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## Cuckoo wasps manipulate foraging and resting activities in their hosts

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11 **Cuckoo wasps manipulate host foraging and resting activities through**  
12 **behavioural interactions**

13

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18 Short title: Host manipulation by social parasite wasp

19

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26

27       **ABSTRACT**

28       Parasite-induced alterations in host behaviour have been reported in a large number of  
29 taxa. However, some parasites are better than others to exploit the resources offered by their  
30 hosts. To date, our understanding of the extent to which some obligate parasites exploit social  
31 insect colonies is still limited. In this study, we examined parasite-mediated behavioural  
32 alterations of *Polistes biglumis* wasps parasitized by the obligate social parasite *P.*  
33 *atrimandibularis* by comparing host female-activity in parasitized and non-parasitized  
34 colonies. Host foundresses foraged more and rested less in parasitized than in non-parasitized  
35 colonies. Next, we used short-term parasite removal experiments to investigate how social  
36 parasites manipulate their hosts. These experiments allowed us to confute the alternative  
37 hypothesis that changes in host behaviour were the result of changes in colony needs (usually  
38 greater in parasitized than non-parasitized colonies). Parasitized host-foundresses foraged  
39 more and their adult female offspring rested less when social parasites were on the nest rather  
40 than after their removal. *P. atrimandibularis* may use behavioural interactions (such as  
41 antennation and trophallaxis) to manipulate host activities, rather than visual, acoustic, or  
42 chemical signals as other parasites do.

43

44       Key words: *Polistes*, social insects, host-parasite system, behavioural manipulation,  
45 proximate mechanism, brood parasitism, dominance-subordinance interactions

46

## 47        **INTRODUCTION**

48        In interactions between parasites and their hosts, parasites are selected for their ability to  
49        manipulate their hosts and enhance their opportunities for reproduction, transmission, or host  
50        encounter (Combes 1991; Poulin and Thomas 1999; Combes 2001). Examples of changes in  
51        host phenotype induced by endoparasites have been documented in a large number of taxa,  
52        ranging from viruses to protozoan, and from flatworms to helminths (reviewed in Schmid-  
53        Hempel 1998; Thomas et al. 2005a; Lefèvre et al. 2008). For instance, a nematode changes  
54        the colour and behaviour of infected Turtle ants (*Cephalotes*) which are its intermediate hosts  
55        leading to trophic transmission into birds, the final host (Yanoviak et al. 2008). Similarly,  
56        another nematode induces a bioluminescent coloration in its host insect larva, causing avian  
57        predators to avoid affected larvae as prey and thus preventing itself and its host from being  
58        eaten (Fenton et al. 2011). The alteration of host behaviour by parasites is a strategy of host  
59        manipulation that is especially impressive and is well documented in viruses, bacteria,  
60        protozoan, arthropods, and birds (e.g., Soler et al. 1995a; Soler et al. 1995b; Berdoy et al.  
61        2000; Moore 2002; Klein 2003; Ponton et al. 2006; Rogers and Bates 2007). An obligate  
62        endoparasitic strepsipteran induces its host wasps, for example, to desert their colonies and  
63        aggregate outside, enhancing parasite opportunity for mating (Hughes et al. 2004).

64        Ectoparasites manipulate and alter host phenotypes by exploiting the chemistry,  
65        physiology, morphology, and behaviour of their hosts (Nash and Boomsma 2008). For  
66        example, cowbird young use begging calls to elicit enhanced food provisioning by their host  
67        parents (Gloag and Kacelnik 2013). The larvae of a parasitic wasp induce their spider hosts to  
68        build a modified web for their own protection (Eberhard 2010). Social parasites can limit  
69        attacks by their social insect hosts using chemical weapons (e.g., D'Ettorre et al. 2000; Mori  
70        et al. 2000), and/or intercepting the host communication-code, which facilitates host nest  
71        invasion and integration (Lenoir et al. 2001; Thomas et al. 2005b; Nash and Boomsma 2008;

72 Bagnères and Lorenzi 2010). Host manipulation by social parasites is impressive because it  
73 involves entire colonies rather than one or a few hosts (Hughes 2008).

