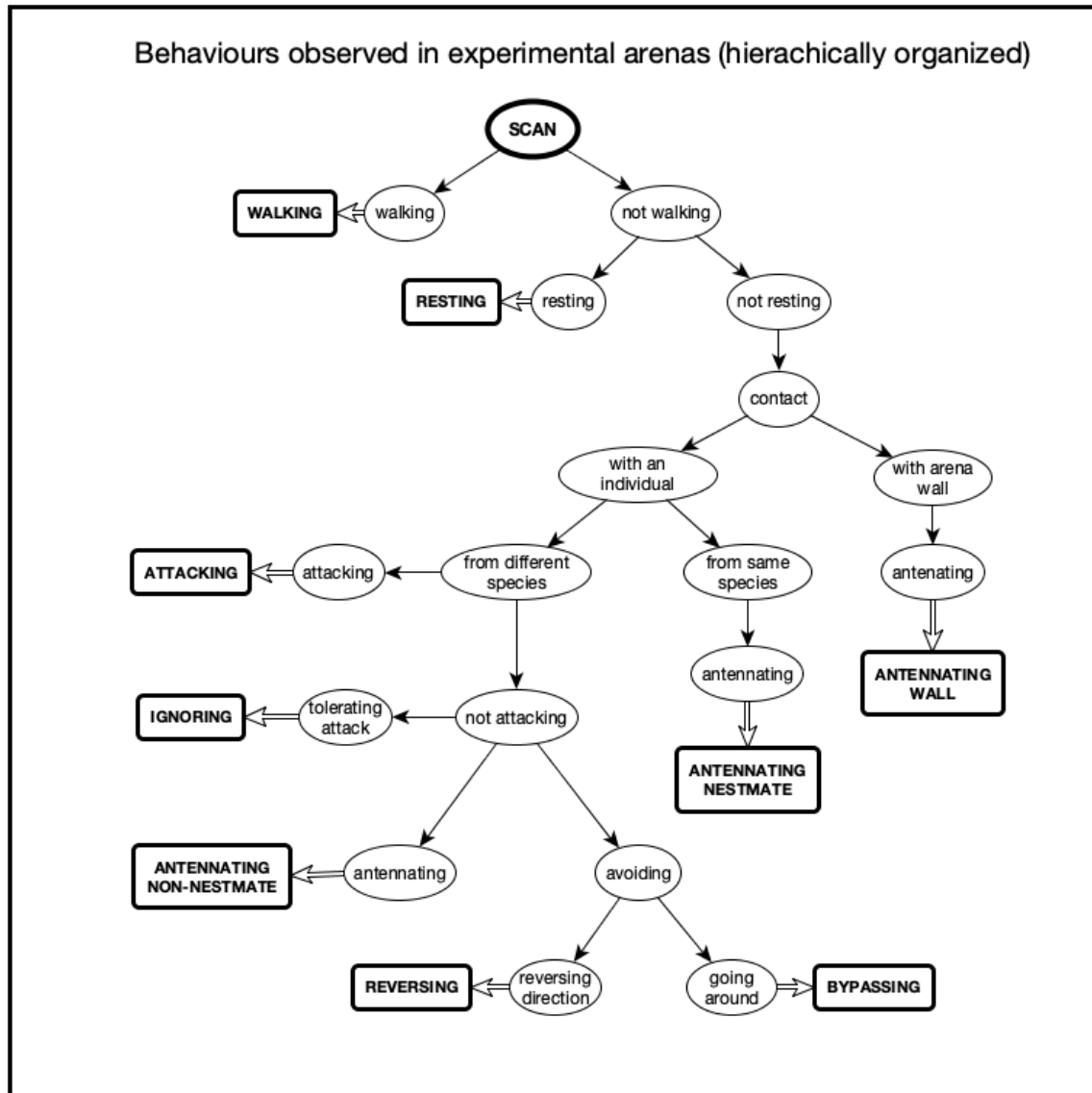
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212 **Table 1.** Behavioural description based on preliminary observations. We defined nine observable  
213 behaviours of relevance to our scope using ten additional video-samples. For statistical analysis, we  
214 classified each behaviour in two ways: (i) either as within-species or between-species; and (ii) either as  
215 aggressive or non-aggressive.

