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Slave Drivers; Increased Foraging by Host Workers under the Slave-Making Ant *Plotomognathus Americanus*

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1 Slave Drivers: Increased Foraging by Host Workers under the Slave-Making Ant

2 *Protomognathus americanus*

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5 **Summary**

6 In parasite-host interactions, the host is a part of the extended phenotype of the parasite and
7 thus acts, often to its own detriment, in such a way that increases the parasite's fitness. This
8 study examines how the obligate slave-making parasite *Protomognathus americanus* alters
9 the 1) foraging and 2) nest preferences of its *Temnothorax* spp. hosts. After comparing the
10 foraging activity of 115 colonies with and without the parasite, parasitized colonies have a
11 greater proportion of *Temnothorax* workers foraging for food, a shorter discovery time of
12 food when it is available, and a greater proportion of total workers at a food source once it
13 has been found. This novel behavioural manipulation may be explained in part by the greater
14 depletion of fat reserves in the host worker force due to a disproportionate number of
15 trophallactic exchanges between the parasite and the host. The nest preferences of parasitized
16 colonies did not differ from those of nonparasitized colonies. Indeed, neither parasitized nor
17 nonparasitized colonies showed a preference for nests based on entrance width, cavity height,
18 or floor area. These results conflict with previous studies on related *Temnothorax* spp. that
19 show distinct nest preferences based on the parameters listed above.

20 **Key words** parasite control of host behaviour, social parasitism, foraging behaviour, nest
21 selection, slave-making ants, *Protomognathus americanus*

22 **1. INTRODUCTION**

23 It is estimated that up to half of all animal species are parasitic [1]. An increasing
24 number of parasites have not only been shown to evade detection by their hosts, but to also

25 manipulate their host's behaviour [2]. The hairworm parasite *Spinochordodes tellinii* induces
26 its katydid host to jump into freshwater where the parasite then reproduces [3]. In social
27 insects, endoparasitic strepsipterans drive their *Polistes* wasp hosts to gather with other
28 infected wasps outside the nest to facilitate mating [4]. Rainforest ants infected by *Cordyceps*
29 fungi climb up a plant and bite down on the underside of a leaf or stem, at which point the
30 fungus then grows a stalk and releases spores on other ants below [5].

31 Ants themselves can be parasitic, either social or otherwise. Around 230 ant species
32 are social parasites of other ants [6]. The obligate slave-making ant *Protomognathus*
33 *americanus* parasitizes *Temnothorax curvispinosus*, *T. longispinosus*, and *T. ambiguus*. The
34 parasite is unable to forage, feed itself, or take care of its own brood [7]. *Protomognathus*
35 *americanus* raid *Temnothorax* colonies, temporarily expelling the workers and the queen(s),
36 and then bring back captured pupae to their own nest. After the host pupae eclose, they
37 perceive the parasitic ants as their kin through chemical imprinting [6], a by-product of
38 normal ant development, and subsequently forage, care for the brood, and feed the slave-
39 making ants via trophallaxis. For this study, I conducted two experiments to test for novel
40 manipulation of two host behaviours by the parasite *P. americanus*: 1) foraging and 2) nest
41 selection.

42 In social insects, a minority of individuals forage, a risky activity, for the benefit of
43 the rest of the colony. It is presumed that *Temnothorax* spp. forage for detritus, sugars, or
44 microinvertebrates living in the leaf litter. Parasitized ant workers are an extension of the
45 parasite's phenotype and should behave, even if it is to their own detriment, in such a way
46 that is optimal for the parasite [8]. Therefore, a greater number of host workers in a
47 parasitized colony could be foragers or forage at a greater rate, even if they put themselves in
48 danger by doing so, in order to increase the nutrition and fitness of the parasite. In my first

49 experiment, I test the hypotheses that: 1) a greater proportion of *Temnothorax* workers from
50 parasitized colonies than from nonparasitized colonies are foraging for food; 2) slave workers
51 reach food faster than free living workers once it becomes available, and 3) a greater
52 proportion of parasitized *Temnothorax* workers than nonparasitized workers reach a food
53 source after it is found.