74 Among the primitively eusocial *Polistes* wasps (Hymenoptera, Vespidae, Polistinae), there  
75 are three species of obligate and permanent social parasites: *P. sulcifer*, *P. semenowi*, and *P.*  
76 *atrimandibularis*. As obligate parasites, they depend entirely on host social structures, lack  
77 the worker caste, and use their host workforce to rear their own brood, which is composed  
78 exclusively of reproductives (Cervo and Dani 1996). *Polistes* parasites have evolved  
79 morphological and chemical adaptations that facilitate invasion and integration in host  
80 colonies (Cervo and Dani 1996; Cervo 2006; Lorenzi 2006; Bagnères and Lorenzi 2010). To  
81 date, no evidence exists of a pheromonal control in *Polistes* wasps and dominance-  
82 subordination interactions are almost entirely behaviourally mediated (Pardi 1948; West-  
83 Eberhard 1969; Reeve 1991). Similarly, behavioural dominance acts seem to be the only way  
84 social parasites establish relationships with their hosts, as neither pheromonal nor acoustic  
85 communication channels play any role (Cervo, 2006). *Polistes* social parasites may therefore  
86 manipulate and alter host activities through behavioural interactions. A similar strategy is  
87 used by *P. fuscatus* queens to regulate the activity of their own workers (e.g. foraging effort)  
88 and monopolize egg-laying (Reeve and Gamboa 1983, 1987), although this strategy is not  
89 widespread (Jha et al. 2006).

90 In this study, we used the *P. biglumis* - *P. atrimandibularis* host-parasite system to assess  
91 whether and how social parasites controlled and altered their host behaviour. We  
92 hypothesised that parasites used behavioural interactions to induce host females to forage  
93 intensively to the advantage of parasite brood. To test this hypothesis, we compared host  
94 behaviour in parasitized and non-parasitized colonies and ran short-term parasite removal  
95 experiments. Our experiments simulated a naturally-occurring phenomenon: each day  
96 parasites leave their nests several times to forage (Cervo 2006) and sometimes they do not

97 return, possibly due to fatalities (personal observations). Removal experiments have been  
98 routinely used in the study of social regulation in *Polistes* colonies (e.g., Reeve and Gamboa  
99 1987; Tibbetts and Huang 2010).

100

101       **MATERIALS AND METHODS**

102       *The Species and their Interaction*

103       *Polistes biglumis* wasps live in mountain zones (1600-2350 m a.s.l.) in Southern Europe.  
104       The severe climatic conditions reduce the length of the nesting period to 3.5-4 months (from  
105       late May to September). Colonies are always strictly founded by single foundresses (solitary  
106       foundation) and are small, i.e., they produce less than 30 individuals throughout the nesting  
107       season (Lorenzi and Turillazzi 1986). In the studied population, the single foundress is the  
108       most active female even after brood emergence, as most of the emerging females are actually  
109       reproductive females (Fucini et al. 2009; Lorenzi and Thompson 2011). Although *P. biglumis*  
110       wasps have efficient recognition systems (Lorenzi et al. 1997; Lorenzi and Filippone 2000),  
111       their nests are targeted by cleptoparasites (Uboni and Lorenzi 2013), by conspecific social  
112       parasites (Lorenzi and Cervo 1995), and by obligate social parasites (*P. atrimandibularis*)  
113       (Cervo et al. 1990b). Obligate social parasites overcome host detection by possessing few  
114       recognition cues and gradually matching those of their hosts, so that hosts accept their  
115       parasites as nestmates (Bagnères et al. 1996; Lorenzi et al. 1999; Lorenzi and Bagnères 2002;  
116       Lorenzi 2003; Uboni et al. 2012). Obligate social parasites may invade *P. biglumis* colonies  
117       about a month after their foundation, when the foundress is still the only adult wasp in the  
118       colony (pre-emergence phase; Cervo et al. 1990a). Since parasites peacefully invade host  
119       colonies and do not kill or harm host foundresses, parasite and host foundress cohabit in the  
120       parasitized nest (Lorenzi et al. 1992). When parasites enter host colonies, they destroy host  
121       eggs and young larvae (but spare old larvae and pupae of the host), suppress host foundress  
122       reproductive capacity, and begin laying their own eggs (Cervo et al. 1990a; Cervo and  
123       Lorenzi 1996). Parasitized colonies will then produce first host brood and later parasite  
124       brood.

125

126 *Study Site and Field Methods*

127 Behavioural observations and experiments were conducted in the field, near Montgenève  
128 (44°55'N, 6°43'E, Hautes Alpes, France, 1850 m a.s.l.), in a typical Alpine environment with  
129 *Pinus silvestris*, *Larix decidua*, and wide meadows. We analysed a *P. biglumis* population  
130 where *P. atrimandibularis* has been recorded since 1958. Up to 20-40 % of founded nests  
131 may be parasitized annually (Lorenzi and Thompson 2011).