216

Behaviour	Description	Type of encounter	Type of interaction
RESTING	Focal animal remains stationary at the same place	non-aggressive	within-species
WALKING	Focal animal moves freely around the arena	non-aggressive	within-species
ANTENNATING WALL	Focal animal reaches the arena wall and performs only antennation	non-aggressive	within-species
ANTENNATING NESTMATE	Focal animal encounters nestmate and performs only antennation	non-aggressive	within-species
ANTENNATING NON-NESTMATE	Focal animal encounters non-nestmate and perform only antennation	non-aggressive	between-species
IGNORING	Focal animal encounters non-nestmate and do not react	non-aggressive	between-species
REVERSING	Focal animal encounters non-nestmate and perform u-turn manoeuvre	non-aggressive	between-species
PASSING	Focal animal encounters non-nestmate and perform a bypass manoeuvre	non-aggressive	between-species
ATTACKING	Focal animal encounters non-nestmate and performs aggression	aggressive	between-species

217



218

219 **Figure 2.** Behavioural flowchart used for annotation. Labels are hierarchically organised to allow  
 220 stepwise classification of behaviours. We defined nine observable behaviours in preliminary  
 221 observations. Combined to a behavioural description presented in Table 1, this flowchart served as a  
 222 reference for annotation.

223

224 We adopted focal animal sampling (Altmann, 1974) with observations taken from video-  
 225 samples to capture interactions between hosts and inquiline individuals. We recorded a total of  
 226 20 video-samples of five minutes (10 using closed arenas, 10 using open arenas). Behaviours  
 227 performed by host workers (HW), host soldiers (HS), inquiline workers (IW) and inquiline  
 228 soldiers (IS) were annotated for each video-sample using the flowchart described above. For  
 229 each one of these categories, an individual was arbitrarily selected for focal observation  
 230 (hereafter, focal animal). Using a 14" LED 1080p screen to watch video samples, we took three-  
 231 seconds observations (hereafter, scans) for each focal animal. Scans were taken at regular time  
 232 intervals of 10 seconds, indicated to observers by scheduled sound signals. This method



233 provided 31 scans *per* focal animal for each video-sample. Finally, we organised all behavioural  
234 annotation in files including all relevant information (e.g. observer, date and time of recording,  
235 room temperature) data analyses.

236

### 237 ***Measuring aggressiveness and host-inquiline interactivity***

238 To measure host's and inquiline's aggressiveness in closed arenas, we classified  
239 behavioural observations into two mutually exclusive categories regarding the type of  
240 encounter: (i) aggressive encounter, when focal animals encountered non-nestmates and  
241 performed aggression (i.e. attack); and (ii) non-aggressive encounter, when focal animals  
242 interacted with non-nestmates but did not perform aggression (i.e. antennating non-nestmate,  
243 reversing, bypassing, ignoring). To measure interactivity between hosts and inquilines in closed  
244 arenas, we classified behavioural observations into two mutually exclusive categories regarding  
245 the type of interaction: (i) within-species, when focal animals performed actions either by  
246 themselves (i.e. resting, walking, antennating wall) or with nestmates (i.e. antennating  
247 nestmate); and (ii) between-species, when focal animals performed actions after establishing  
248 physical contact with non-nestmates (i.e. antennating non-nestmate, ignoring, bypassing,  
249 reversing, attacking).

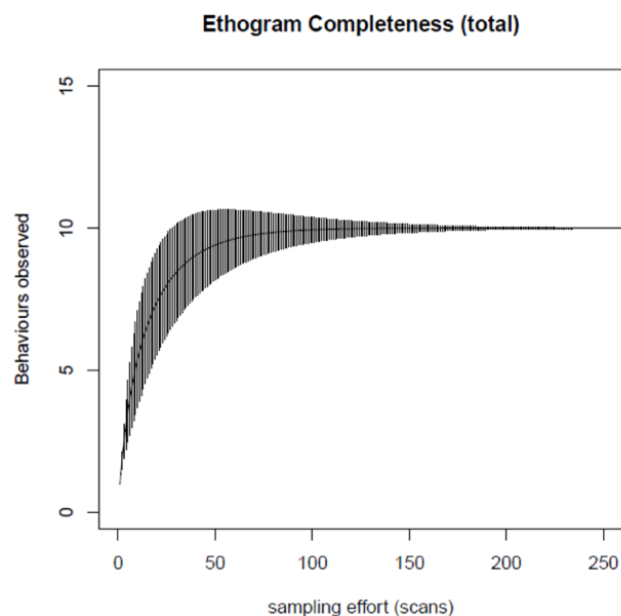
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### 251 ***Assessing behavioural profiles***

