

1 **Title: Individual versus collective decision-making: optimal foraging in the**
2 **group hunting termite predator *Megaponera analis***

3 **Short Title: Optimal foraging in the ant *Megaponera analis***

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22 **Abstract**

23 Collective decision-making is one of the main mechanisms of organization in social insects.
24 However, individual decision-making can also play an important role depending on the type
25 of foraging behaviour. In the termite-hunting ant species *Megaponera analis* information
26 about foraging sites is collected by only a handful of individual scouts that have to convey
27 this information to the colony as accurately as possible to optimize their foraging behaviour.
28 We therefore look at predictions made by optimal foraging theory to better understand the
29 interplay between collective and individual decision making in this obligate group-raiding
30 predator. We found a clear positive relation between raid size (200 – 500 ants) and termite
31 abundance at the foraging site thereby confirming predictions of the maximization of energy
32 theory. Furthermore selectivity of the food source increased with distance, thus confirming
33 central place prediction theory. The confirmation of these theories suggests that individual
34 scouts must be the main driver behind raid size, choice and raiding behaviour. Marginal value
35 theorem is also confirmed by our results, time spent at the hunting ground increased with
36 distance and prey quantity. This raises questions on how foraging time at the food source is
37 regulated in a group-hunting predator. Hunger decreased selectivity of scouts in respect to
38 food sources, while average raid size increased and more scouts left the nest in search of prey.
39 Thus implying that scouts are aware of the hunger state of the colony and adapt their decision
40 making accordingly. Remarkably most central place foraging behaviours in *M. analis* were
41 not achieved by collective decisions but rather by individual decisions of scout ants. Thereby
42 having 1% of the colony (10-20 scouts) deciding the fate and foraging efficiency of the
43 remaining 99%.

44 **Keywords:** central place foraging | hunger state prediction | marginal value theorem |
45 maximization of energy | myrmecology | predator prey interaction | raiding behaviour |
46 social insect

47 Group living animals are able to increase the accuracy of a decision, at the cost of time,
48 through collective decisions (Chittka, Skorupski, & Raine, 2009). Collective decisions have
49 been extensively studied in social insects and are considered to be one of the main
50 mechanisms for regulating behavioural choices, like nest or food choice (Bert Hölldobler &
51 Wilson, 2008; Mallon, Pratt, & Franks, 2001). There are certain species however where the
52 choice of a food source cannot be taken by collective decisions. The foraging success of
53 species that rely on independent foragers directly depends on the individual decisions made
54 by them (Pohl & Foitzik, 2011). In species where a large portion of the colony forages
55 independently, the mistakes made by individuals do not weigh heavily. However, in species
56 where the colony depends on scouts for obtaining accurate information to send large numbers
57 of individuals to the food source, mistakes become far more risky. We therefore looked at the
58 foraging behaviour of the termite-hunting ant *Megaponera analis* to better understand the
59 interplay between collective and individual decision-making in their raid choice and the
60 precision of these choices.

61 *Megaponera analis* is a strictly termitophagous ponerine ant species found in sub-Saharan
62 Africa from 25°S to 12°N (Schmidt & Shattuck, 2014), specialized in raiding termites of the
63 subfamily Macrotermitinae at their foraging sites (Lepage, 1981; Levieux, 1966). Colony size
64 varies between 440 to 1400 adult ants (Lepage, 1981). The general foraging pattern of *M.*
65 *analis* starts with scout ants searching an area of approximately 50 m radius around the nest
66 for termite foraging sites. This searching phase can last up to one hour and in unsuccessful
67 cases the scout returns to the nest in a circuitous route (Longhurst & Howse, 1979). Once a
68 scout ant has found a potential site it investigates it, while avoiding contact with the termites.
69 After this investigation the scout returns in a direct route to the nest to recruit nestmates for a
70 raid (Longhurst & Howse, 1979). It recruits approximately 200-500 nestmates and leads them
71 to the termites in a column-like march formation (Bayliss & Fielding, 2002; Longhurst &
72 Howse, 1979). During the raid division of labour occurs (Corbara & Dejean, 2000); larger

73 ants (majors) break open the protective soil cover created by the termites while the smaller
74 ants (minors) rush into these openings to kill and pull out the prey (Villet, 1990). After 13-20
75 minutes the hunt ends and the ants start collecting the dead termites and injured ants in need
76 of assistance (Frank et al. 2017, Yusuf, Gordon & Pirk 2013). Majors grasp up to seven
77 termites between their mandibles and minors grasp up to three, the majority however return
78 empty (Yusuf, Gordon & Pirk 2013). After collecting the termites the column forms again
79 and the hunting party returns to the nest together. *Megaponera analis* seems to show certain
80 prey preferences, preferring to attack termite species that are easier to hunt and that have
81 weaker defence capabilities (Yusuf, Gordon & Pirk 2013).

82 The high variance in raid distances and raid sizes made us wonder how well the scouts used
83 the information gathered at the prey site and how accurate these decisions were in light of
84 optimal foraging theory. Optimal foraging theory has been applied on various animals to
85 understand their foraging patterns and behaviours (Macarthur & Pianka, 1966; Olsson, Brown,
86 & Helf, 2008; Pearce-Duvet, Elemans, & Feener, 2011). Central place foraging theories
87 expanded upon present theories of optimal foraging to include animals that carry food back to
88 a central place (Orians & Pearson, 1979; Schoener, 1979), as is the case for most ant species.
89 We thus expect that increased accuracy of information conveyed by scouts will better match
90 predictions of central place foraging theory. Additionally, although central place foraging
91 theory has been extensively studied in honeydew feeding ant species (Bonser, Wright,
92 Bament & Chukwu, 1998) and solitary foraging ants (Pearce-Duvet et al., 2011) little is
93 known about how well central place foraging theory predicts the foraging patterns of group
94 recruiting predatory ant species, like *M. analis*. These ants behave markedly different to other
95 ant species in their raiding behaviour, though certain similarities to some bee species can be
96 observed (Abou-Shaara, 2014; Nieh, 2004), which will be addressed in the discussion.
97 Recruitment and foraging behaviour in ants is often regulated through pheromone trails. Food
98 choices are passively regulated by the reinforcement of trails that lead to good food sources

99 faster (Hölldobler & Wilson, 1990). In predatory species the time after detection by the prey
100 has to be minimized as much as possible (Witte, Schliessmann & Hashim, 2010). Widespread
101 foraging strategies of predatory ants therefore include solitary foraging (most ponerines) and
102 group foraging (like driver ants) (Peeters & Crewe, 1987), in both cases no recruitment occurs.
103 In group mass-recruiting predatory ant species only a very small percentage of the colony
104 leaves the nest in search for food sources before recruiting a substantial portion of the colony
105 to go out to exploit it. If their foraging behaviour would be optimized in accordance with
106 central place foraging theory, it would imply that the scouts exert an extensive control on the
107 colony, since only they hold all the information necessary for optimizing raiding behaviour.
108 Decision-making would therefore not be regulated collectively but by individuals.
109 *Megaponera analis* offers itself therefore as an ideal model organism to study these questions.