132 We found 98 *P. biglumis* colonies in different summers (1997, 1998, 2001, 2002, 2006,  
133 and 2007). We individually marked the adult members of each colony on the thorax (i.e., the  
134 host foundress, its adult female offspring, and the parasite female, where present) with unique  
135 colour combinations of enamel paint. In few cases, colonies were discovered later in the  
136 season than others. In this case, foundresses were identified by their worn wings. The tips of  
137 wasp wings become more and more worn as the wasp performs its daily activities. Thus, the  
138 longer a wasp has emerged as an adult, the more worn its wings are.

139

140 *Behavioural Observations in Parasitized vs. Non-parasitized Colonies*

141 We conducted behavioural observations on 33 parasitized and 35 non-parasitized colonies  
142 (hereafter, untreated colonies) during both the host pre- and post-emergence phases, for a  
143 total of 368 h, by using a Canon MV960 camcorder, placed at approximately 20 cm from the  
144 nest (two observations per colony, each about 2 hours long, see Table 1 for details).

145 Behavioural observations were performed at least 10 days after the period when parasites  
146 invade host nests, so that in parasitized colonies all larvae were parasite brood. Behavioural  
147 observations were performed on sunny days, between 10:00-16:00 h local time, after  
148 checking the number of brood in the nest (eggs, larvae and pupae). For data elaboration, we  
149 calculated the amount of time spent by the host females motionless or grooming (hereafter,  
150 resting). We also recorded departure and return times from/to nests to quantify the time spent

151 foraging. These behaviours (staying motionless, grooming, leaving the nest, returning to the  
152 nest) are easily scored and clearly distinguishable from any other behaviour. Behavioural data  
153 were analysed as proportion of observation time.

154

#### 155 *Parasite Removal Experiment*

156 Colony productivity is typically higher in parasitized than in non-parasitized colonies  
157 (mean number of larvae  $\pm$  SD:  $36 \pm 11$  vs.  $24 \pm 13$ ; Lorenzi et al. 1992), and therefore the  
158 number of larvae is larger in parasitized than in non-parasitized colonies. Thus, the two types  
159 of colonies presumably differ in the amount of food required to feed larvae (i.e, in colony  
160 needs). Additionally, in parasitized colonies, enhanced foraging activity of host foundresses  
161 and their adult offspring might be caused by begging by parasite larvae, rather than by  
162 manipulation of host behaviour by adult parasite. To test whether differences in host  
163 behaviours were associated to the presence of adult parasites on the nest or rather to its brood  
164 begging hosts for food, we performed short-term parasite removal experiments on another  
165 group of parasitized colonies (hereafter called treated colonies,  $n = 30$ ). Short-term removal  
166 experiments have been previously used to test how queens regulate their worker activities in  
167 *Polistes* colonies (Reeve and Gamboa 1987). Experiments were conducted in the field and  
168 were not blind because of visible morphological differences between species. However, wasp  
169 behaviours were sufficiently clear to avoid subjective interpretation by the observer. All  
170 observations were performed by the same observer (S.F.) who recorded the time when the  
171 behaviours of interest begun or stopped (no video recording).

172 We performed 4-hour behavioural observations on these colonies, as follows. Before  
173 parasite removal, we performed a 2-hour behavioural observation (control observation) on  
174 each colony, for a total of 58 h of observation. Then, each parasite was removed from its  
175 colony and kept in a fresh box with water and honey for 4 hours. A 2-hour behavioural

176 observation (experimental observation) was performed during the 3<sup>rd</sup> and 4<sup>th</sup> h after parasite  
177 removal, for a total of 54 h. Therefore each experiment lasted 6 hours. Few behavioural  
178 observations were slightly shorter than two hours, due to changes in weather conditions that  
179 interrupted wasp activity, leading to a total of 112 hours of observation. The time period of  
180 parasite removal was limited to 4 hours to limit potential damages to these rare social  
181 parasites. At the end of the experiment, each parasite was re-introduced into its host colony  
182 and both parasites and hosts soon resumed their typical activities. Therefore, no parasite was  
183 harmed during the parasite-removal experiments. The number of larvae did not vary within  
184 the 2-hour intervals before and after parasite removal. Eleven colonies used in this  
185 experiment were in the pre-emergence phase (n = 6 in 2001, n = 5 in 2002), while 19 were in  
186 the post-emergence phase (n = 11 in 2001, n = 8 in 2002). [In 10 pre-emergence and 10 post-](#)  
187 [emergence colonies, the pre-parasite removal observation was conducted between 10:00 and](#)  
188 [12:00, while the post-parasite removal observation was conducted between 14:00 and 16:00.](#)  
189 [As a control for effect of time of the day on wasp behaviour, we conducted pre-parasite](#)  
190 [removal observations on 1 pre-emergence and 9 post-emergence colonies between 12:00 and](#)  
191 [14:00 and paired these observations to post-parasite removal observations conducted at the](#)  
192 [same time the following day.](#)