54 The foraging behaviour of *Temnothorax* is not well known; however, the collective
55 decision making behaviour of *T. curvispinosus* during nest selection is well studied [9, 10].
56 When a worker ant finds a potential nest site (frequently a hollow acorn or hickory nut on the
57 forest floor), it first recruits nest mates to the new site by using tandem runs (follow-the-
58 leader) and then by physically transporting nest mates to the new site after a threshold
59 number of recruiting ants is reached [11]. The “quorum sensing” ensures that a nest with
60 preferred qualities is selected over inferior nests, even when individual ants may only inspect
61 one potential site [12]. *Temnothorax curvispinosus* selects cavity nests based on, among
62 other parameters, volume, ceiling height, and entrance width. In general, the ants prefer
63 smaller entrances, larger cavity volumes, and high-ceilinged cavities [13]. Adult *P.*
64 *americanus* are generally larger than their hosts and may consequently prefer nests with
65 larger specifications. For my second experiment, I test the hypotheses that parasitized
66 colonies show a preference for nests with 1) larger entrance widths, 2) larger ceiling heights,
67 and 3) larger floor areas compared to the nest preferences of nonparasitized colonies.

68 **2. MATERIALS AND METHODS**

69 **(a) Ant collection and care**

70 Between October 2011 and September 2012, I collected colonies of *T. curvispinosus*
71 (from the Pocono Mountains, PA, Tibbetts Brook Park, Yonkers, NY, and Forest Park,
72 Queens, NY) and colonies of *T. longispinosus* (from Black Rock Forest and Storm King State

73 Park, West Point, NY). I also collected *P. americanus* colonies containing *T. curvispinosus*
74 (from the Poconos) and *T. longispinosus* (BRF, SKSP) during the same time frame. The
75 colonies were housed in artificial nests made of a 0.8 mm x 25 mm x 75 mm balsa wood
76 sheet sandwiched between two microscope slides. The top slide had a 2 mm wide entrance
77 drilled through it so that the ants could enter a cavity cut out of the balsa sheet with a ~912
78 mm² floor area. Each nest (hereby referred to as a “holding nest”) was placed in a 20 mm x
79 60 mm Petri dish. All nests were kept in an environmental chamber under a constant 25° C,
80 60% humidity, and photoperiod (12 hr light per day). Each colony was fed Bhatkar ant diet
81 [14] *ad libitum* about twice weekly. Host pupae were added to parasitized colonies as needed
82 to replenish their supply of host workers. Parasitized colonies only received host pupae
83 collected from the same field site.

84 **(b) Experimental design of foraging experiment**

85 For each colony used in this experiment, I recorded the number of *Temnothorax*
86 foragers (i.e., any individuals outside the nest that were not carrying out midden work) before
87 any ant diet was placed in the holding dish. After placing ~50 mg of ant diet 45 mm from the
88 nest entrance, I recorded the time it took for the first ant in each colony to reach the food
89 source and how many workers arrived at the food source before the first worker returned to
90 the nest and performed trophallaxis with a nest mate (or otherwise recruited a nest mate to the
91 food source). In this way, I only recorded individual ants that foraged without having been
92 recruited by returning foragers. For this experiment, 16 parasitized colonies (1 parasitized *T.*
93 *curvispinosus* from Poconos, 5 parasitized *T. longispinosus* from BRF, and 10 parasitized *T.*
94 *longispinosus* from SKSP) and 99 host colonies (1 *T. curvispinosus* from Forest Park, 3 *T.*
95 *curvispinosus* from TB park, 13 *T. curvispinosus* from Poconos, 27 *T. longispinosus* from
96 BRF, and 55 *T. longispinosus* from SKSP) were examined.