252 To analyse the influence of specific behaviours in the general profile of hosts and  
253 inquilines, we developed a network analysis using the free software yEd Graph Editor version  
254 3.14.4 (yWorks, 2015). To build graphs for each caste, we performed the following procedure:  
255 using behavioural sequences extracted from annotations, we constructed adjacent matrices  
256 containing the behavioural change for each caste (Supplementary Material, **Table S2**), which  
257 later was imported to yEd to draw the graphs. As typically done in standard network analysis  
258 (Newman, 2003), graphs consisted of networks of nodes linked by connecting edges (*i.e.*  
259 directional arrows). In our case, however, nodes represented specific observable behaviours  
260 executed by individuals, whereas connecting edges represented behavioural changes from a  
261 given behaviour to another one. That is, if individuals changed from rest to walking behaviour,  
262 the behavioural change annotated would be rest-walk. With nine observable behaviours defined  
263 in our scope (**Table 1**), 81 types of behavioural change could be possibly observed. With the  
264 constructed graphs, we calculated centrality measures (Freeman, 1978) using the number of  
265 incoming connecting edges for each node (Brandes & Erlebach, 2005). Then, using the  
266 calculated centrality scores, we adjusted the size of nodes to visually represent the degree of  
267 influence exerted by each behaviour upon profiles (*i.e.* the larger the size of a node, the higher  
268 its influence on the network).

## 269 **Ethogram validation**

270 We adopted a procedure suggested by Dias et al. (2009) to validate our ethograms.  
271 Following this approach, we used behavioural accumulation curves (BAC) to assess an optimal  
272 balance between (i) effort with sampling and (ii) ethogram completeness. A minimum of 250  
273 independent observations would be required to efficiently capture a total of ten observable  
274 behaviours (**Fig. 3**). In our study, we extrapolated this number and performed 1240 discrete  
275 observations for the nine observable behaviours previously defined (that is, 31 scans x 2 castes  
276 x 2 species x 10 replicates = 1240 scans).



277  
278 **Figure 3.** Ethogram completeness using Behavioural Accumulation Curves (Dias et al., 2009): the X-axis  
279 represents sampling effort, that is, the number of scans performed to observe all behaviours (in our case,  
280 31 scans x 2 castes x 2 species x 10 replicates = 1240 scans); the Y-axis represents the accumulative  
281 number of behaviours experimentally observed in trials.

## 282 283 **Statistical analyses**

284 We performed the statistical analyses in R, version 3.5.2 (R Development Core Team,  
285 2018) using Generalized Linear Modelling (GLM) under Binomial errors with log-link. As a  
286 conservative approach, the significance of treatments was accessed using the following  
287 procedure: we compared complex models to simpler ones achieved by combining treatment  
288 levels (Crawley, 2012). When simplification did not provoke significant changes, simpler models  
289 were accepted, and the combined treatments were considered equivalent to each other. We  
290 then submitted adjusted models to a residual analysis as to check the suitability of the  
291 modelling equation and normality of error distribution. If required, error distribution was  
292 adjusted using Quasi-binomial distribution. In all tests conducted, we considered an  $\alpha = 0.05$  to  
293 assess statistical significance.