110 In the following section we list our major predictions of central place foraging theory when
111 applied to the foraging behaviour of *M. analis*.

112 Maximization of energy: Animals forage so as to maximize their net energy intake per unit
113 feeding time, by minimizing the energy invested and selective food choice (Schoener, 1971).
114 We expect *M. analis* to select food sources with a high amount of energy gained per unit time
115 (i.e. hunting as many termites as possible per ant in as little time as possible). Furthermore, to
116 minimize energy investment, raid size should vary according to the size of the patch and the
117 density of foraging termites (so as to optimize the ratio of termites per ant).

118 Central place prediction: As distance from the central place increases, selectivity should
119 increase (Orians & Pearson, 1979). Since food sources further away take more time and
120 energy to reach, they should be richer in termites to compensate for the longer travel time.
121 *Megaponera analis* should therefore only conduct raids to far away termite sources if they
122 were of high quality.

123 Marginal value theorem: The optimal time a predator should spend at a food source before
124 moving on to another site depends on the distance between feeding sites, assuming that food
125 intake rate at a hunting site decreases over time (Charnov, 1976). Applied to the central place
126 foraging theory this implies that the longer the travel time the longer one should exploit the
127 food source before returning to the nest. *Megaponera analis* should therefore spend more
128 time at feeding sites further away from the nest.

129 Hunger state prediction: Food selectivity depends on the consumer's hunger state, with
130 increased food intake leading to increased diet selectivity and specialization (MacArthur &
131 Pianka, 1966; Schoener, 1971). We expect *M. analis* to start conducting raids on less
132 favourable termite sources if no successful raids occurred for a while and the hunger state of
133 the colony is high. Furthermore, foraging behaviour is expected to become more risk prone
134 (Cartar & Dill, 1990).

135 The combination of laboratory and field experiments allowed us to test these hypotheses and
136 shed light on the mechanisms regulating the foraging behaviour of group recruiting predators.
137 Do the individual scouts or collective decisions by the colony regulate it?

138 **METHODS**

139 *Study area and organism*

140 The study area is a humid savannah woodland located in the Comoé National Park, northern
141 Côte d'Ivoire (Ivory Coast), at the Comoé National Park Research Station (8°46'N, 3°47'W).
142 The annual rainfall is 1500-2200 mm, mostly falling from May to September (Konaté &
143 Kampmann, 2010). Colonies of *Megaponera analis* were located in a radius of approximately
144 2000 m from the research station. The distances between the colonies varied between 10 to
145 200 m. Nests were most commonly located by following a raiding column or scout ant return
146 to the colony. In total 450 raids of 54 different colonies were observed. In these raids the

147 predominantly hunted termite species was *Pseudocanthotermes* sp. but raids on *Macrotermes*
148 *bellicosus* were also observed. Out of these 450 field raids, data on the raiding parameters for
149 this study were collected in 144 raids (134 for undisturbed colonies and 10 for hungry
150 colonies). Colony size for 12 excavated colonies was between 900-2300 ants, a result
151 comparable to previous studies in other regions (Villet, 1990; Yusuf, Crewe, & Pirk, 2013).

152 *Data collection*

153 Observations in April 2013 established that raiding activity was highest in the morning and
154 afternoon hours between 6:00–11:00 and 15:00–19:00 local time, which corresponds to prior
155 observations (Bayliss & Fielding, 2002; Longhurst & Howse, 1979; Yusuf et al., 2014). Night
156 raiding was also observed, but was not included in this study. Experiments and observations
157 in the field were therefore carried out from 7:00–11:00 and 15:00–18:00 from April to
158 September 2013, August to October 2014, January to March and July to September 2015 as
159 well as March to May 2016. Even though *M. analis* is known to show monophasic allometry
160 within its worker sizes (Crewe, Peeters, & Villet, 1984; Villet, 1990), for statistical analysis
161 and illustration, the workers were divided into majors (head width > than 2.40 mm), minors
162 (head width < 1.99 mm) and intermediates (head width 2.40 - 1.99 mm) as proposed by Villet
163 (Villet, 1990).

164 *Laboratory colonies*

165 A total of 4 excavated colonies were placed in artificial nests in the field stations lab. The
166 20x20x10 cm large nests, made of PVC plastic, were connected to a 1x1 m arena. To enable
167 raids this arena was connected to a second arena (1x1 m) by a corridor of either 10 or 30 m
168 length. The ground was covered with soil from the natural habitat around the field station.
169 The experiments were conducted after giving the ants 7 days to habituate to the artificial nests.
170 Between experiments each ant colony was fed twice a day in the first arena, with a total of

171 300 termites per day, so as to assure constant conditions. For the experiments *Macrotermes*
172 *bellicosus* termites were placed in the second arena. These termites were found by scouts and
173 triggered raiding behaviour on which we performed the experiments. Termites were placed in
174 the second arena either at 8:00 or 16:00 and observed until a raid occurred or until 3 hours
175 elapsed. All lab experiments were repeated 3 times per colony (for a total $N=12$ per
176 experiment). Due to time constraints the hunger experiments for large and small hunting
177 grounds could only be repeated 5 times each with a total of 3 colonies. All colonies were
178 released into the wild again at the end of the study (to their original nest location in the wild).
179 For further details on lab keeping see Yusuf et al. (Yusuf et al., 2013).

180 Although our results showed that field raids were predominantly conducted on
181 *Pseudocanthotermes militaris*, we also observed raids on *M. bellicosus* in the field. We can
182 thus safely assume that the species predated in the laboratory, *M. bellicosus*, is not an
183 unnatural prey choice. We chose *M. bellicosus* as prey species due to the ease of collection
184 (collected from the surrounding area by attracting them with a pot filled with dry grass over
185 night). Both species, *M. bellicosus* and *P. militaris*, forage principally on wood, grass or litter
186 on the surface and cover their food with a thin layer of soil. The main difference between both
187 species is the larger worker and soldier size of *M. bellicosus*. This might have affected the
188 injury rate of *M. analis* during a raid, although this was not analysed in this study, but see
189 (Frank et al., 2017) for details about injured ants.

190 *Experiments*

191 Data about raid size (number of ants participating in a raid) and termite carriers (number of
192 ants carrying termites on the return journey) was collected by counting the individuals of the
193 raiding column on the outward and return journey. The duration of the different raid phases
194 (outward journey, time at the hunting ground and return journey) was also timed. Hunting

195 time was defined as the time between the arrival of the ants at the food source and the start of
196 the departure of the return column.

