

1 **Reduced foraging investment as an adaptation to patchy food sources: a**
2 **phasic army ant simulation**

3

4 **Abstract**

5 Colonies of several ant species within the subfamily Dorylinae alternate
6 stereotypical discrete phases of foraging and reproduction. Such phasic cycles are
7 thought to be adaptive because they minimize the amount of foraging and the related
8 costs, and at the same time enhance the colony-level ability to rely on patchily
9 distributed food sources. In order to investigate these hypotheses, we use here a
10 simple computational approach to study the population dynamics of two species of
11 virtual ant colonies that differ quantitatively in their foraging investment. One species,
12 which we refer to as “phasic”, forages only half of the time, mirroring the phasic
13 activity of some army ants; the other “non-phasic” species forages instead all the
14 time. We show that, when foraging costs are relatively high, populations of phasic
15 colonies grow on average faster than non-phasic populations, outcompeting them in
16 mixed populations. Interestingly, such tendency becomes more consistent as food
17 becomes more difficult to find but locally abundant. According to our results, reducing
18 the foraging investment, for example by adopting a phasic lifestyle, can result in a
19 reproductive advantage, but only in specific conditions. We thus suggest phasic
20 colony cycles to have emerged together with the doryline specialization in feeding on
21 the brood of other eusocial insects, a resource that is hard to obtain but highly
22 abundant if available.

23

24

25 Introduction

26 Within several taxa belonging to the ant subfamily Dorylinae (*sensu* Brady et al.,
27 2014), species are considered “phasic” or “non-phasic” according to their lifestyle
28 (Schneirla, 1971; Gotwald, 1995; Kronauer, 2009). In phasic species, broods develop
29 synchronously in distinct cohorts of the same age, and colonies undergo virtually
30 discrete phases of foraging and reproduction based on the presence or absence of
31 food-demanding larvae (Schneirla, 1971; Gotwald, 1995; Ravary and Jaisson, 2002;
32 Kronauer, 2009; Teseo et al., 2013). In non-phasic species, larvae are not
33 synchronized in their development, and foraging and reproduction are not strictly
34 coordinated with reproductive cycles. Within army ants, non-phasic taxa include the
35 genera *Dorylus* and *Labidus*, whereas phasic taxa include some species within the
36 Old World genus *Aenictus* and the New World genera *Eciton* and *Neyvamyrmex*
37 (Kronauer, 2009). Outside army ants, phasic groups include some species in the
38 genera *Sphinctomyrmex* (Buschinger et al., 1989), *Leptanilloides* (Brandão et al.,
39 1999; Donoso et al., 2006), *Cerapachys* (Wilson, 1958a; Ravary and Jaisson, 2002),
40 and to some extent *Simopelta* within the Ponerinae subfamily (Gotwald and Brown,
41 1967), and *Leptanilla japonica* within Leptanillinae (Masuko, 1990). Found in loosely
42 related groups, phasic colony cycles have recently been suggested to have evolved
43 repeatedly and early in army ant evolution, and to have been secondarily lost in
44 genera such as *Dorylus* and *Labidus* (Kronauer, 2009).

45 Whereas the phasic cycles of *Eciton* and *Neyvamyrmex* have been extensively
46 studied in the field throughout the 20th century (Hagan, 1954a, 1954b, 1954c,
47 Schneirla, 1934, 1945, 1944a, 1944b; Topoff et al., 1980; Topoff, 1984), the “clonal
48 raider ant” *Cerapachys biroi* is the only species in which the mechanistic aspects of
49 phasic colony cycles have been thoroughly studied in highly controlled laboratory
50 experiments (Ravary and Jaisson, 2002; Ravary et al., 2006; Teseo et al., 2013;
51 Ulrich et al., 2015). In this parthenogenetic queenless species, the presence of larvae
52 inhibits the ovarian activation in workers and stimulates foraging behavior. This
53 results in developmentally synchronized cohorts of larvae and phasic foraging activity
54 limited to when larvae are present.

55 Although the molecular, individual and colony-level mechanisms underlying the
56 alternation of phases are now beginning to be understood (Ravary and Jaisson,
57 2002; Ravary et al., 2006; Teseo et al., 2013; Oxley et al., 2014; Ulrich et al., 2015),
58 the adaptive significance of the phasic lifestyle is still to some extent unknown. At

59 present, a single study (Kronauer, 2009) has formulated explicit hypotheses about
60 the adaptive value of the phasic lifestyle, suggesting that it likely provides several
61 main benefits. First, in some army ant species, colonies migrate throughout the
62 foraging phases. Migrations probably maximize the foraging success and help
63 avoiding resource depletion at a local scale (Wilson, 1958b; Franks and Fletcher,
64 1983; Gotwald, 1995). Second, phasic cycles minimize the time invested in foraging,
65 which in turn minimizes the costs involved in foraging activity and emigrations. Third,
66 stationary reproductive phases are sometimes necessary because, in raid-
67 conducting genera such as *Eciton* and *Neyvamyrmex* (but not in *C. biroi*),
68 physogastric egg-laying queens are not mobile or cannot be transported by workers.
69 Finally, doryline ants are in fact specialized predators of the brood of other social
70 insect colonies (Brady et al., 2014; Borowiec, 2016), a food source that is difficult to
71 find but may be overabundant when found (Kronauer, 2009). Developmentally
72 synchronized cohorts of larvae should, in principle, consume more efficiently the
73 large quantities of rapidly decaying prey that become unpredictably available during
74 foraging phases compared to non-synchronized broods including eggs and pupae.