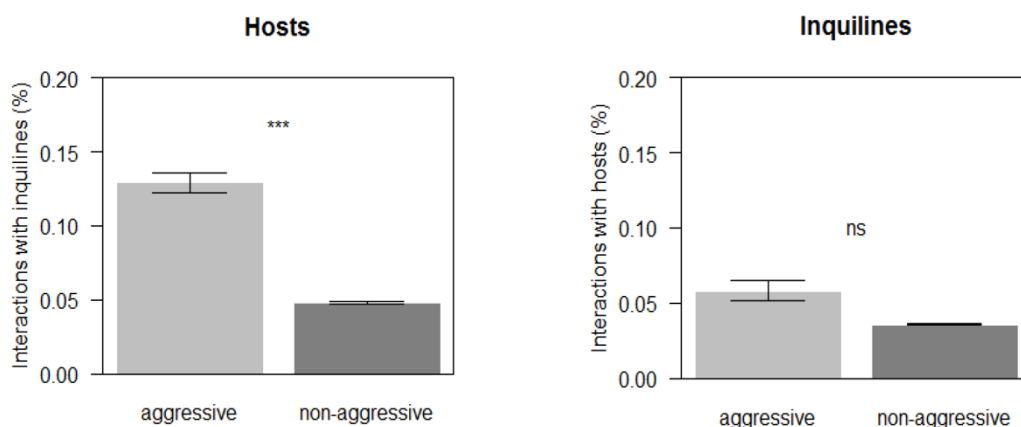
## 294 Results

295

### 296 *Inquilines suffered attacks from hosts but responded with low aggressiveness*

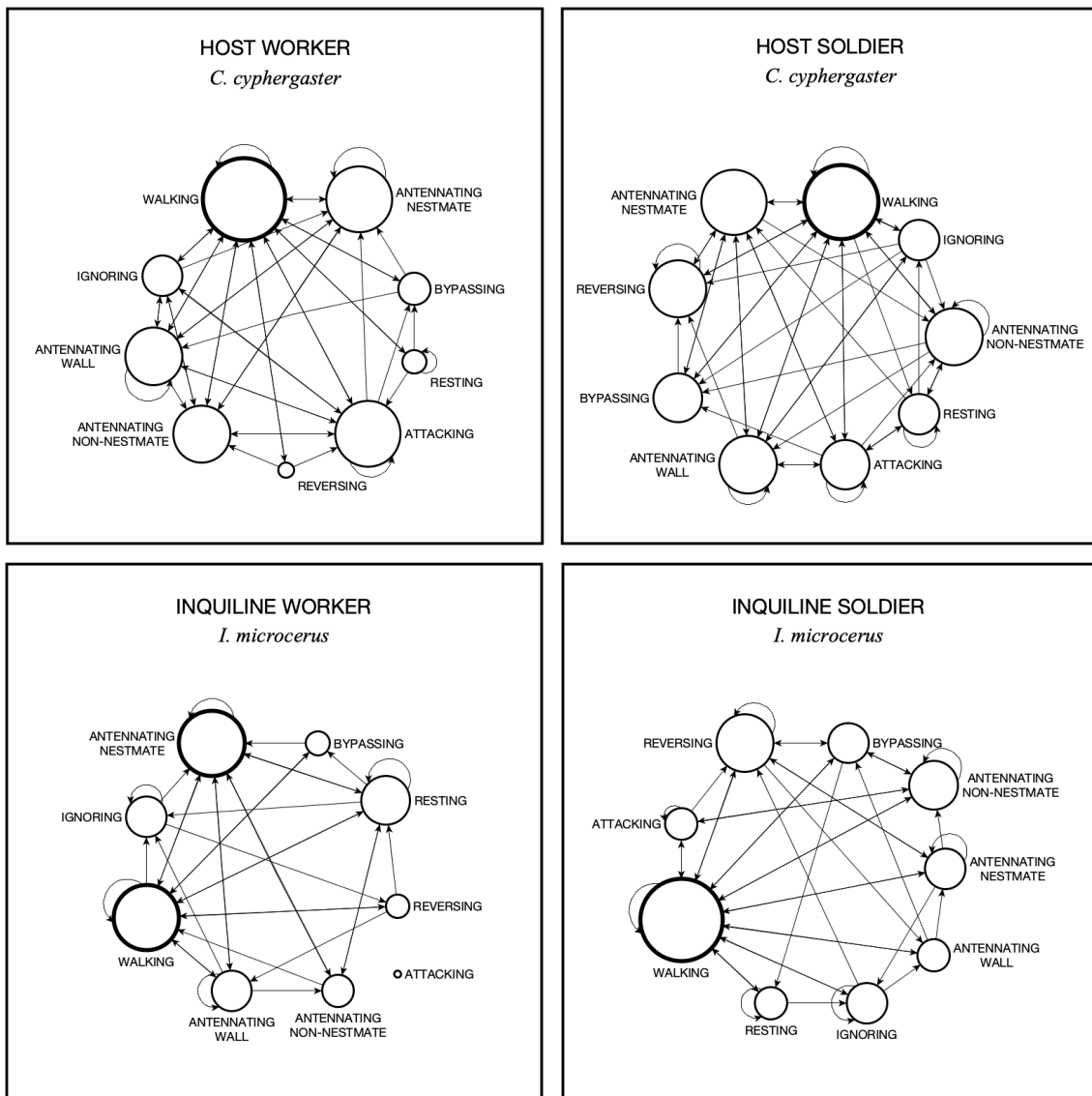
297 In closed arenas, the proportion of aggressive interactions initiated by hosts when  
298 encountering inquilines was significantly higher than the proportion of non-aggressive  
299 interactions (GLM;  $F_{1,98}=16.72$ ,  $P<0.001$ ; **Fig. 4**). As expected, caste was determinant in the type  
300 of aggression inflicted by individuals. While host workers physically injured inquilines by biting  
301 them in several portions of their softy bodies, host soldiers frequently adopted an agonistic  
302 display, characterised by an abrupt movement with stretched antennae. In *C. cyphergaster*,  
303 soldiers present a snout-like protuberance in their head that contains a frontal gland. Such an  
304 apparatus produces a mixture of terpenoids, often used against targets in defensive actions (for  
305 details, see Cristaldo et al., 2015). In this study, however, we were not always able to detect  
306 whether an agonistic display was followed by chemical spray.