197 In the field, distance to the termite-feeding site was measured by using a 40 m long measuring
198 tape. In the laboratory, distance to the food source was either 10 or 30 m.

199 The termite abundance in the laboratory experiments was manipulated by offering either 50
200 termites in an area of 50 cm² (small hunting ground) or 250 termites in an area of 1260 cm²
201 (large hunting ground). The areas where the termites were released were closed off with
202 plastic barriers, thus preventing them from leaving the designated hunting area. Furthermore,
203 the area where the termites were released was kept moist and had dry grass on it (in contrast
204 to the surrounding area, which consisted of dry soil) so that the termites could build galleries.
205 The termites were given 1–2 hours time to build their galleries before the ants gained access
206 to the arena. Scout numbers were quantified by counting the ants outside the nest before each
207 experiment. This number was only a conservative estimate though since individual scouts
208 entered and left the nest frequently making it impossible to clearly quantify the number of
209 scouts (i.e. if a new scout left the nest or if it was the same one that previously entered the
210 nest).

211 The hunger state of the colonies was manipulated by preventing raids for 48 hours. In the
212 field this was done by placing 30 cm high PVC walls around the nest, which were dug 10 cm
213 into the ground (to include all nest entrances within the enclosure). Observations throughout
214 the starvation period confirmed that the scouts were unable to leave the enclosure (they were
215 observed to search for exits during the activity period). In the lab, colonies were simply not
216 fed for 48 hours.

217 *Statistical analysis*

218 For statistical analysis and graphical illustration we used the statistical software R v3.1.2 (R
219 Core Team, 2013) with the user interface RStudio v0.98.501 and the R package ggplot2
220 v2.1.0 (Wickham, 2009). We tested for deviations from the normal distribution with the
221 Shapiro Wilks test ($P>0.05$). A Bartlett test was used to verify homoscedasticity ($P>0.05$). If
222 data was normally distributed and homoscedastic an ANOVA was used to compare the
223 significance of the results with a Tukey HSD test for post hoc analysis. If this was not the
224 case a Kruskal-Wallis rank sum test was used, followed by a Dunn's test with Holm-
225 Bonferroni correction. Linear correlations were calculated with a Pearson's correlation test.
226 Median values in the text are followed by a median absolute deviation.

227 **RESULTS**

228 *Raiding behaviour*

229 In the field, raids of *M. analis* occurred 2–5 times a day per colony. Raiding activity was
230 highest in the morning and afternoon but also seemed to be strongly influenced by
231 temperature, rainfall and humidity. During the dry season (January – March) raiding activity
232 was more pronounced during the night. The main termite species hunted in our study site was
233 *Pseudocanthotermes militaris*, making up 95 % of the analysed raids ($N=134$).

234 *Maximization of energy and central place prediction*

235 In the field, raids of *M. analis* varied in size between 50 and 800 ants conducting raids up to
236 48 m away from the nest (Fig. 1). The median percentage of ants carrying termites back to the
237 nest after a raid was 29 ± 19 % (efficiency), of which each individual carried a median of $3 \pm$
238 2 termites ($N=50$). The percentage of termite-carriers was not significantly influenced by
239 either distance or raid size (linear model: raid size: $F_{1,116}=1.41$, $R^2=0.011$, $P=0.25$; distance:
240 $F_{1,116}= 0.05$, $R^2<0.01$, $P=0.82$). Small raids (less than the median raid size of 318) conducted

241 to far away locations (further than half the maximum raid distance, i.e. >24 m) made up only
242 2.2 % of the raids (3 out of 134; Fig.1, lower right quadrant).

243 In the lab, raid size clearly correlated with termite abundance at the feeding site rather than
244 distance (Fig. 2 & Table A1), with rich termite sites generally being exploited by large raids.
245 Ant colony size also positively affected raid size (Fig. A1a; Pearson correlation: $r= 0.58$, $N=$
246 68 , $P<0.001$). The percentage of the colony participating in a raid decreased with colony size.
247 Small colonies conducted raids consisting of up to 75 % of the colony, while larger colonies
248 only allocated 35 % of the colony to a raid (Fig. A1b; Pearson correlation: $r= -0.65$ $N= 67$,
249 $P<0.001$).

250 *Marginal value theorem*

251 In the field, hunting time at the foraging site increased significantly with distance from the
252 nest (Fig. 3a, Pearson correlation: $r= 0.38$ $N= 126$, $P<0.001$). Hunting time was defined as the
253 time interval between the arrival of the ants at the food source and the start of the departure of
254 the return column. The number of termites killed per minute during the hunting period
255 decreased with longer stays at the foraging site (Fig. 3b, Pearson correlation: $r= -0.16$, $N=114$,
256 $P=0.026$). In the lab, hunting time also increased with food abundance and distance (Fig. 4 &
257 Table A2).

258 *Hunger state prediction*

259 In the field, starved colonies tended to conduct raids to significantly shorter distances (median
260 1.9 ± 0.9 m; $N=10$) compared to control colonies (median $12 \pm 8,9$ m; $N=134$; Wilcoxon test:
261 $W=1320$, $P<0.001$). Raid size also varied strongly, with very small raids (50 ants) being
262 conducted to very short distances (1 m; Fig. A2). The number of scouts leaving the nest in
263 search of food also clearly increased with increasing hunger, with two to three times as many
264 scouts leaving the nest in starved colonies (30-50 scouts per colony, compared to 10-20 scouts

265 in control colonies, although these numbers are only approximations, since the exact number
266 could not be determined).

267 In the lab, our experiments showed that raid size for starved colonies was significantly larger
268 in comparison to normal raids (Fig. 5 & Table A3), both for small and large termite
269 abundances at the hunting ground, although a larger sample size would be necessary to state
270 this with certainty (Wilcoxon test $W=7$, $P=1$, effect size=0.19; power=0.057). The time
271 between the discovery of the food site by the scout and the start of the raid was also
272 significantly shorter in starved colonies (425 ± 145 sec) when compared to satiated colonies
273 (1040 ± 889 sec; Wilcoxon test: $W = 0.81$, $P < 0.001$).

274

275 **DISCUSSION**

276 We confirmed various central place foraging theory predictions for *M. analis*. The scout not
277 only collects qualitative information about the food source, but also conveys this information
278 accurately to the colony. This gave us new insights on the importance of different factors for
279 their raiding behaviour, like termite quantity and distance. Remarkably, most of the decisions
280 that optimize their raiding behaviour are not regulated collectively, but by individual scout
281 ants.