75 In this study, we use simple computer simulations to explore some of the
76 hypotheses regarding the adaptive value of phasic cycles in army ants, with the goal
77 of understanding whether these may have appeared as an adaptation to specific
78 ecological conditions. In nature, colonies of phasic ant species only forage in the
79 presence of developing larvae, a period corresponding approximately to half the
80 duration of a complete reproductive cycle in *E. burchelli* or *C. biroi* (Schneirla, 1971;
81 Ravary and Jaisson, 2002). In such species, however, colonies need to reach a
82 certain threshold size in order to successfully split, via fission, into two viable
83 daughter colonies. Accordingly, the main assumption of our model is that, everything
84 else being equal, phasic colonies invest in foraging only half of their time. Therefore,
85 due to the reduced investment in foraging, growth and reproduction in phasic
86 colonies are restricted to around only half of their potential. From an evolutionary
87 perspective, in a hypothetical ancestral population in which different ant colonies
88 make quantitatively different foraging investments, colonies with a low foraging
89 investment should grow and reproduce relatively slower and eventually become
90 extinct; on the other hand, colonies with a high foraging investment should grow and
91 reproduce faster, invading the population. Our model aims to understand the
92 evolution of phasic cycles by investigating the conditions in which reducing rather

93 than maximizing the time invested in foraging may result in a selective advantage for
94 virtual ant colonies. In particular, we ask whether and how the cost of foraging, the
95 probability to find food items and the size of the food items affect the population
96 dynamics of low- and high-foraging virtual ant colonies, which we respectively refer to
97 as “phasic” and “non-phasic”. These two colony types, or species, behave exactly the
98 same way, with the only exception that the foraging investment of phasic colonies is
99 only half of that of non-phasic colonies.

100 In our simulations, we first examine the growth of monospecific populations of
101 phasic or non-phasic colonies. Then, we explore the outcome of competition for food
102 in mixed populations consisting of phasic and non-phasic colonies. We show that
103 phasic colonies reproduce more than, and outcompete, non-phasic colonies when
104 the cost of foraging is relatively high. Interestingly, this tendency becomes more
105 consistent as food becomes more patchily distributed. Our results suggest that the
106 more locally abundant and rare food sources are, the better phasic colonies
107 outperform non-phasic colonies. Minimizing the foraging investment, for example by
108 adopting a phasic lifestyle, could thus result in a reproductive advantage in specific
109 conditions.

110

111 **The models**

112 **Logistic density-dependent growth of phasic or non-phasic colonies**

113 Our simulations are based on a variation of the continuous density-dependent
114 growth model in single-species populations. In our model, growth depends on the
115 food income and the cost of foraging. The growth of a colony can thus be expressed
116 by the differential equation:

117

$$\frac{dn}{dt}(t) = f(p - c) n(t) \left(\frac{1 - n(t)}{N} \right)$$

118

119 where $n(t)$ is the number of individuals in the colony, p is the food income for the
120 colony, c is the cost of foraging, f is a factor that describes the foraging investment
121 and takes different values for phasic ($f=1/2$) and non-phasic ($f=1$) populations, and N
122 is the maximal size that a colony can reach, expressed as its number of individuals.
123 When $p=c$, the population growth equals zero and the system is in an unstable state

124 of equilibrium. With $p < c$, the colony experiences negative growth and goes through
125 extinction, whereas with $p > c$ it grows until the maximal size is reached.

126 In our first set of simulations, we examine the growth curve of populations
127 constituted of either only phasic or only non-phasic colonies, in discretized time. In
128 each simulation, the total population is composed by a variable number of colonies
129 and is represented by a vector \bar{n} , which we refer to as the population vector. Each
130 element n_i within \bar{n} represents the number of individuals within the i -th colony. The
131 length of \bar{n} represents the number of colonies in the population, and varies with time
132 depending on colony death and reproduction. At each time iteration (identified by the
133 subscript t), the discrete variation of the size of each colony is computed according to
134 the following equation:

135

$$\Delta n_{i,t} = f(p_{i,t} - c) n_{i,t} \left(\frac{1 - l_t}{L} \right)$$

136

137 where $n_{i,t}$ is the number of individuals in the i -th colony at the t -th time iteration, f is
138 the “foraging” factor varying for phasic ($f=1/2$) and non-phasic ($f=1$) populations, $p_{i,t}$ is
139 the food income, c is the foraging cost, l_t is the number of colonies at time t , and L is
140 the carrying capacity for the population, expressed as the maximal number of
141 colonies that are able to survive in the environment. The idea behind our simulations
142 is that virtual ant colonies explore the environment in search of food, and may
143 encounter food items of various sizes and at different probabilities. The time unit of
144 the simulation corresponds to one colony cycle, a period in which each colony may
145 find a food item and, depending on its size, possibly reproduce or die. In our
146 algorithm, colonies find on average the same quantity of food, but food distribution is
147 parametrically controlled to allow testing and comparing differential scenarios. To
148 keep the average food income constant among scenarios, the size of the available
149 food items and the probability to encounter them are inversely proportional. For
150 example, in a given scenario, food items are small and easy to find, whereas in
151 another one they are large and difficult to find. We thus implement the food income
152 $p_{i,t}$ as a stochastic variable depending on the random number x , which is uniformly
153 distributed in the interval $[0,1]$, in the following way:

154

$$\begin{cases} p = w & \text{if } x \leq s/w \\ p = 0 & \text{elsewhere} \end{cases}$$

155

156 where s represents the average food income per colony, w is the parameter used
157 to tune food distribution in the different scenarios (it regulates the probability of
158 finding food without changing the average food income over time per colony), and
159 s/w is the probability of finding food. The model is based on the iteration of an
160 algorithm modelling a virtual ant colony cycle, which is taken as the time unit (Figure
161 1a). The algorithm begins with the generation of a random number x . If x is smaller
162 than s/w , the colony finds and consumes a quantity w of food, which results in a size
163 increase; if x is larger than s/w , the colony does not encounter food and does not
164 increase in size. In addition, as foraging is costly, colonies lose individuals at each
165 time iteration. This limits the growth of the colonies that encounter food items, and
166 results in negative growth for colonies that do not encounter food items. Changing
167 the value of w modifies the probability at which each colony receives food and the
168 size of the food items, but does not affect the average quantity of food received. For
169 example, with s fixed at 0.4, if $w=1$ colonies receive food items of size 1 with a
170 probability 0.4; on the other hand, if $w=2$, colonies receive food items of size 2 with a
171 probability 0.2, and if $w=0.5$, they receive food items of size 0.5 with a probability 0.8
172 (Figure 1b). Implementing different values of w allows testing and comparing the
173 performances of phasic and non-phasic colonies in various scenarios.

174 Colonies of phasic army ant species generally reproduce via fission by splitting in
175 two equally sized daughter colonies when they reach a certain threshold size. In
176 order to reproduce such dynamics, the algorithm checks the size of each colony at
177 the end of each time iteration. If a colony reaches the maximal size, which we refer to
178 as m , it splits into two colonies of size $m/2$. If during the simulations the size of a
179 given colony falls below the value $m/10$, the colony is considered not viable anymore,
180 and is eliminated from the population vector. At the beginning of the simulations, the
181 population always consists of a single colony of size $m/2$.

182 In the first set of simulations, we studied the dynamics of monospecific populations
183 of phasic or non-phasic species, without inter-specific interactions. For each species,
184 for each of 4 values of w (0.7; 1; 2; 4), we explored values of c uniformly distributed
185 in the interval $[0, 0.7]$. We focused exclusively on the cases in which $p \geq c$ because
186 populations always go through extinction when $p < c$. The duration of each simulation

187 was set to 500 time units to allow populations to reach, in most cases, an almost
188 stable state. Each simulation was repeated 1000 times. The maximal colony size (m)
189 was fixed to 1000 individuals, and the carrying capacity L to 300 colonies. These
190 values were changed to check their effect on the simulation outcome (data not
191 shown), but as long as they were kept sufficiently high to assure a good statistical
192 representation, they did not appear to affect the results.

193

194 **Competition between phasic and non-phasic colonies**

195 Simulating the density-dependent growth of phasic or non-phasic colonies
196 provides insight into the population dynamics of monospecific populations in various
197 ecological conditions; however, it does not allow predicting the outcome of
198 competition for food in populations made up of colonies of both species. In our
199 second set of simulations, we implement a resource competition scenario within a
200 mixed population of phasic and non-phasic colonies. In this case there are two
201 population vectors, one for phasic colonies and the other for non-phasic ones, but the
202 carrying capacity is computed on the total population, i.e. the sum of phasic and non-
203 phasic colonies. Consistently with our monospecific model, at each time iteration
204 (identified by the subscript t) the discrete size variation of each colony is computed
205 according to the following equations, for phasic and non-phasic populations
206 respectively:

207

$$\Delta n_{1,t} = 1/2(p_{i,t} - c)n_{1,t} \left(\frac{1 - l_t}{L} \right)$$
$$\Delta n_{2,t} = (p_{i,t} - c)n_{2,t} \left(\frac{1 - l_t}{L} \right)$$

208

209 where n_1 is the population vector of phasic colonies, n_2 is the population vector of
210 non-phasic colonies, l_t is the total number of colonies (phasic and non-phasic) at time
211 t , and L is the carrying capacity expressed as the maximal number of colonies.
212 Concerning reproduction, the same rules of our monospecific model apply here.