193 During these observations, we recorded the amount of time spent by the host females  
194 motionless or grooming (i.e., resting) and departure and return times from/to nests to quantify  
195 the time spent foraging, as described above for the behavioural observations on untreated  
196 colonies. Before parasite removal, the observer also noted the behavioural interactions  
197 between parasites and their hosts, and whether the host or the parasite started them. All  
198 interactions were analysed as rates (number of acts/h) and classified as either strongly  
199 aggressive (darts, dominance-subordinance interactions, and sting attempts), or non-

200 aggressive (antennation and trophallaxis). All these behaviours are clear-cut and easily  
201 identified in the small colonies of this species.

202

### 203 *Statistical Analyses*

204 To avoid pseudoreplications, each colony supplied a single datum. Differences in host  
205 behaviour between parasitized and non-parasitized colonies were analysed using Generalized  
206 Linear Mixed Models for binomially distributed data and logit link function (e.g., time  
207 foraging/total observation time). Wasp activities may be affected by the number of larvae, as  
208 well as by the time of the day and the day of season. Therefore, we included in the models the  
209 number of larvae, time of the day and day of the season as covariates. We also included year  
210 as a random factor. We used Paired sample t-test in pairwise comparisons (i.e., to analyse  
211 data from parasite removal experiments). Statistical analyses were performed using SPSS  
212 21.0 statistical package (SPSS Inc, Chicago, IL).

213

214       **RESULTS**

215       *Behavioural Observations in Parasitized vs. Non-parasitized Colonies*

216       *Foundress behaviour*

217       Foundresses foraged significantly more and rested significantly less in parasitized than in  
218 non-parasitized colonies and in both the pre- and post-emergence phase (Fig. 1a, b). The  
219 variations in foundress foraging and resting between parasitized and non-parasitized colonies  
220 were larger in the pre-emergence than in the post-emergence phase (as shown by the  
221 significant interaction term colony status \* phase) (GLMM on foraging, colony status:  $F_{1,76} =$   
222 1284.845,  $P < 0.0001$ ; pre/post-emergence phase:  $F_{1,76} = 1524.528$ ,  $P < 0.0001$ ; colony status  
223 \* phase:  $F_{1,76} = 1206.252$ ,  $P < 0.0001$ ; number of larvae:  $F_{1,76} = 3349.922$ ,  $P < 0.0001$ ; time  
224 of the day:  $F_{1,76} = 3767.891$ ,  $P < 0.0001$ ; day of the season:  $F_{1,76} = 1033.981$ ,  $P < 0.0001$ ;  
225 random factor year:  $Z = 1.224$ ,  $P = 0.221$ ) (GLMM on resting, colony status:  $F_{1,76} =$   
226 1350.196,  $P < 0.0001$ ; pre/post-emergence phase:  $F_{1,76} = 11147.573$ ,  $P < 0.0001$ ; colony  
227 status \* phase:  $F_{1,76} = 2551.289$ ,  $P < 0.0001$ ; number of larvae:  $F_{1,76} = 3497.269$ ,  $P < 0.0001$ ;  
228 time of the day:  $F_{1,76} = 3497.269$ ,  $P < 0.0001$ ; day of the season:  $F_{1,76} = 1307.007$ ,  $P <$   
229  $0.0001$ ; random factor year:  $Z = 1.224$ ,  $P = 0.221$ ) (Fig. 1a, b).