282 *Maximization of energy*

283 In the lab, there was a clear positive relation between raid size and termite abundance at the
284 foraging site thereby confirming predictions of the maximization of energy theory. These
285 results support our hypothesis that scouts have to be able to assess the richness of a food
286 source while examining it.

287 In the field, the median percentage of termite-carriers in a raid was 29 % regardless of
288 distance or raid size. Termites were very rarely observed to be left behind at the hunting

289 ground (in any obvious quantity), we assume that the ants try to adjust their raid size to the
290 richness of the food source, leading to only 30 % of the ants having to transport back termites.
291 The other ants have other essential roles in the hunting process, like killing the termites and
292 potentially also protecting the termite carriers on the return journey. This was supported by
293 experiments in the lab, with smaller raids only going for smaller hunting grounds (Fig. 2). We
294 believe that the lab results can be extrapolated to the field since the information of patch
295 quality, for regulation of raid size, is collected by scouts in the field and in the lab under
296 similar conditions (the termites in the lab have 1-2 hours to create foraging galleries prior to
297 investigation by the scouts). Of course once the actual hunt starts these raids are markedly
298 different, thus information on hunting time and percentage of termite carriers should be
299 compared with care.

300 Our field observations are in line with prior observations (Lepage, 1981; Levieux, 1966;
301 Longhurst & Howse, 1979). Other studies in Tanzania and Kenya seem to imply that colony
302 size is the main factor for raid size variation (Bayliss & Fielding, 2002; Yusuf, Gordon,
303 Crewe, & Pirk, 2014). While this factor also plays a role in our observations (Fig. A1a), the
304 variation of raid size within the colonies can probably best be explained by adaptation of the
305 raid size to the termite foraging site. Intercolonial differences in raid size were also not
306 proportionate to colony size. Large colonies seemed to conduct raids barely larger than those
307 of small colonies (Fig. A1b), suggesting that raid size is limited by other factors. Some
308 possible limitations could be the recruitment capacity of the scout, raid organisation or lack of
309 richer/larger hunting grounds. Larger colonies seem to also have the advantage of conducting
310 two raids simultaneously (personal observation).

311 Individual learning by the scouts might have influenced our results in the lab with the scouts
312 learning the position of the food sources. Although this should not have influenced our main
313 results, in the field the same site can also be exploited multiple times. The number of termites
314 at the feeding site changes constantly, depending on humidity, time of day and activity of the

315 termites, it is therefore still always necessary for the scout to properly assess the feeding site
316 to adapt the raid size accordingly, which is also what we observed in the lab.

317 In ants individuals are able to assess the quality/quantity of a food source to decide if they
318 want to recruit other ants or exploit the food source individually, thereby optimising the
319 energy investment according to the food source (Hölldobler & Wilson, 1990; Witte et al.,
320 2010). In *M. analis* individual exploitation of a food source is not an option. Conducting large
321 raids to small hunting grounds would lead to a waste of energy, unnecessarily occupying a
322 portion of the colony. The ability of *M. analis* to adjust their raid size to the hunting ground
323 allows a more flexible allocation of limited resources (ants) in the foraging process and relies
324 on individual decisions made by scouts, which collect the necessary information.

325 *Central place prediction*

326 At short distances the full spectrum of raid sizes was observed. With increasing distance away
327 from the nest the minimal raid size started to increase, thereby reducing the variance until
328 98% of the raids were large at the furthest distances (Fig. 1). In the previous section we show
329 that raid size positively correlated to termite abundance at the foraging site. We therefore
330 conclude that food selectivity increases with distance. Furthermore, our lab experiments
331 showed that raid size depended on termite abundance at the foraging site and not on its
332 distance (Fig. 2), thereby confirming central place prediction theory.

333 The efficiency of a single ant seems to be independent of raid size or distance (Fig. 1). At the
334 same distance a large raid to a large food source is as efficient as a small raid to a small food
335 source, from an energetic point of view. Why then do the ants not conduct small raids to far
336 distances? An explanation to this pattern may arise by looking at the foraging process from
337 the perspective of the individual scout rather than the raid. Scouts are exposed to considerably
338 larger risks when searching for food sources alone. Scouts that move further away from the
339 nest spend more time traveling and are therefore exposed longer to predation risks. This

340 increased risk can potentially only be outweighed if it leads to conducting raids to rich
341 foraging sites.

342 Distance also seems to have an effect on raid size, although the significant differences are
343 clearer when looking at the termite abundance at the food source. An outlier is the result for
344 large raids conducted at far distances for poor termite sites in the lab (Fig. 2). It is worth to
345 keep in mind however that the experimental setup removes the possibility of choice, forcing
346 the ants to exploit the presented food source. If no other choices are present it makes sense for
347 the ants to even exploit an, under natural circumstances, unfavourable food source.

348 In conclusion, these experiments allowed us to identify food source quality rather than
349 distance as the main factor affecting raid size. However, we still do not fully understand the
350 raiding behaviour in light of present theories due to the lack of observations of small raids to
351 far locations.

352 *Marginal Value theorem*

353 The hunting time at a food source in *M. analis* seems to be in line with what marginal value
354 theorem predicts. Hunting time increases with distance (Fig. 3a) but killing/collecting speed
355 decreases over time (Fig. 3b), while richer food sources are exploited longer than poorer food
356 sources (Fig. 4).

357 The diminishing returns over time at a raiding site are likely more pronounced in termites
358 when compared to more passive food sources. Termites start to actively retreat into their
359 galleries as soon as the ants arrive, with the soldiers staying behind to protect the retreating
360 workers (Corbara & Dejean, 2000). Nevertheless a clear positive relation was observed
361 between hunting time, distance and termite abundance, both in the lab and in the field. Since
362 in the lab termites were unable to retreat, this may lead to less natural behaviour by the
363 termites when being attacked. Something to consider is also the handling time after the fight
364 (i.e. collecting the dead termites), this phase is included in our definition of hunting time and

365 could depend on the number of termites killed at the food patch. We believe that the handling
366 time remains relatively constant since the raid size depended on the termite number (i.e. more
367 ants were available to handle more termites). Furthermore, results for hunting grounds with
368 the same termite number showed an increase in hunting time at greater distances (Fig. 4). We
369 therefore believe that it is safe to assume that the hunting behaviour is in line with what
370 marginal value theorem predicts.