213 In this set of simulations, we studied the same values of c , w and s considered in
214 the monospecific simulations. For each value of these parameters, we repeated the
215 simulation 1000 times; each simulation consisted of 500 time iterations; we fixed m ,
216 the maximal colony size, to 1000, and the carrying capacity L to 300. Concerning the

217 choice of such values, the same considerations made for the previous model apply
218 here. All the simulations were carried out in a Python environment ({van Rossum},
219 1995) with the module Numpy (Walt et al., 2011). Our scripts are provided in the
220 supplementary electronic material.

221

222 **Results**

223 **Logistic density-dependent growth of phasic and non-phasic colonies**

224 Our results show that, as expected, both phasic and non-phasic colonies perform
225 best when the cost of foraging is low. When the cost of foraging (c) exceeds a certain
226 value that depends on w (the number that regulates the probability of finding food
227 without changing the average quantity of food received over time by each colony),
228 the population size at the end of the simulations decreases, and the probability of
229 extinction increases (Figures 2a, b). When the cost of foraging and the probability to
230 find food (p) approach the same value, i.e. close to the line described by the
231 equivalence $p=c$ (Figures 2a, b), the probability to go through extinction increases for
232 both phasic and non-phasic populations. In general, at each value of c , the final
233 population size increases with p , and the probability of extinction decreases (Figures
234 2a, b). The range of c and p values at which populations go through extinction
235 becomes wider with increasing values of w . In particular, the extinction zone is wider
236 for non-phasic colonies (Figure 2a) compared to phasic ones (Figure 2b), meaning
237 that, for the same values of c , non-phasic colonies need more food than phasic
238 colonies in order to avoid extinction.

239 For phasic colonies, for each value of c and at increasing values of p , the
240 probability of extinction decreases and reaches zero (Figures 2b); on the other hand,
241 for non-phasic colonies, the extinction probability decreases more slowly and never
242 reaches zero, indicating that non-phasic colonies always face a risk of extinction
243 (Figures 2a). Overall, higher extinction rates of non-phasic colonies lower their final
244 population size across simulations.

245

246 **Competition between phasic and non-phasic colonies**

247 At relatively low values of w , i.e. when food items are small but found frequently,
248 non-phasic colonies outcompete phasic colonies and invade the population in most
249 conditions (Figures 3a). On the other hand, phasic colonies tend to invade the

250 population at values close to the line described by the equivalence $p=c$, in relatively
251 more difficult conditions (Figures 3b).

252 As c increases, both populations need more food to avoid extinction, and with food
253 becoming more difficult to find but locally abundant (i.e. at increasing values of w),
254 survival becomes increasingly difficult for both types of colonies (Figure 3a). With
255 $w=4$, for example, the carrying capacity is reached exclusively at relatively low
256 foraging costs. However, similar to what happens in monospecific populations,
257 phasic colonies go through extinction more slowly compared to non-phasic colonies,
258 in that their prevalence increases at increasing values of w (Figure 3b). Even though
259 for high values of w the total final population size is much lower than for low w
260 values, phasic colonies outcompete non-phasic colonies in most conditions (Figures
261 3a, b).

262

263 Discussion

264 In this study, we have explored the population dynamics of two species of virtual
265 ant colonies that differed quantitatively in their foraging investment. Our goal was to
266 understand whether and when, under the assumptions of our model, colonies with a
267 reduced foraging investment (or “phasic”) may have a better reproductive success
268 compared to colonies that maximize their foraging effort (or “non-phasic”). We first
269 studied monospecific populations of phasic or non-phasic colonies, and then mixed
270 populations in which the two species competed for resources. When food was found
271 frequently and the cost of foraging was set to relatively low values, monospecific
272 populations of non-phasic colonies grew faster than phasic populations. On the other
273 hand, due to their lower foraging investment, phasic colonies lost fewer individuals
274 per iteration compared to non-phasic colonies, which resulted to be advantageous in
275 challenging conditions. In fact, with the foraging cost set at relatively high values,
276 phasic colonies survived through long series of iterations in which they could not
277 access any food. This made them less likely to go through extinction, and also
278 allowed them to reach larger population sizes compared to non-phasic colonies.
279 Finally, and most interestingly, phasic populations performed increasingly better than
280 non-phasic populations with food becoming rarer and locally abundant (higher values
281 of w). Consistent to what we observed in monospecific populations, the dynamics of
282 mixed populations depended as well on the distribution of the food items. When food
283 was available only in small quantities but found easily, non-phasic colonies invaded

284 the population in most conditions, and reached the carrying capacity of the
285 environment. On the other hand, even though they did not reach the carrying
286 capacity, phasic colonies tended to invade the population as food became rarer and
287 more locally abundant, because they were less likely to go through extinction
288 compared to non-phasic colonies.