97 **(c) Experimental design of nest selection experiment**

98 I placed two newly constructed artificial nests in an experimental arena (a 150 X 25
99 mm Petri dish with polytetrafluoroethylene on the inside wall to prevent escape) 75 mm apart
100 from each other. The two nests differed from a holding nest by only one parameter, entrance
101 width (4 mm vs. 1 mm), cavity height (2.4 mm vs. 1.6 mm), or floor area (1237.5 mm² vs.
102 825 mm²). I flipped a coin to determine which type of nest was on which side of the arena.
103 Then I placed a holding nest containing either a parasitized or nonparasitized colony into the
104 arena 75 mm from each of the empty nests. I removed the top slide to encourage nest
105 relocation and, 48 hours later, recorded which of the two possible nest sites the colony chose.
106 If all the larvae were in one nest, I counted that as a selection, but if the larvae were split
107 between both nests then I did not count that trial in the results. For this experiment, 20
108 parasitized and 20 nonparasitized colonies went through one trial per nest parameter in a
109 random order with at least a 24 hr break between trials.

110 All the colonies were collected from SKSP and therefore contained *T. longispinosus*
111 workers. I removed workers and brood so that each nonparasitized colony consisted of 1
112 queen, 15 workers, and 15 larvae and each parasitized colony consisted of 4 slave-makers, 15
113 host workers, and 15 larvae. The 20 parasitized colonies were obtained by dividing up 10
114 parasitized colonies. Each "sub-colony," and therefore each individual ant, participated in
115 only one trial per nest parameter.

116 By maintaining a consistent number of *Temnothorax* workers, I could control for the
117 effects of colony size on nest selection. Additionally, I conducted entrance width tests with
118 "whole" colonies of varying sizes (16 parasitized *T. longispinosus*, 16 nonparasitized *T.*
119 *longispinosus*, and 10 nonparasitized *T. curvispinosus*), assuming that colony size does not
120 affect entrance width preference. I used the same criteria as above to determine nest choice.

121 **(d) Statistical analysis**

122 All statistical tests were carried out in JMP 9 (SAS Institute). I used a nonparametric
123 Wilcoxon rank sum test to compare, between the parasitized and nonparasitized colonies, 1)
124 the mean number of initial foragers, 2) mean number of total foragers, 3) mean discovery
125 time per initial forager, 4) proportion of workers foraging before the appearance of food, and
126 5) the proportion of workers at the food source after its appearance. I used a nonparametric
127 test instead of the parametric Student's t test because the samples were not normally
128 distributed.

129 I used a Chi-square test for association to determine if parasitization was correlated
130 with nest choice based on cavity height and floor area. I used a Fisher's exact probability test
131 to determine whether there was a difference in nest preference based on entrance width
132 because of smaller sample sizes in the data. I also performed a Chi-square test for association
133 to determine if parasitization was correlated with entrance width preference of the "whole"
134 colonies. I performed a Wilcoxon rank sum test to determine if mean colony size was
135 different between those colonies that selected the 4 mm entrance and those that selected the 1
136 mm entrance, because, again, the data were not normally distributed.