307 When attacked by hosts, the proportion of aggressive reactions initiated by inquilines  
308 was not significantly higher than the proportion of non-aggressive interactions (GLM;  $F_{1,98}=1.74$ ,  
309  $P=0.18$ ; **Fig. 4**). When threatened, or even severely injured by hosts, inquiline workers never  
310 retaliated (attacking; **Fig. 5**). Instead, individuals were more likely to adopt evasive manoeuvres  
311 and quickly divert from aggressors. These actions occurred immediately after an active contact  
312 with host individuals was established, and included behaviours that avoided the opponents  
313 (reversing, bypassing; **Fig. 5**). Besides escaping from host threats, inquiline workers also  
314 performed ignoring behaviour. In this case, individuals actively touched by hosts did not react  
315 to such a stimulus, remaining completely stationary (ignoring; **Fig. 5**).



316

317 **Figure 4.** Interactions observed in closed arenas for hosts, *C. cyphergaster* (right), and inquilines, *I.*  
318 *microcerus* (left). Proportions were calculated by the number of aggressive and non-aggressive  
319 interactions observed, divided by the total number of observations taken from video-samples (N=10).  
320 Behaviours that do not preclude interaction (i.e. resting, walking and antennating wall) are not  
321 represented. For this reason, frequencies do not sum up to 100%. Light bars: aggressive interactions;  
322 Dark bars: non-aggressive interactions.



323

324 **Figure 5.** Behavioural profiles observed for each caste. Nodes represent behaviours performed by  
 325 individuals, whereas connecting edges (arrows) represent behavioural changes occurred from one  
 326 behaviour to another. Behaviours with the highest influence on the network are highlighted with thicker  
 327 node contours. Node size was adjusted using calculated centrality measures to visually represent the  
 328 degree of influence exerted by each behaviour upon the profiles. Obs.: For inquiline worker, attacking  
 329 never happened and, therefore, this behaviour is not connected to the network. A version containing  
 330 calculated scores is included in the Supplementary material (Figure S1).

331

332 The behaviour of inquiline soldiers was an exception to such a lack of aggressiveness  
 333 among inquilines. As opposed to inquiline workers, inquiline soldiers performed aggression in  
 334 retaliation to host assaults (Supplementary Material, **Video S1**), even though this occurred not  
 335 so frequently (attacking, **Fig. 5**). Aggression performed by inquiline soldiers consisted of  
 336 snapping attacks, a sudden release of slender mandibles pressed against each other producing  
 337 powerful strikes over opponents (Supplementary Material, **Video S2**).

338 ***Inquilines interacted little with hosts even when locally restricted***

339 Inquilines exhibited low interactivity with host individuals, even when locally restricted  
340 and presumably more prone to meet, such as in closed arenas. The proportion of between-  
341 species observations was considerably lower than the proportion of within-species  
342 observations (*GLM*;  $F_{1,178} = 71.73$ ,  $P < 0.001$ ). Besides, regarding the behavioural change,  
343 inquiline workers exhibited a loop between resting, walking and antennating nestmate, all  
344 behaviours with no contact with the host (**Figure S3**). The **Table S1** of Supplementary Material  
345 contains absolute numbers for between- and within-species observations for each one of the  
346 castes.

347

348 ***Hosts were active in arenas, while inquilines were lethargic***

349 When placed in closed arenas, host individuals performed antennation on the arena wall  
350 more frequently than inquiline individuals (*GLM*;  $F_{1,78} = 4.73$ ,  $P < 0.005$ ), an indication that hosts  
351 could be possibly attempting to broaden their patrolled area. We confirmed this suspicion with  
352 results from the second experiment, with open arenas: host individuals quickly moved to the  
353 external area passing through the gate as soon as they found it. Either in the presence or  
354 absence of inquiline individuals, there was no difference in the mean time spent by host  
355 individuals to leave the internal area ( $19.93 \pm 3.56$  seconds,  $F_{1,9} = 0.34$ ,  $P = 0.57$ ), meaning that  
356 inquilines did not threaten hosts. Inquilines, in turn, were more prone to remain stationary and  
357 never left the internal area, a result that seem to confirm the putative lethargic behaviour of  
358 inquilines.