289 According to our results, reducing rather than maximizing foraging activity can, in
290 specific conditions, provide a significant reproductive advantage to ant colonies.
291 Relying exclusively on costly, rare but locally abundant food is thus sustainable if the
292 colony-level foraging investment is parsimonious; instead of foraging and raising
293 brood continuously, phasic ants have evolved a system in which foraging, to which
294 colony growth, reproduction and fitness are proportional, is reduced to phases
295 virtually as short as the development of a single larva.

296 Most phasic ants, like many Dorylinae, are predators specialized in feeding on the
297 brood of other social insects (Brady et al., 2014; Borowiec, 2016). Typically this is
298 costly because prey colonies defend their nests and are in principle difficult to feed
299 on. However, social insect colonies also generally house large amounts of brood,
300 representing consistent food quantities for successful predator colonies. Our results
301 thus suggest the possibility that the phasic lifestyle may have emerged together with
302 the specialization in feeding on the brood of social insect colonies. Ecological
303 pressures, such as inter-colony competition, might have pushed generalist non-
304 phasic hunting ancestors to specialize in feeding on social insect brood. This might
305 have selected for colonies that restricted their foraging investment, eventually
306 resulting in the evolution of phasic cycles. In army ants, such a transition towards
307 phasic activity may have occurred concurrently with the transition from individual to
308 cooperative hunting (Wilson, 1958b; Hölldobler and Wilson, 1990; Kronauer, 2009),
309 possibly through the re-activation of the gene networks responsible, in solitary-living
310 Hymenoptera, for the alternation of foraging and reproductive phases (Amdam et al.,
311 2006; Oxley et al., 2014).

312 The evolution of phasic activity cycles in ants needs to be further investigated a
313 theoretical perspective. Our population dynamics approach, for example, could be
314 integrated with a recently proposed mathematical model suggesting phasic colony
315 cycles to be adaptive in species where the investment required to feed a single larva
316 is high, but decreases as the number of larvae increases (Garnier and Kronauer,
317 2016). Previous research in theoretical ecology has made use of cellular automata to

318 simulate the behavior of *Eciton burchelli* colonies (Britton et al., 1996), and analyze
319 the effects on habitat quality and extension on population survival (Partridge et al.,
320 1996; Britton et al., 1999). Using such cellular automata to model an interspecific
321 competition scenario may help explore more specific questions about the adaptive
322 value of phasic cycles. Such an approach would allow, for example, explicitly
323 implementing the spatial and chronological dynamics of virtual ant colonies with
324 differential degrees of phasic behavior, and testing whether and how phasic cycles
325 may have a role in preventing colonies from depleting food resources at a local scale
326 (Wilson, 1958b; Franks and Fletcher, 1983; Gotwald, 1995).

327 At present, empirically studying the adaptive value of phasic colony cycles
328 appears to be challenging. A possible approach would likely consist in comparing
329 phasic and non-phasic populations of the same or of closely related species. In
330 particular, one could challenge such phasic and non-phasic colonies by feeding them
331 either frequently with low amounts of food, or rarely with large amounts of food.
332 Measuring the subsequent fitness of such experimental colonies would likely help
333 understand whether phasic cycles are better suited for relying on rare but locally
334 abundant food sources. At present, however, such an experiment would be hard to
335 set up, mostly because phasic ant species are still poorly understood, cryptic and
336 difficult to manipulate, especially in laboratory conditions. The only phasic ant that
337 can be consistently studied in laboratory experiments is *C. biroi*. Using gene-
338 silencing techniques on this species, an interesting approach would be “switching off”
339 the mechanisms inhibiting worker ovarian activity in the presence of larvae, which
340 would possibly result in producing non-phasic colonies. One could then test non-
341 phasic and wild type colonies with differential feeding regimes.

342 The biology of doryline ants is still relatively poorly known. This is mainly because
343 many taxa within the group are rare or difficult to encounter because of their
344 hypogeaic lifestyle. In addition, a poor knowledge of the taxonomy of doryline ants,
345 and a classification that until recently did not accurately take into account their
346 evolutionary relationships have been an obstacle to comparative studies within the
347 subfamily (Borowiec, 2016). A deeper understanding of the systematics and the
348 behavior of Dorylinae is needed to gain new insights into the evolution of phasic
349 colony cycles.

350

351

353 **References**

354

355 Amdam, G.V., Csondes, A., Fondrk, M.K., Page, R.E., 2006. Complex social
356 behaviour derived from maternal reproductive traits. *Nature* 439: 76-78.

357

358 Borowiec, M., 2016. Generic revision of the ant subfamily Dorylinae (Hymenoptera,
359 Formicidae). *ZooKeys* 608: 1-280.

360

361 Brady, S.G., Fisher, B.L., Schultz, T.R., Ward, P.S., 2014. The rise of army ants and
362 their relatives: diversification of specialized predatory doryline ants. *BMC Evol. Biol.*
363 14:93.

364

365 Brandão, C.R.F., Diniz, J.L.M., Agosti, D., Delabie, J.H., 1999. Revision of the
366 Neotropical ant subfamily Leptanilloidinae. *Syst. Entomol.* 24: 17-36.