137 **3. RESULTS**

138 **(a) Foraging**

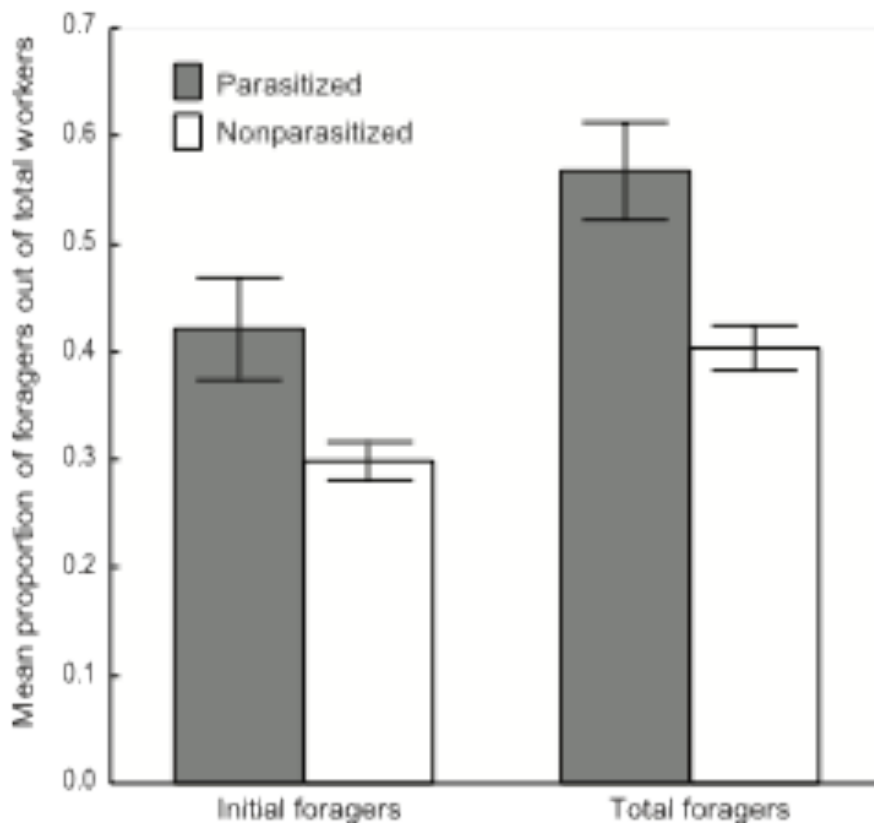
139 Parasitized colonies had a significantly greater mean number of initial foragers ($\bar{x} \pm$
140 $SE = 17.8 \pm 3.7$) and total foragers ($\bar{x} \pm SE = 24 \pm 4.8$) than the nonparasitized colonies (\bar{x}
141 $\pm SE = 9.9 \pm 0.8$ and 13.5 ± 1 , respectively) ($Z = 2.0231$, $p = 0.0431$ and $Z = 2.14373$, $p =$
142 0.0321 , respectively). Parasitized colonies also had a significantly greater proportion of the
143 work force foraging before the appearance of food (Fig. 1, $Z = 2.46503$, $p = 0.0137$) and a
144 significantly greater proportion of host workers at the food source after its appearance (Fig. 1,

145 $Z = 2.91774$, $p = 0.0035$). The parasitized colonies had a shorter discovery time (s) than the
146 nonparasitized colonies ($\bar{x} \pm SE = 23.43 \pm 7.7$ and 29 ± 2.8 for parasitized and
147 nonparasitized colonies, respectively) ($Z = -2.12665$, $p = 0.0334$) and had a shorter discovery
148 time per initial forager (Fig. 2, $Z = -2.32358$, $p = 0.0201$). Also, parasitized colonies had a
149 greater number of internal nest workers leave the nest to forage ($\bar{x} \pm SE = 6.13 \pm 1.69$) than
150 nonparasitized colonies ($\bar{x} \pm SE = 3.81 \pm 0.5$) and a greater proportion of the total work
151 force were internal nest workers that left to forage ($\bar{x} \pm SE = 0.15 \pm 0.03$) than
152 nonparasitized colonies ($\bar{x} \pm SE = 0.11 \pm 0.01$). However, the difference was not significant
153 for either ($Z = 1.637$, $p = 0.1016$ and $Z = 1.44391$, $p = 0.1488$, respectively)