371 Marginal value theorem has been extensively studied in solitary foraging animals and ants
372 (Olsson et al., 2008; Pearce-Duvet et al., 2011). Studies on ants mostly focus on single prey
373 loaders (Pearce-Duvet et al., 2011), in which marginal value theorem does not apply
374 (Charnov, 1976). There are some studies on honeydew feeding ants (like *Lasius niger*, *L.*
375 *fuliginosus*, *Myrmica ruginodis*), which observe foraging strategies in line with marginal
376 value theorem (Bonser et al., 1998). Our study is the first though to show these patterns in a
377 group hunting predatory ant species like *M. analis*. The processes that regulate this for group
378 foraging ants remain unclear. *Megaponera analis* has various reasons, like predation risk, to
379 return back to the nest together and they take great care to do so (Bayliss & Fielding, 2002;
380 Longhurst & Howse, 1979). We propose a quorum decision-making process as the regulating
381 mechanism for the hunting time. The ants could have a certain termite encounter threshold,
382 which at a certain point leads the ants to switch from hunting termites to collecting dead
383 termites. Further experiments are necessary though to crystalize a clear regulatory mechanism
384 for the hunting time.

385 *Hunger state prediction*

386 We observed that with increased hunger prey selectivity decreased and average raid size
387 increased. We also observed more scouts searching for prey, in some cases doubling the
388 number of scouts when compared to satiate colonies.

389 Field experiments showed that raids were conducted to much shorter distances (1.9 ± 0.9 m
390 compared to 12 ± 8.9 m), some of them even being conducted to locations so near (~ 1 m) that
391 a trail to the termites was formed rather than a normal raid, with very few ants participating.
392 Additionally our lab experiments showed that hungry colonies always tended to conduct
393 overly large raids (Fig. 5), with shorter investigation of the hunting ground by the scouts
394 beforehand (425 ± 145 sec compared to 1040 ± 889 sec for satiated colonies).

395 We hypothesize that a reduction in distance suggests that scouts become less selective in their
396 prey choice, conducting a raid to the first termite location they find. This would imply that
397 under normal circumstances scouts encounter termite foraging sites much more frequently but
398 decide against exploiting them if they are too small. The reduced investigation time in hungry
399 colonies likely make it harder for the ants to adapt their raid size to the feeding site (due to a
400 lack of accurate information) and may explain the lack of raid size variation in hungry
401 colonies. An alternative hypothesis could be that hungry ants in the colony are easier to
402 recruit, thus always leading to larger raids for the same recruitment effort (Fig. 5).

403 These results suggest that foraging behaviour becomes more risk-prone under hunger,
404 supporting hunger state prediction theory and observations in bumblebees (Cartar & Dill,
405 1990). Furthermore, bumblebees also became more sensitive to recruitment pheromones in
406 hungry colonies (Molet et al. 2008). We hypothesize that by conducting large raids to feeding
407 sites, which in principle would not need it, the colony invests a larger portion of its resources
408 (ants) for the small chance of gaining more termites. The reduced food site selectivity and
409 investigation time by the scouts suggest that they prefer to conduct a raid to a potentially
410 unfavourable feeding site, thereby reducing the risk of being discovered at the cost of
411 information. This implies an interesting interplay between collective and individual selectivity
412 of prey choice. The colony would need to convey their hunger state to the scouts so that they
413 can adapt their individual prey selectivity accordingly.

414 *Individual decision-making*

415 Most of our results suggest a high degree of control by individual scouts on the foraging
416 behaviour of the entire colony. Individual scout ants regulate most optimal foraging
417 behaviours observed in this study. Scouts have to be acutely aware of the hunger state of the
418 colony to know how selective they can be with their prey choice. They need to collect
419 sufficient information of a termite foraging site to decide whether to conduct a large or small
420 raid, while keeping distance from the nest in mind. This information then has to be passed on
421 to the colony so that the appropriate raid can be conducted. Unlike honeybees it is not
422 necessary for the scouts to pass on detailed information about the location of the feeding site
423 to the others, since the scout leads the column of ants to the termites. Thus the only
424 information that is vital during recruitment is the termite abundance at the food source,
425 thereby varying the amount of raiding ants. Scouts do not always succeed with recruitment
426 after finding a foraging site (personal observation), suggesting that some control by the
427 colony in the collective decision to conduct a raid is present. The number of scouts searching
428 for food also seems to depend on the hunger state of the colony and is therefore likely
429 regulated collectively, potentially through thresholds regarding hunger. Although it is
430 possible that also the hunting time at the foraging site is regulated by scouts (by giving a
431 signal when to stop), we believe that it is more likely a collective decision by the raiding ants
432 (quorum decision making).

433 *Scouts in social insects*

434 The foraging behaviour of *M. analis* can to some extent be compared to that of slave-making
435 ants (Pohl & Foitzik, 2011). In the slave-making ant *Protomognathus americanus* the colony
436 also depends on the accuracy of the decisions made by individual scouts for their raiding
437 efficiency. Individual scouts are able to assess the size of a potential host colony and make
438 their decision accordingly, with larger colonies offering more pupae to be stolen (Pohl &

439 Foitzik, 2011). One big difference to *M. analis* is that these colonies only include a handful of
440 ants (3-6 slave-maker ants) compared to over 1000, which are present in *M. analis*.
441 Furthermore, just because a prey can be hunted in group does not imply that it will.
442 *Ophthalmopone berthoudi* for example is a solitary hunting termite specialist and belongs to
443 the sister genus of *Megaponera* (Peeters & Crewe 1987). There are various strictly
444 termitophagous ant species that hunt solitarily or in group. It is unclear though how exactly
445 this different strategies for the same food source evolved and there are likely various factors
446 that influence it (Peeters & Crewe 1987).

447 Honeybees (*Apis mellifera*) and some stingless bee species (Nieh, 2004) also have a certain
448 proportion of workers scouting for food while the rest waits in the nest to be recruited (Abou-
449 Shaara, 2014). Both, *A. mellifera* and *M. analis*, hunt a stationary temporal food source:
450 termite foraging sites do not normally change position if left undisturbed and are only active
451 at certain times of day, similar to nectar and pollen in flowers. This is an important
452 prerequisite since the time taken by a scout to return to the nest and recruit nestmates would
453 be problematic when hunting mobile prey, although there are exceptions where scouts are
454 present like in the ponerine ant *Leptogenys diminuta* (Witte, Schliessmann & Hashim, 2010).
455 The necessity for scouts in group-hunting species can also be bypassed by directly foraging in
456 groups, like *Leptogenys* sp. does in Cambodia (Peeters & DeGreef 2015). These ants hunt
457 large millipedes in groups of several dozen workers, subduing their prey would otherwise be
458 difficult. Thus the millipede can be overwhelmed immediately without first recruiting
459 nestmates, which would increase the risk of losing such mobile prey (Witte, Schliessmann &
460 Hashim, 2010).