367

368 Britton, N.F., Partridge, L.W., Franks, N.R., 1999. A model of survival times for
369 predator populations: The case of the army ants. *Bull. Math. Biol.* 61: 469-482.

370

371 Britton, N.F., Partridge, L.W., Franks, N.R., 1996. A mathematical model for the
372 population dynamics of army ants. *Bull. Math. Biol.* 58: 471-492.

373

374 Buschnger, A., Peeters, C., Crozier, R.H., 1989. Life-Pattern Studies on an
375 Australian *Sphinctomyrmex* (Formicidae: Ponerinae; Cerapachyini): Functional
376 Polygyny, Brood Periodicity and Raiding Behavior. *Psyche J. Entomol.* 96: 287-300.

377

378 Donoso, D.A., Donoso, D.A., Vieira, J.M., Wild, A.L., 2006. Three new species of
379 Leptanilloides Mann from Andean Ecuador (Formicidae: Leptanilloidinae). *Zootaxa*

380

381 Franks, N.R., Fletcher, C.R., 1983. Spatial patterns in army ant foraging and
382 migration: *Eciton burchelli* on Barro Colorado Island, Panama. *Behav. Ecol.*
383 *Sociobiol.* 12, 261–270. doi:10.1007/BF00302894

384

385 Garnier, S., Kronauer, D.J.C., 2016. The adaptive significance of phasic colony
386 cycles in army ants. bioRxiv 091934. doi:10.1101/091934

387

388 Gotwald, W.H., 1995. *Army Ants: The Biology of Social Predation*. Cornell University
389 Press, Ithaca

390

391 Gotwald, W.H., Brown, W.L., 1967. The ant genus *Simopelta* (Hymenoptera:
392 Formicidae). *Psyche* 73: 261–277.

393

394 Hagan, H.R., 1954a. The reproductive system of the army-ant queen, *Eciton* (*Eciton*)
395 Part 1, General anatomy. *American Museum novitates*. 1663: 1-12.

396

397 Hagan, H.R., 1954b. The reproductive system of the army-ant queen, *Eciton* (*Eciton*)
398 Part 2, Histology. *American Museum novitates* □ 1664: 1-17.

399

400 Hagan, H.R., 1954c. The reproductive system of the army-ant queen, *Eciton* (*Eciton*)
401 Part 3, The oöcyte cycle. *American Museum novitates*. 1665: 1-20.

402

403 Hölldobler, B., Wilson, E.O., 1990. *The ants*. The Belknap Press of Harvard
404 University Press, Cambridge, MA.

405

406 Kronauer, D.J., 2009. Recent advances in army ant biology (Hymenoptera:
407 Formicidae). *Myrmecol. News* 12: 51-65.

408

409 Masuko, K., 1990. Behavior and ecology of the enigmatic ant *Leptanilla japonica*
410 *Baroni Urbani* (Hymenoptera: Formicidae: Leptanillinae). *Insectes Sociaux* 37: 31-57.

411

412 Oxley, P.R., Ji, L., Fetter-Pruneda, I., McKenzie, S.K., Li, C., Hu, H., Zhang, G.,
413 Kronauer, D.J.C., 2014. The Genome of the Clonal Raider Ant *Cerapachys biroi*.
414 *Curr. Biol.* 24: 451-458.

415

416 Partridge, L.W., Britton, N.F., Franks, N.R., 1996. Army Ant Population Dynamics:
417 The Effects of Habitat Quality and Reserve Size on Population Size and Time to
418 Extinction. *Proc. R. Soc. Lond. B Biol. Sci.* 263: 735-741.

419

420 Ravary, F., Jahyny, B., Jaisson, P., 2006. Brood stimulation controls the phasic

- 421 reproductive cycle of the parthenogenetic ant *Cerapachys biroi*. *Insectes Sociaux* 53:
422 20-26.
423
- 424 Ravary, F., Jaisson, P., 2002. The reproductive cycle of thelytokous colonies of
425 *Cerapachys biroi* Forel (Formicidae, Cerapachyinae). *Insectes Sociaux* 49: 114-119.
426
- 427 Schneirla, T.C., 1971. *Army ants*: a study in social organization. Freeman, San
428 Francisco
429
- 430 Schneirla, T.C., 1945. The Army-Ant Behavior Pattern: Nomad-Statary Relations in
431 the Swarms and the Problem of Migration. *Biol. Bull.* 88: 166-193.
432
- 433 Schneirla, T.C., 1944a. Studies on the Army-Ant Behavior Pattern - Nomadism in the
434 Swarm-Raider "*Eciton burchelli*." *Proc. Am. Philos. Soc.* 87: 438–457.
435
- 436 Schneirla, T.C., 1944b. The Reproductive Functions of the Army ant Queen as Pace-
437 Makers of the Group Behavior Pattern. *J. N. Y. Entomol. Soc.* 52: 153-192.
438
- 439 Schneirla, T.C., 1934. Raiding and Other Outstanding Phenomena in the Behavior of
440 Army Ants. *Proc. Natl. Acad. Sci. U. S. A.* 20: 316–321.
441
- 442 Teseo, S., Kronauer, D.J.C., Jaisson, P., Châline, N., 2013. Enforcement of
443 reproductive synchrony via policing in a clonal ant. *Curr. Biol.* 23: 328–332.
444
- 445 Topoff, 1984. Social organization of raiding and emigrations in army ants. *Adv. Stud.*
446 *Behav.* 14: 81–126
447
- 448 Topoff, H., Mirenda, J., Droual, R., Herrick, S., 1980. Onset of the nomadic phase in
449 the army ant *Neivamyrmex nigrescens* (Cresson) (Hym. Form.): Distinguishing
450 between callow and larval excitation by brood substitution. *Insectes Sociaux* 27: 175-
451 179.
452
- 453 Ulrich, Y., Burns, D., Libbrecht, R., Kronauer, D.J.C., 2015. Ant larvae regulate
454 worker foraging behavior and ovarian activity in a dose-dependent manner. *Behav.*