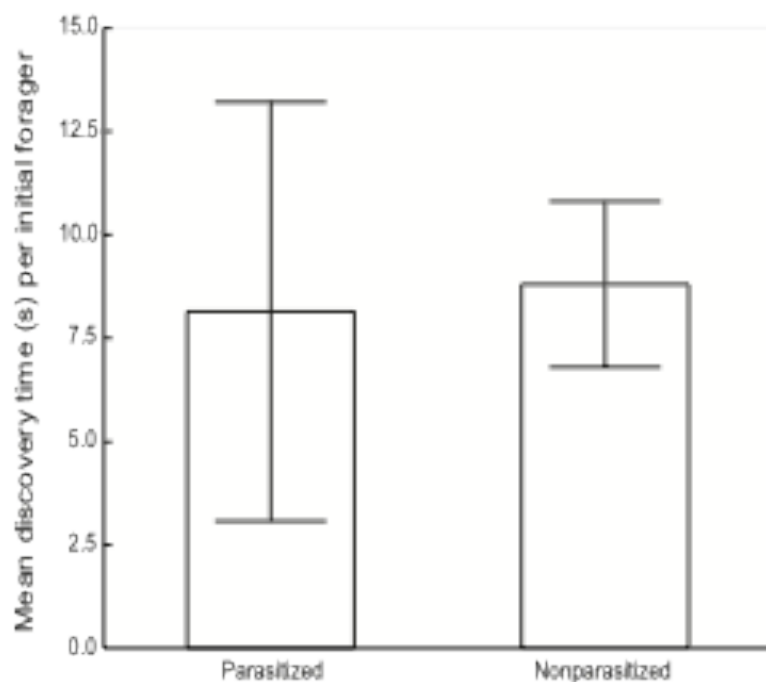
154 Of the 99 nonparasitized *Temnothorax* colonies used in this experiment, 40 were
155 queenless, while the other 59 colonies had at least one queen. In order to see if the presence
156 or absence of a host queen had an effect on the foraging behaviour of the colony, I conducted
157 a Wilcoxon rank sum test for each pair: queenright and parasitized, queenless and parasitized.
158 The proportion of initial foragers ($\bar{x} \pm SE = 0.29 \pm 0.02$ and 0.31 ± 0.03 for queenright and
159 queenless, respectively) and the proportion of total foragers ($\bar{x} \pm SE = 0.39 \pm 0.02$ and 0.41
160 ± 0.03 for queenright and queenless, respectively) were significantly greater in the parasitized
161 colonies compared to either the queenright ($Z = -2.34765$, $p = 0.0189$ and $Z = -2.8651$, $p =$
162 0.0042 respectively) or queenless colonies ($Z = -2.23111$, $p = 0.0257$ and $Z = -2.52163$, $p =$
163 0.0117 respectively).

164 Also, since all but one of the parasitized colonies for this experiment contained *T.*
165 *longispinosus*, I compared 15 parasitized *T. longispinosus* and 82 nonparasitized *T.*
166 *longispinosus* colonies based on proportion of initial foragers ($\bar{x} \pm SE = 0.43 \pm 0.05$ and
167 0.31 ± 0.02 for parasitized and nonparasitized, respectively), mean discovery time ($\bar{x} \pm SE$

168 = 17.4 ± 5 and 26.6 ± 2.66 for parasitized and nonparasitized, respectively), and proportion
 169 of total foragers ($\bar{X} \pm SE = 57 \pm 0.05$ and 0.44 ± 0.02 for parasitized and nonparasitized,
 170 respectively). Still, the parasitized colonies had a greater proportion of initial foragers (Z
 171 = 2.40988 , $p = 0.0160$), shorter discovery time ($Z = -2.35649$, $p = 0.0184$), and greater
 172 proportion of total foragers ($Z = 2.34006$, $p = 0.0190$).



173
 174 **Fig 1.** Mean number of both initial foragers and total foragers out of the total number of
 175 workers for parasitized ($\bar{X} \pm SE = 0.42 \pm 0.05$ and 0.57 ± 0.04 , respectively) and
 176 nonparasitized ($\bar{X} \pm SE = 0.29 \pm 0.01$ and 0.4 ± 0.02 , respectively) colonies. Using a
 177 Wilcoxon rank sum analysis, there is a significant difference between the parasitized and
 178 nonparasitized colonies for both initial foragers ($p = 0.0137$) and total foragers ($p = 0.0035$).
 179 The bars denote 1 standard error from the mean.