359

360 ***Inquiline's defecation prevented host aggression***

361 We observed an unexpected response among inquiline workers: when threatened by  
362 hosts, inquiline workers deposited faecal pellets always towards the direction from which they  
363 suffered threats (Supplementary Material, **Video S3**). Rather than usual defecation, this  
364 behaviour seemed to be elicited by host aggressions in a particular way: when receiving attacks  
365 from backwards, individuals immediately placed faecal pellets in front of aggressors and  
366 escaped forward. Threats coming from any other direction, however, triggered a slightly  
367 different response: before defecating, individuals first adjusted their posture accordingly,  
368 placing themselves in a way that they could quickly drop faecal pellets in front of the aggressors.  
369 Only after such a move, inquiline workers defecated and escaped forward. We observed this  
370 behaviour 33 times, and in all occurrences, faecal pellets immediately prevented inquilines of  
371 being chased or receiving further attacks from aggressors. Although we did not measure  
372 whether inquiline faeces have a repellent effect over hosts, it was evident in our recordings that

373 areas containing faeces were less visited by host individuals (Supplementary Material, **Video**  
374 **S3**).

375

### 376 ***Caste types showed unique behavioural profiles***

377 We found striking differences when comparing the behavioural profile of hosts and  
378 inquilines (**Fig. 5**). Visual representations obtained from network analyses revealed unique  
379 configurations for each of the castes analysed. For all caste types, walking was the behaviour  
380 with the highest centrality score (walking; **Fig. 5**), that is, with the highest influence. The only  
381 caste type that presented two behaviours equally influential to the network was that of  
382 inquiline workers. In this group, besides walking, conspecific antennation also reached the  
383 highest centrality score (antennating nestmate; **Fig. 5**). As highlighted above, because inquiline  
384 workers never performed an attack, this behaviour presented the lowest centrality score and did  
385 not connect to the network (attacking; **Fig. 5**).

386

### 387 **Discussion**

388

389 In environments where individuals are constantly surrounded by potential aggressors,  
390 the evolution of a “peaceful behaviour” may appear, at first, counter-intuitive. Our results  
391 demonstrate, however, that for inquilines (*I. microcerus*) non-aggressive behaviour is a valid  
392 strategy that mitigates detrimental consequences of unexpected encounters with hosts (*C.*  
393 *cyphergaster*). More important, it seems to secure housing for inquiline colonies within host  
394 nests in the long-term. Evasive behaviour by inquilines has been previously suggested as one of  
395 the proximate causes in inquilinism, as it reduces the frequency of encounter between colonies.  
396 Here, besides providing substantial behavioural data supporting this idea, we showed that once  
397 inevitably exposed to hosts, inquiline individuals can modulate their behaviour to a less  
398 threatening profile and circumvent confrontation. As compared to other termite species, this  
399 suggests a degree of adaptation towards a more flexible behaviour which could, in turn, strongly  
400 favour cohabitation.

401

### 402 **The behavioural adaptations of a peaceful guest**

403 A set of behaviours seem to support our interpretation of inquilines as peaceful guests  
404 within host nests. First, when encountering host individuals, inquilines suffered several attacks  
405 but did not react with the same level of aggressiveness. Lack of aggression was markedly  
406 evident among inquiline workers. This caste not only never performed a single attack during  
407 our experiments but also managed to move away from aggressors with evasive manoeuvres  
408 (reversing, bypassing; **Fig. 5**). The same was not observed for inquiline soldiers, who did



409 retaliate host attacks with snapping (attacking; **Fig. 5**). It is worth mentioning, however, that  
410 soldiers are rare in natural colonies of *I. microcerus* (Cunha et al., 2003), and sometimes even  
411 absent (HH, pers. obs.). Thus, it is unlikely that the aggressive behaviour of a minority would  
412 contribute to increase the species aggressiveness substantially. Although we did not find  
413 evidence pointing in such a direction, we acknowledge the necessity of more studies evaluating  
414 the interplay between worker's and soldier's behaviour in field conditions, something that was  
415 clearly beyond the scope of the present work.