455 Ecol. Sociobiol. 70(7): 1011-1018.

456

457 van Rossum, G., 1995. Python tutorial, Technical Report CS-R9526.

458

459 Walt, S. van der, Colbert, S.C., Varoquaux, G., 2011. The NumPy Array: A Structure
460 for Efficient Numerical Computation. Comput. Sci. Eng. 13: 22–30.

461

462 Wilson, E.O., 1958a. Observations on the behavior of the Cerapachyine ants.
463 Insectes Sociaux 5: 129–140.

464

465 Wilson, E.O., 1958b. The Beginnings of Nomadic and Group-Predatory Behavior in
466 the Ponerine Ants. Evolution 12 : 24–31.

467

468

469

470

471

472

473

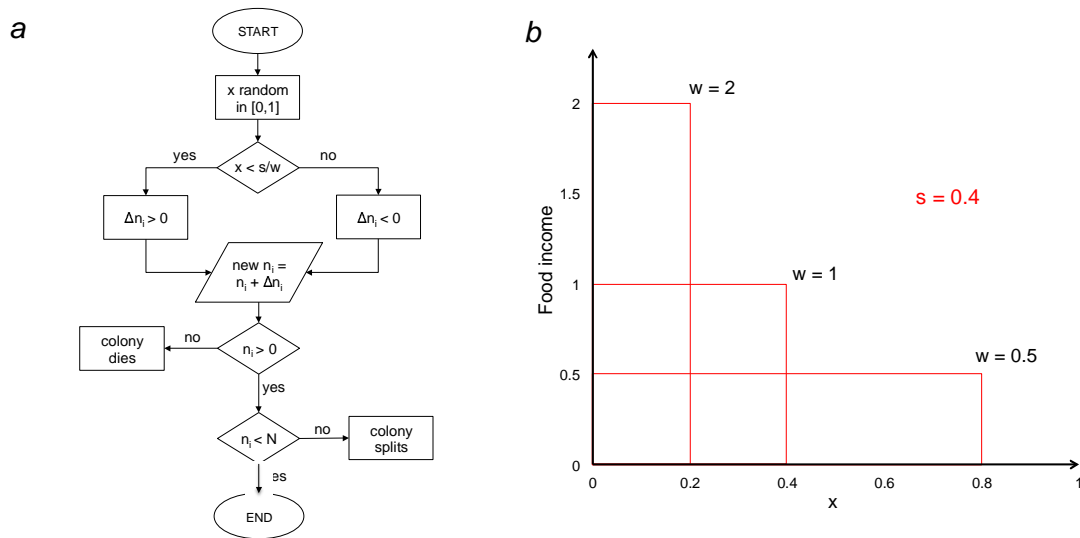
474

475

476

477

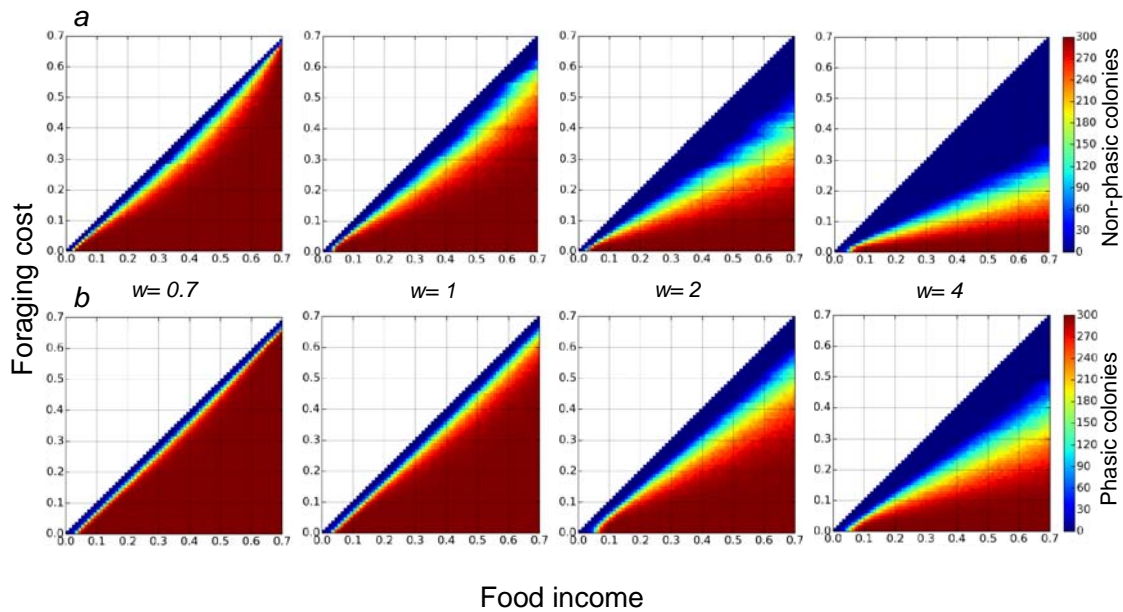
478 **Figures**



479

480 **Figure 1. The simulation algorithm. a)** At each time iteration, for each colony,
 481 our algorithm extracts a random number x . If x is smaller than s/w , the colony
 482 consumes a quantity w of food; if the value of the extracted x is larger than s/w , the
 483 colony does not consume any food, and does not grow in size. If a colony reaches
 484 the maximal size, it splits in two daughter colonies, whereas if its size falls below a
 485 given minimal value (one tenth of the maximal size), it dies. **b)** With s fixed at 0.4, if
 486 $w=1$ colonies receive food items of size 1 with a probability 0.4; if $w=2$, colonies