461 One very clear difference between honeybees and *M. analis* is the ratio of scouts to recruits.
462 In honeybees 5–25 % of the workers act as scouts, foraging individually and recruiting if need
463 be (Seeley 1983), while in *M. analis* it is roughly 1 %. This stark difference could be due to

464 the number of foraging trips. While *M. analis* will only exploit 3-5 food sources over a day,
465 honeybees exploit dozens of different sources in the same time window (Abou-Shaara, 2014)
466 and more importantly are able to do so alone. Since *M. analis* requires only a few hunting
467 trips per day a much smaller number of scouts could suffice to find enough adequate food
468 sources. This could be comparable to certain cleptoparasitic stingless bee species, like the
469 genus *Lestrimelitta*, which invade other bee nests for food (Gruter, von Zuben, Segers, &
470 Cunningham, 2016). Bumblebees (*Bombus terrestris*) offer an interesting example of a
471 eusocial species foraging on stationary food sources without clear recruitment (Dornhaus &
472 Chittka 2004a). The current scientific reasoning for this is that the benefits of recruitment
473 decrease with increasing patchiness of food sources (Dornhaus & Chittka 2004b).
474 Bumblebees forage mostly in open meadows in a very heterogeneous environment with many
475 food sources (Dornhaus & Chittka 2004a), so while activation of nestmates can be observed,
476 there is no need for direct recruitment to a specific location. Ultimately the foraging
477 behaviour of *M. analis* can be compared to many other social insects (stingless bees, slave-
478 making ants), further studies are necessary though to crystalize the factors that truly regulate
479 scout numbers and group/solitary foraging in a cross family comparison.

480 *Conclusion*

481 In conclusion we were able to show that most central place foraging predictions are fulfilled
482 by the raiding behaviour of *M. analis*. Remarkably this is not only achieved by collective
483 decisions but rather by an interplay between individual decisions by scout ants and collective
484 responses by the colony. Thereby having 1 % of the colony (10–20 scouts) potentially
485 deciding the fate and foraging efficiency of the other 99 %.

486

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581

582 **TABLES**

583 Table A1. Statistical differences in raid size depending on distance and food quality in Fig. 2

Caste 1	Caste 2	Z	P
Kruskal-Wallis			<0.001
Small HG 10 m	Small HG 30 m	-1.90	0.11
Small HG 10 m	Large HG 10 m	2.33	0.049
Small HG 10 m	Large HG 30 m	3.90	<0.001
Small HG 30 m	Large HG 10 m	0.15	0.44
Small HG 30 m	Large HG 30 m	1.44	0.15
Large HG 10 m	Large HG 30 m	-1.44	0.22

584 Kruskal Wallis rank sum test ($X^2_3=15.7$) followed by Dunn's test; Small hunting ground (HG) 10 m: $N=15$;585 Small HG 30 m: $N=8$; Large HG 10 m: $N=12$; Large HG 30 m: $N=13$.

586

587 Table A2. Statistical differences in hunting time depending on distance and hunting ground as shown in Fig. 4

Caste 1	Caste 2	Z	P
Kruskal-Wallis			<0.001
Small HG 10 m	Small HG 30 m	1.43	0.077
Small HG 10 m	Large HG 10 m	-3.06	0.001
Small HG 10 m	Large HG 30 m	4.80	<0.001
Small HG 30 m	Large HG 10 m	-1.23	0.11
Small HG 30 m	Large HG 30 m	-2.66	0.004
Large HG 10 m	Large HG 30 m	1.58	0.057

588 Kruskal Wallis rank sum test ($X^2_3=24.7$) followed by Dunn's test; Small hunting ground (HG) 10 m: $N=15$;589 Large HG 10 m: $N=12$; Hunger: $N=8$.

590

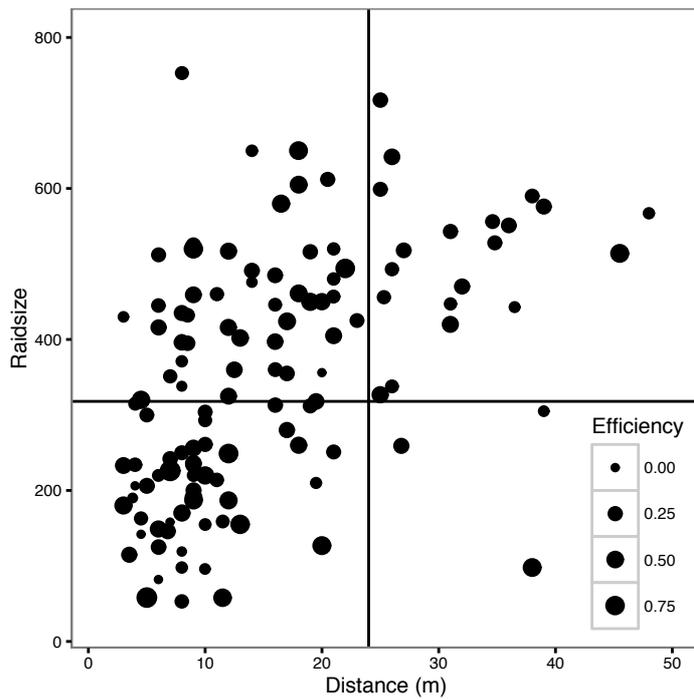
591 Table A3. Statistical differences in raid size depending on hunger state and hunting ground as shown in Fig. 5

Caste 1	Caste 2	Z	P
Kruskal-Wallis			<0.001
Small HG 10 m	Large HG 10 m	-2.29	0.011
Small HG 10 m	Small Hunger	-2.99	0.0014
Small HG 10 m	Large Hunger	-3.66	<0.001
Large HG 10 m	Small Hunger	-1.56	0.05
Large HG 10 m	Large Hunger	-1.88	0.03
Small Hunger	Large Hunger	-0.004	0.5

592 Kruskal Wallis rank sum test ($X^2_3=19.0$) followed by Dunn's test; Small hunting ground (HG) 10 m: $N=15$;
 593 Large HG 10 m: $N=12$; Hunger small: $N=5$; Hunger large: $N=5$.