416 A second behaviour linked to the levels of aggressiveness reported (**Fig. 3**) was the  
417 reduced mobility of inquilines. Consequently, the interaction between hosts and inquilines in  
418 arenas was limited. In open arenas, only hosts moved to the external area over time, whereas  
419 inquilines remained quiet in the inner portion. Such spatiotemporal segregation could be a  
420 direct consequence of the behavioural profile of hosts. As we have shown, walking was a  
421 commonly performed behaviour among all castes, but at the same hosts spent less time  
422 remaining stationary in the same place (resting, **Fig. 5**). Theoretically, as they walk more  
423 intensively and explore sites more efficiently, gates would be more readily found. In this regard,  
424 the presence or absence of non-nestmates in arenas did not affect the time spent by hosts to  
425 pass through the gate and access the external area. This result indicates that inquilines did not  
426 necessarily triggered the collective motion of hosts to the external area. Dynamics of both  
427 collective behaviour and environment have been suggested to regulate group-level properties in  
428 ants (Gordon, 2019). In termites, some studies have explored principles of collective behaviour  
429 (Sumpter, 2006) using agent-based models to understand self-organisation of groups, from nest  
430 construction processes (Deneubourg, 1977) to aspects of social facilitation (Miramontes &  
431 DeSouza, 1996; DeSouza et al., 2001). Still, for nest-sharing termite species, to what extent  
432 individual behaviour shape collective motion patterns, remains a topic to be fully understood.

433 A third component that seemingly affected the amount of aggression we observed in  
434 arenas was defecation by inquilines. Presence of faecal pellets shortened host-inquiline contact  
435 in virtually all occasions, and consequently, host attacks towards inquilines were less frequent.  
436 This result indicates that faeces may improve evasion by preventing host aggressions. In fact,  
437 defecation as an evasive mechanism is not exclusive of *I. microcerus*, being first described for  
438 termites by Coaton (1971) in *Skatitermes* sp. (Termitidae: Apicotermitinae). Such a defensive  
439 behaviour may have important implications for cohabitation: if faeces indeed repel hosts, single  
440 pellets placed in narrowed galleries throughout the nest could prevent host contact in a very  
441 efficient, inexpensive way. Besides, it is possible that while placing the pellets, *I. microcerus*  
442 would be spreading their scent throughout the entire nest, making it harder for hosts to locate  
443 the core of their colonies. Accordingly, while studying the cohabitation of another host-inquiline  
444 pair (*C. cavifrons* and *I. inquilinus*, respectively), Jirošová et al. (2016) showed that walls from

445 the inquiline portion of nests contain levels of C12 alcohols, a repellent for host individuals.  
446 According to these authors, chemically mediated spatial separation of hosts and inquilines may  
447 aid to avoid conflict. Among other non-related groups, such as the cuckoo bumblebee, repellent  
448 odours are known to reduce host attacks (Lhomme et al., 2012), suggesting that this is an  
449 effective mechanism across taxa.

450

#### 451 **The meaning of an interspecific encounter**

452 The non-aggressive behaviour observed among inquilines raises the question of  
453 whether such a strategy would be useful within the nest. After all: are encounters with the host  
454 species a real threat for inquiline colonies? We provide evidence that there are, indeed,  
455 detrimental consequences of encountering hosts. As mentioned before, aggression among hosts  
456 was performed not only by soldiers but also by workers. (attacking, **Fig. 5**), which seems to  
457 indicate that defence would be integrated between castes. While host soldiers attack individuals  
458 spraying chemicals and provoking disruptive reactions, host workers provided with functional  
459 mandibles, are the ones who inflict the physical damage. In *C. cyphergaster*, terpenoids sprayed  
460 from the frontal gland of soldiers function as an effective alarm pheromone (Cristaldo et al.  
461 2015). Thus, once a target is sprayed, it recruits nestmates to converge upon the site and deploy  
462 themselves around it (Eisner et al., 1976). In such a harsh environment, where virtually all  
463 individuals are potential aggressors, it is plausible that a peaceful behaviour, rather than a  
464 costly aggressive profile, could be a simpler alternative solution. All in all, as compared to a  
465 belligerent set of behaviours, a non-threatening profile would demand less elaborated actions,  
466 plausibly resulting in lower activity and reduced probability of interspecific encounter.

467

#### 468 **The mechanism of conflict avoidance**

469 Behaviours preventing confront escalation are widespread. When attacked by host ant  
470 workers, for instance, parasite ant queens do not react aggressively and, instead, quickly move  
471 towards the fungus garden remaining quietly there (Nehring et al., 2015). In another typical  
472 social parasite, *Maculinea rabeli* (Lycaenidae), larvae individuals are known to suppress  
473 aggression from their host ants by mimicking aspects of the brood's pheromone (Akino et al.,  
474 1999; Pierce et al., 2002). Among bees, changes in the host's behaviour towards non-aggressive  
475 types have been also reported: in the presence of the cuckoo bumblebee *Bombus vestalis*, host  
476 colonies decrease worker aggressiveness towards alien individuals, possibly due to changes in  
477 the host worker's discrimination (Lhomme et al., 2012). Examples of aggressiveness being  
478 affected by external factors are not exclusive to social insects, extending to other invertebrate  
479 and vertebrate groups (Aureli et al., 2002; Baan et al., 2014; Gobush & Wasser, 2009; Thierry et  
480 al., 2008). In termites, aggressiveness may depend on factors such as diet (Florane et al., 2004),