230

231       *Worker behaviour*

232       Similarly to their foundresses, workers foraged significantly more and rested significantly  
233 less in parasitized than in non-parasitized colonies (Fig. 1a, b) (GLMM on foraging, colony  
234 status:  $F_{1,43} = 3574.681$ ,  $P < 0.0001$ ; number of larvae:  $F_{1,43} = 7834.205$ ,  $P < 0.0001$ ; time  
235 of the day:  $F_{1,43} = 1323.201$ ,  $P < 0.0001$ ; day of the season:  $F_{1,43} = 15189.188$ ,  $P < 0.0001$ ;  
236 random factor year:  $Z = 1.222$ ,  $P = 0.222$ ) (GLMM on resting, colony status:  $F_{1,37} =$   
237 6568.117,  $P < 0.0001$ ; number of larvae:  $F_{1,37} = 1830.293$ ,  $P < 0.0001$ ; time of the day:

238  $F_{1,37} = 1301.789, P < 0.0001$ ; day of the season:  $F_{1,37} = 49999.297, P < 0.0001$ ; random  
239 factor year:  $Z = 1.225, P = 0.221$ ) (Fig. c).

240

#### 241 *Parasite Removal Experiment*

##### 242 *The pre-emergence phase*

243 During the pre-emergence phase, host foundresses foraged significantly less and rested  
244 significantly more after parasite removal (compared to before parasite removal; Paired  
245 sample t-test, foraging:  $t = 4.071, df = 10, P = 0.002$ ; resting:  $t = -3.922, df = 10, P = 0.003$ ;  
246 Fig. 2a).

247

##### 248 *The post-emergence phase*

249 The same variations in host foundress behaviour were observed during the post-emergence  
250 phase, as host foundresses foraged less and rested more after parasite removal (foraging:  $t =$   
251  $4.763, df = 18, P < 0.0005$ ; resting  $t = -3.771, df = 18, P = 0.001$ ; Fig. 2b).

252 Adult host female offspring responded to parasite removal by significantly increasing the  
253 time spent resting ( $t = -2.100, df = 18, P = 0.050$ ), but did not change the time spent foraging  
254 ( $t = 1.435, df = 18, P = 0.168$ ; Fig. 2c).

255

##### 256 *Behavioural interactions*

257 Before parasite removal, parasites started non-aggressive interactions towards host  
258 foundresses significantly more often than host foundresses did towards their parasites, both in  
259 the pre- and the post-emergence phase (pre-emergence:  $t = -4.935, df = 10, P = 0.001$ ; post-  
260 emergence:  $t = -4.843, df = 18, P < 0.0005$ ; Fig. 3a). Strongly-aggressive interactions were  
261 very rare from both parts and were started by parasites as often as by host foundresses (pre-  
262 emergence:  $t = -0.279, P = 0.784$ ; post-emergence:  $t = -1.531, P = 0.157$ ; Fig. 3b).

263 Parasites interacted significantly more often with adult host offspring than host  
264 foundresses did (non-aggressive interactions:  $N = 19$ ,  $t = -3.966$ ,  $df = 18$ ,  $P = 0.001$ ; strongly-  
265 aggressive interactions:  $N = 19$ ,  $t = -2.162$ ,  $df = 18$ ,  $P = 0.044$ ; Fig. 3c).  
266

267        **DISCUSSION**

268        This field study provides evidence that *P. atrimandibularis* obligate social parasites deeply  
269 altered the time that hosts allotted to different activities on their colony. *P. atrimandibularis*  
270 parasites possibly used behavioural interactions to manipulate host behaviour.

271        The observations in untreated colonies indicated that there were behavioural changes in  
272 both host foundresses and their adult offspring. Indeed, foundresses in parasitized colonies  
273 foraged more and rested less than those in non-parasitized colonies in both the pre-emergence  
274 and the post-emergence phase. Similarly, host offspring foraged more and rested less in  
275 parasitized than in non-parasitized colonies. These results were obtained controlling for the  
276 number of larvae in the nest, the time of the day, and the day of the season. In all cases the  
277 analyses showed that these variables had a significant impact on host foraging and resting,  
278 but nest status (i.e., whether the nest was parasitized or not) was a highly significant predictor  
279 of host behaviour. Therefore, these results suggest that either adult parasites or parasite larvae  
280 (e.g., through “begging” signals; Cervo et al. 2004) directly stimulated an enhanced activity  
281 level in the hosts of parasitized colonies.