594

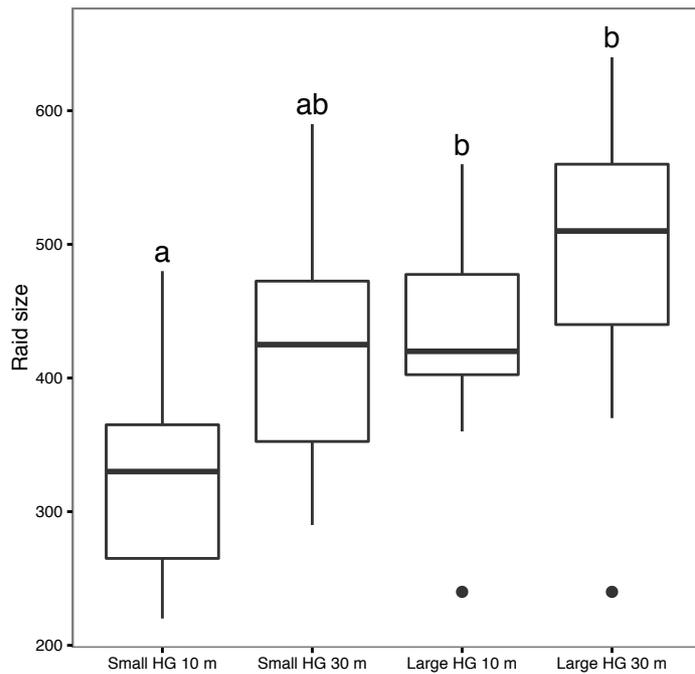
595 **FIGURES**



596

597 **Figure 1.** Correlation of raid size to distance. Efficiency: Percentage of ants carrying termites
 598 after the raid; dot size corresponds to the percentage of efficiency. Raid size: number of ants
 599 participating in raid. $N=134$. Horizontal line: median raid size (318 ants). Vertical line: Half
 600 of the maximum raid distance (24 m).

601

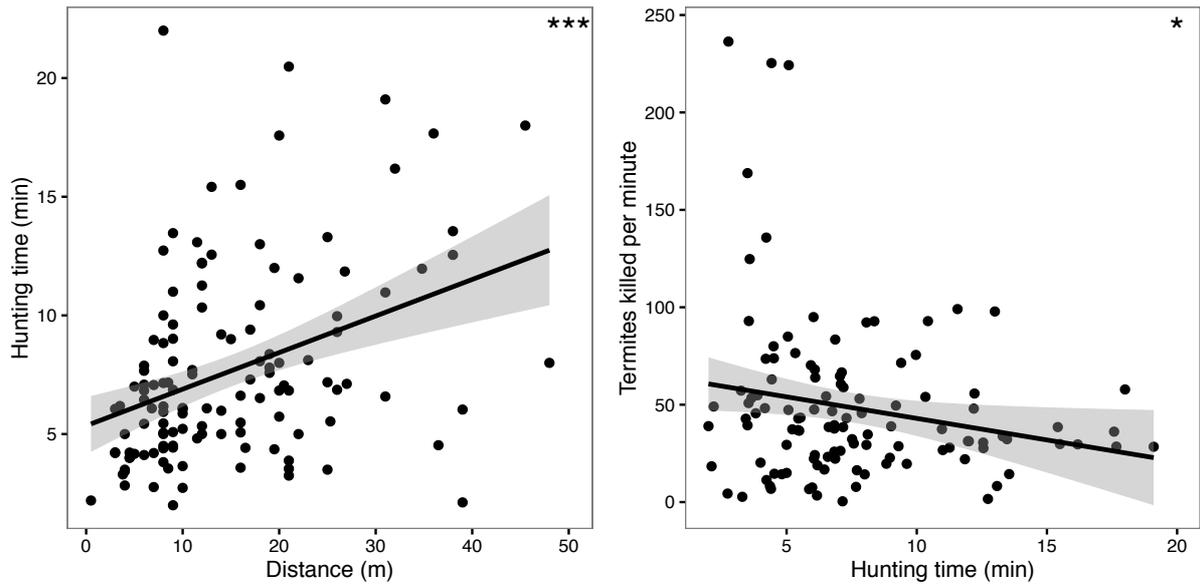


602

603 **Figure 2.** Raid size for differing distance and food quantity. Box-and-whisker plot for raids
 604 conducted in the lab ($N=12$ per experiment). Small HG: Small Hunting ground (50 termites in
 605 an area of 50 cm^2); Large HG: Large Hunting ground (250 termites in an area of 1260 cm^2).
 606 10 m and 30 m: distance from the nest to the feeding site. Box-and-whisker plot show median
 607 (horizontal line), interquartile range (box), distance from upper and lower quartiles times 1.5
 608 interquartile range (whiskers), outliers ($> 1.5X$ upper or lower quartile) and significant
 609 differences (different letters; $P<0.05$).

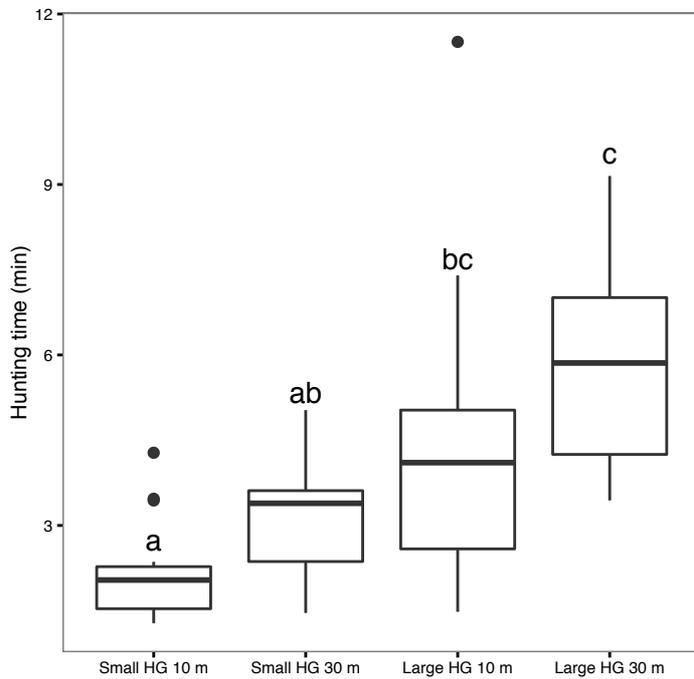
610

611



612

613 **Figure 3.** Relation of hunting time to distance and killing rate. Scatterplot with linear
 614 regression line and 95% confidence interval (shaded area) for (a) time spent at the hunting
 615 ground in relation to distance from the nest and (b) the number of termites killed per minute
 616 during the hunting period to the time spent at the hunting ground. $*$ = $P<0.05$; $**$ = $P<0.01$;
 617 $***$ = $P<0.001$.