180

181 **Fig. 2** Mean discovery time (s) per ant foraging outside the nest before the availability of
 182 food. Using a Wilcoxon rank sum analysis, there is a significant difference between the
 183 parasitized (8.14 ± 5) and nonparasitized colonies (8.8 ± 2) ($p = 0.0201$). The bars denote 1
 184 standard error from the mean.

185

186 **(b) Nest selection**

187

For the nest selection tests for entrance size, cavity height, and floor area (Table 1), a

188

Chi-square test of independence showed that there was no association between parasitization

189

and cavity height ($\chi^2 = 0.468$, $p = 0.491$) or floor area ($\chi^2 = 0.508$, $p = 0.4760$). A Fisher's

190

exact probability test, necessitated by small sample sizes, showed there was no association of

191

parasitization and entrance width preference ($p = 0.0958$). Using a Pearson Chi-square

192

goodness-of-fit test, parasitized colonies showed no preference for nests based on entrance

193

width (10 chose 4 mm entrance, 10 chose 1 mm entrance; $\chi^2 = 0.0$, $p = 1.0$), cavity height (6

194

chose 2.4 mm high ceiling, 12 chose 1.6 mm high ceiling; $\chi^2 = 2.0$, $p = 0.1573$), or floor area

195

(8 chose 1237.5 mm² floor area, 8 chose 825 mm² floor area; $\chi^2 = 0.0$, $p = 1.0$). Likewise,

196

nonparasitized colonies had no preference based on cavity height (8 chose 2.4 mm high

197 ceiling, 10 chose 1.6 mm high ceiling; $\chi^2 = 0.2222$, $p = 0.6374$) or floor area (10 chose
 198 1237.5 mm² floor area, 6 chose 825 mm² floor area; $\chi^2 = 1.0$, $p = 0.3173$). However,
 199 nonparasitized colonies did show a preference for the *larger* entrance width (16 chose 4 mm
 200 entrance, 4 chose 1 mm entrance; $\chi^2 = 7.2$, $p = 0.0073$).

201 For the “whole” colony entrance width test (Table 2), colonies of parasitized *T.*
 202 *longispinosus*, nonparasitized *T. longispinosus*, and nonparasitized *T. curvispinosus* showed
 203 no nest preference ($\chi^2 = 0.25$, $p = 0.6171$; $\chi^2 = 0.25$, $p = 0.6171$; $\chi^2 = 0.0$, $p = 1.0$
 204 respectively). A Wilcoxon rank sum test for each revealed no difference in mean number of
 205 *Temnothorax* workers between colonies that selected the 4 mm entrance and those that
 206 selected the 1 mm entrance (parasitized *T. longispinosus*: $Z = 0.0$, $p = 1.0$; *T. longispinosus*: Z
 207 $= 0.4234$, $p = 0.6720$; and *T. curvispinosus*: $Z = -0.10476$, $p = 0.9166$).

208 **Table 1.** Contingency tables for parasitized and nonparasitized colonies in nest selection tests
 209 based on entrance width, cavity height, and floor area. Numbers in each cell correspond to the
 210 number of colonies that selected a given nest. 4 colonies in the cavity height test and 8
 211 colonies in the floor area test were split and not counted in the tables. Parasitized colonies
 212 consisted of 4 *P. americanus* adults, 15 *T. longispinosus* workers, and 15 larvae.
 213 Nonparasitized workers consisted of 1 *T. longispinosus* queen, 15 of her workers, and 15 of
 214 her larvae.

	Entrance width			Cavity height			Floor area		
	4 mm	1 mm	Total	2.4 mm	1.6 mm	Total	1237.5 mm ²	825 mm ²	Total
Parasitized	10	10	20	6	12	18	8	8	16
Nonparasitized	16	4	20	8	10	18	10	6	16
Total	26	14	40	14	22	36	18	14	32

215
 216 **Table 2.** Contingency table for three colony types in a nest selection test based on entrance
 217 width. Numbers in each cell correspond to the number of colonies that selected a given nest.