282        Parasite removal experiments indicated that parasite presence caused hosts to increase  
283 their activity levels and highlighted that parasites manipulated their host behaviour during the  
284 whole nesting season. We found that host foundresses and host offspring foraged less and  
285 rested more after parasite removal, even though the number of larvae in the nests did not  
286 change during the experiment. Therefore, we found no support for the hypothesis that hosts  
287 foraged more in parasitized colonies because they were stimulated by signals emitted by  
288 parasite larvae (e.g., “begging” signals; Cervo et al. 2004). Moreover, we would usually  
289 expect to find increased foraging activity during warmer hours (i.e., during 20 out of 30 post-  
290 parasite removal observations), due to the positive effect of air temperature on *Polistes*  
291 foraging activity (Fucini et al. 2014). Instead, we found the opposite pattern (i.e., host

292 [foundresses and host offspring foraged less and rested more after parasite removal\). This](#)  
293 [finding gives further support to our hypothesis that parasites induce their hosts to forage more](#)  
294 [and rest less.](#)

295 *P. atrimandibularis* parasites contribute to prey foraging as they plunder larvae from host  
296 nests other than the one they live in (Cervo et al. 1990b; personal observations). Therefore,  
297 removing parasites actually reduced the amount of food brought to the colonies, and should  
298 have increased colony needs and consequently promoted an increase in host activity. This  
299 was not the case in our observations, suggesting that parasites actively induced host  
300 foundresses to forage more and adult host offspring to rest less on the nests. Similarly,  
301 removing *P. fuscatus* queens from their colonies induced a decrease in worker activity (Reeve  
302 and Gamboa 1987).

303 Foraging reduces the opportunity for direct reproduction in social wasps more than any  
304 other colony task because of the high energetic cost and mortality risk (Markiewicz and  
305 O'Donnell 2001). Indeed, foundresses may die prematurely in parasitized nests due to  
306 overworking (Lorenzi et al. 1992). Therefore, *P. atrimandibularis* parasites attain great  
307 benefits by overexploiting their hosts, at enormous costs for their hosts.

308 Additionally, the results of parasite removal experiments suggested that parasites may  
309 stimulate and manipulate host female behaviour via behavioural interactions, i.e. mainly via  
310 non-aggressive interactions. Parasites frequently interacted with their hosts and were also the  
311 main initiators of interactions with host foundresses and their adult offspring. In *Polistes*  
312 wasps, dominant individuals mediate and regulate the activity of subordinate females by  
313 means of behavioural interferences, without relying on pheromones (Pardi 1948; West-  
314 Eberhard 1969; Reeve 1991). *P. atrimandibularis* may use similar means to control the  
315 activity levels of its hosts. Our results support the hypothesis that parasites act as dominant  
316 individuals on host nests.

317        Examples of behavioural manipulations of hosts by social parasites reported in the  
318 literature involve mainly the use of signals produced by parasites and perceived by the hosts,  
319 such as visual, acoustic, or chemical signals (Soler et al. 1995a; Kilner et al. 1999; Lenoir et  
320 al. 2001; Cervo et al. 2004; Bagnères and Lorenzi 2010). In those cases, parasites manipulate  
321 their hosts intercepting specific sensory channels (Combes 2001). After invasion, *P.*  
322 *atrimandibularis* acquires the chemical signature of its host nest (Bagnères et al. 1996).  
323 Therefore, there is no support for the hypothesis that this parasite uses cuticular chemistry to  
324 influence host behaviour. Most probably, behavioural interactions initiated by parasites are  
325 relatively more important than chemical cues as ways for host manipulation. However,  
326 additional studies will be necessary to support this hypothesis.  
327

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333

334

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472

473 Table 1. Sample size of the behavioural observations conducted in the field on untreated  
474 colonies.

	<b>Pre-emergence phase</b>		<b>Post-emergence phase</b>	
	<b>2006</b>	<b>2007</b>	<b>1997</b>	<b>1998</b>
<b>Parasitized colonies</b>	17	2	7	7
<b>Non-parasitized colonies</b>	12	9	3	11

475

476 **Fig. 1** Mean percentage + SE of the observation time spent foraging and resting in  
477 parasitized and non-parasitized colonies by a) host foundresses during the pre-emergence  
478 phase, b) host foundresses during the post-emergence phase, and c) by host female offspring.

479

480 **Fig. 2** Mean percentage + SE of the observation time spent foraging and resting before and  
481 after parasite removal by a) host foundresses during the pre-emergence phase, b) host  
482 foundresses during the post-emergence phase, and c) by host female offspring.

483

484 **Fig. 3** Mean rate of interactions (mean number of acts / h) + SE between parasites and host  
485 foundresses a) in the pre-emergence phase, b) in the post-emergence phase, and c) mean rate  
486 of interactions initiated by parasites and foundresses towards host offspring. Data were  
487 collected on treated colonies before parasite removal.