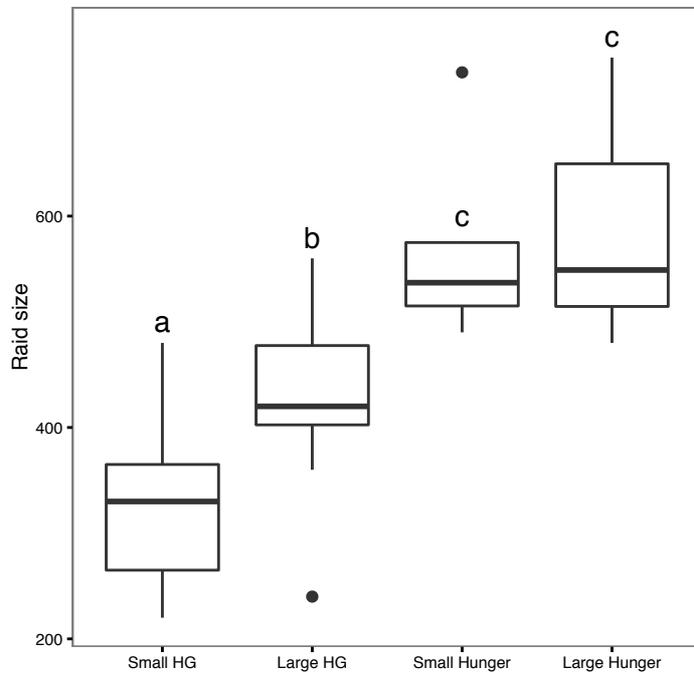


618

619 **Figure 4.** Hunting time for differing distance and food quantity. Box-and-whisker plot for
 620 raids conducted in the lab ($N=12$ per experiment). Hunting time: Time spent at the foraging
 621 site; Small HG: Small Hunting ground (50 termites in an area of 50 cm^2); Large HG: Large
 622 Hunting ground (250 termites in an area of 1260 cm^2). Box-and-whisker plot show median

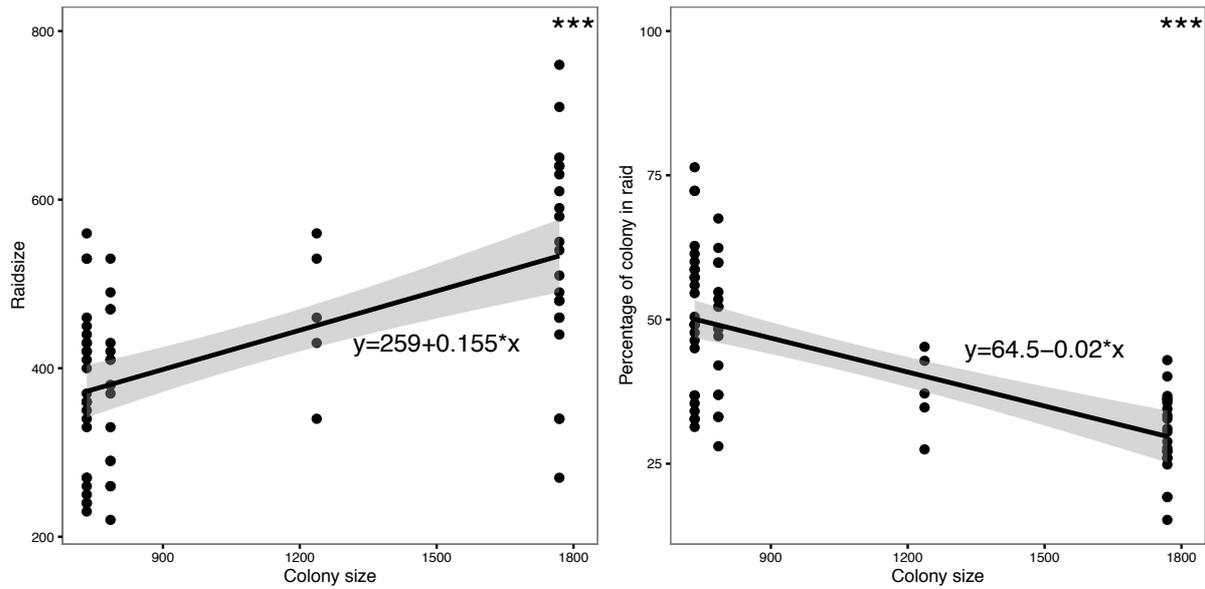
623 (horizontal line), interquartile range (box), distance from upper and lower quartiles times 1.5
624 interquartile range (whiskers), outliers ($> 1.5X$ upper or lower quartile) and significant
625 differences (different letters; $P<0.05$).

626



627

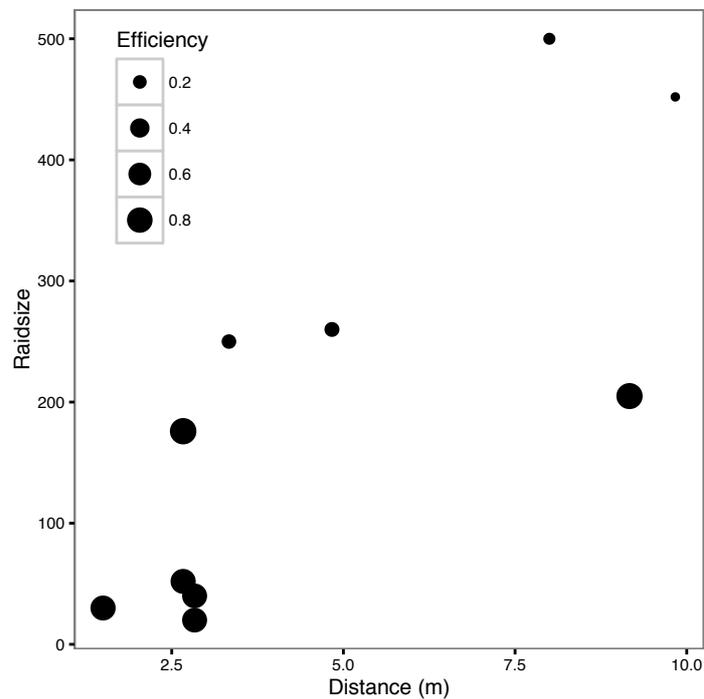
628 **Figure 5.** Raid size for Hungry colonies compared to satiated colonies. Box-and-whisker plot
629 for raids conducted in the lab. Small HG: Small Hunting ground ($N=12$; 50 termites in an area
630 of 50 cm^2); Large HG: Large Hunting ground ($N=12$; 250 termites in an area of 1260 cm^2);
631 Small Hunger: Colony starved for 48 h for small HG ($N=5$); Large Hunger: Colony starved
632 for 48 h for large HG ($N=5$). Box-and-whisker plot show median (horizontal line),
633 interquartile range (box), distance from upper and lower quartiles times 1.5 interquartile range
634 (whiskers), outliers ($> 1.5X$ upper or lower quartile) and significant differences (different
635 letters; $P<0.05$).



636

637 **Figure A1.** Raid size in relation to colony sizes in the lab. Black line: linear regression line
 638 and 95% confidence interval (shaded area). ***= $P < 0.001$; $N = 69$. (a) Raid size in relation to
 639 colony size (b) Percentage of colony participating in raid to total colony size.

640



641

642 **Figure A2.** Correlation of raid size to distance for starved colonies. Efficiency: Percentage of
 643 ants carrying termites after hunt. Raid size: number of ants participating in raid. $N = 10$