	Mean # of <i>Temnothorax</i> workers \pm standard error from the mean	4 mm entrance width	1 mm entrance width	Total
Parasitized <i>T. longispinosus</i>	29.94 \pm 6.96	7	9	16
<i>T. longispinosus</i>	67.44 \pm 10.98	7	9	16
<i>T. curvispinosus</i>	26.30 \pm 6.48	5	5	10
Total	43.36 \pm 5.87	17	23	42

218 4. DISCUSSION

219 This study is among the first to demonstrate parasite manipulation of host foraging by
220 a well-studied slave-making ant. *Temnothorax* workers are more likely to forage for food
221 when *P. americanus* is present in the nest than when it is not. The parasite could be driving
222 this behaviour by inducing its slaves to exchange food via trophallaxis more often than their
223 nonparasitized conspecifics. Consequently, the slave-making ants could be consuming a
224 disproportionate amount of food contained in the social stomach compared to the host
225 workers, thus leading to more risky foraging by the relatively expendable host workers. In
226 support of this explanation, low fat reserves are the most significant factor in inducing an
227 individual *Temnothorax albipennis* ant, a European relative of *T. longispinosus* and *T.*
228 *curvispinosus*, to forage [15]. The quicker discovery time of the slaves could also be a
229 product of their lower fat reserves since the foragers would be leaner and quicker. However,
230 the data for discovery time per initial forager in parasitized colonies has a large standard error
231 of the mean, which may be a result of the small feeding area.

232 Parasitized *Temnothorax* workers have been shown to be more aggressive than
233 their free-living counterparts, and therefore more territorial [16]. There is a possibility
234 that the external nest workers of a parasitized colony are not truly foraging but are
235 instead marking territory. Parasitized colonies would then not have a greater
236 proportion of the work force foraging for food. I do not believe that this is the case
237 because parasitized colonies still had a greater number and greater proportion of
238 workers leave the nest to go to a food source after it was available. This indicates that
239 even the internal nest workers of a parasitized colony have low enough fat reserves to
240 go out and forage without being recruited by a nest mate.

241 If the host workers increase their foraging in response to the parasite using up most of

242 the resources, then the parasite is behaving closer to the “exploitation of host response” end
243 of the manipulation spectrum [17]. However, disproportionate trophallaxis between parasite
244 and host may not be the only mechanism of increased foraging. Of the 16 parasitized colonies
245 used in the foraging experiment, six had but one *P. americanus* individual and two of those
246 colonies had 90 or more slaves. One parasite would have to participate in a very high
247 proportion of the trophallaxis in a nest in order to deplete the fat reserves of so many
248 foragers. If there are other factors at play, the parasite may be manipulating its host *sensu*
249 *stricto* in some way.

250 The nest selection experiment yielded a negative, yet surprising, result. I expected *T.*
251 *longispinosus* to exhibit nest preferences similar to those of *T. curvispinosus* [14]. Most
252 surprising, *T. longispinosus* preferred the *larger* entrances, while previous studies have
253 shown that preferred entrance width of *T. curvispinosus* is around 1 mm. This pattern did not
254 hold when the colony size varied from 15 workers. Perhaps *T. longispinosus* is less choosy
255 than *T. curvispinosus*, or I collected them when they were in a less choosy state. Aspects of
256 the laboratory environment (e.g. greater light intensity than seen on the forest floor) or the
257 length of time maintained in the laboratory (more than a year for some colonies) may have
258 altered the nest selection preferences. Supporting the environmental explanation, *T.*
259 *curvispinosus* were split between the 4 mm entrance and the 1 mm entrance under the same
260 laboratory conditions. Future nest selection experiments comparing parasitized and
261 nonparasitized colonies should not be concerned with controlling for colony size and should
262 instead give colonies a differential nest choice immediately after collection, straight from the
263 acorn.

264

265

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