481 caste ratios (Roisin et al., 1990), nestmate recognition (Delphia et al., 2003; Haverty & Thorne,  
482 1989), group composition (Haverty & Thorne, 1989), territoriality (Adams & Levings, 1987;  
483 Levings & Adams, 1984) and resource availability (Cristaldo et al., 2016b). Even inter-colony  
484 aggression, presumably more predictable due to higher relatedness, is not always consistent  
485 (Binder, 1987). Species may exhibit behavioural plasticity (Ishikawa & Miura 2012), responding  
486 aggressively in some cases (Su & Haverty, 1991), and lacking aggression in others (Delaplane,  
487 1991; Neoh et al. 2012). Altogether, these reports indicate that it is possible to have scenarios in  
488 which termite species adopt low aggressiveness profile, rather than the typical aggressiveness  
489 observed among the group.

490         The symbiosis between *C. cyphergaster* and *I. microcerus* is a case of obligate  
491 inquilinism, meaning that at least for inquilines, nest-sharing has become mandatory (Shellman-  
492 Reeve, 1997). Evolutionary costs and drawbacks of such a specialisation by inquilines remain to  
493 be assessed, although the benefits associated with nest invasion seem to be straightforward:  
494 nest invaders are not required to spend time and energy building their own home. At the same  
495 time, being nest construction a demanding, costly process (Korb & Linsenmair, 1999), one  
496 would expect such inquiline invasions to be not strictly in the interest of hosts. In this sense, it  
497 would be reasonable to think of a scenario in which hosts would endeavour to detect inquilines,  
498 whereas inquilines would try to go unnoticed by hosts. Under such driving forces, it is possible  
499 that an evolutionary arms race would take place (Dawkins & Krebs, 1979), leading hosts and  
500 inquilines to reach well-adjusted behavioural profiles. In doing so, both cohabitant would  
501 become highly specialised in their neighbour (Kilner & Langmore, 2011).

502

### 503 **Cohabitation and conflict**

504         Cohabitation goes way beyond the “living in overlapping spaces”. Instead, it is a result of  
505 multiple interactions over time. Whether interactions contribute for the emergence of stable  
506 relationships depends on the consequences mutually inflicted by the parties involved. With our  
507 approach, we presented findings supporting a notion that hostile interactions do not always  
508 lead to increased aggressiveness between opponents, especially if asymmetric aggression or  
509 lack of reciprocal retaliation is in place. Although a common event in nature, conflict can be a  
510 limiting factor for species coexisting. While surpassing acceptable thresholds, excessively high  
511 levels of aggression can jeopardise relationships between organisms and lead entire colonies to  
512 collapse. The behavioural adaptations we described, seem to allow inquilines to manage the  
513 amount of aggression received from their hosts. Such a non-threatening individual behaviour  
514 may play a fundamental role in cohabitation, as it seems to increase the chances of a stable  
515 (although asymmetric) relationship between host and inquiline colonies considerably. We  
516 suggest that further research should explore the contributions of such individual actions on

517 collective patterns in the system. While in line with previous reports on cohabitation between  
518 termite societies, our findings reinforce the growing view of conflict management as a critical  
519 component of socially complex systems. Finally, descriptions of peaceful mechanisms by  
520 recipients of aggression in locally restricted, hostile environments should contribute to putting  
521 conflict and its consequences in a broader perspective, adding novel insights for studies  
522 involving multiple group-living organisms.

523

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538

## 539 **Author contributions**

540 HH, PFC & ODS conceived the study; HH & PFC developed fieldwork, behavioural recording and  
541 ethogram design. HH conducted data collection, statistical analysis and drafted the paper. PFC &  
542 ODS commented on the manuscript, improving it considerably for submission.

543

## 544 **Ethical statement**

545 We obtained all required permits for the present study, thus complying with relevant  
546 regulations governing animal research in Brazil. This includes: (i) permits from The Brazilian  
547 Institute for the Environment and Renewable Natural Resources (IBAMA, no. 33094); (ii)  
548 permission from The Brazilian Enterprise for Agricultural Research (EMBRAPA) at Sete Lagoas;  
549 (iii) permission from landowners at the Divinópolis site to conduct the study on their property;  
550 and (iv) tacit approval from the Brazilian Federal Government implied by employing authors to  
551 conduct scientific research. None of the sampled species had protected status. No genetic  
552 information was accessed in the study.

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