 487 receive food items of size 2 with a probability 0.2; if $w=0.5$, colonies receive food
 488 items of size 0.5 with a probability 0.8. The area underlying each of the red graphs is
 489 constant across cases.

490



491

492 **Figure 2. Monospecific populations of phasic and non-phasic colonies. a)**

493 The number of non-phasic colonies as a function of food income (p in the text) and

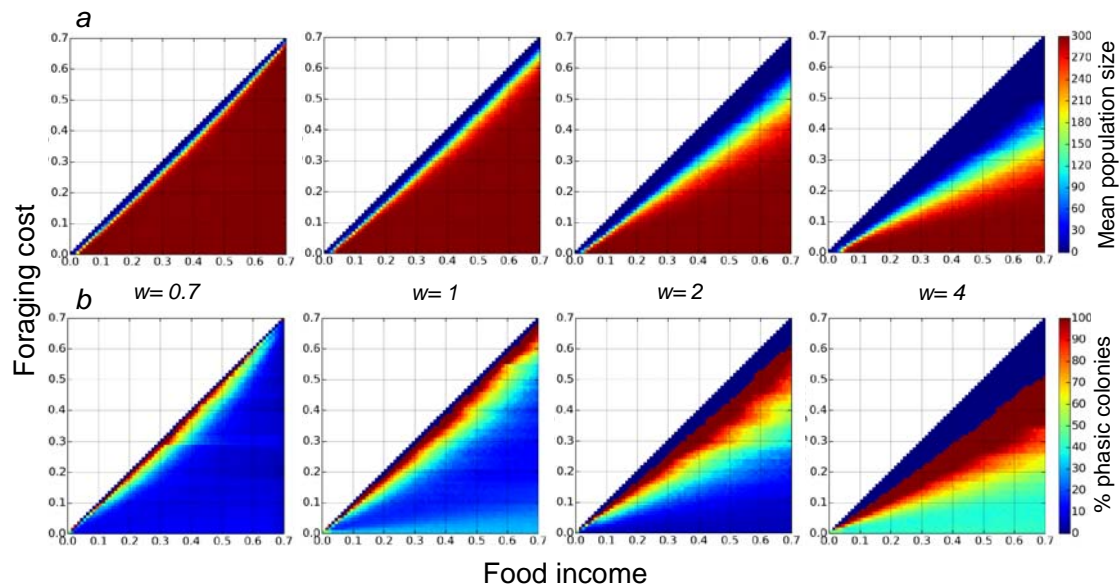
494 foraging cost (c in the text), for four different values of w , in monospecific

495 populations. **b)** Number of phasic colonies in monospecific populations. The color

496 scale represents the mean number of colonies at the end of the simulations. As

497 specified in the text, the probability of finding food decreases at increasing values of

498 w , whereas the food item size increases.



499

500 **Figure 3. Mixed populations of phasic and non-phasic colonies. a)** Mean size
501 of mixed populations at the end of the simulations, as a function of food income (p in
502 the text) and foraging cost (c in the text), for different values of w . As w increases,
503 populations increasingly fail to reach the carrying capacity (300 colonies). **b)** The
504 proportion of phasic colonies within mixed populations. The number of both phasic
505 and non-phasic colonies decreases with the increase of w , whereas the prevalence
506 of phasic colonies increases.

507

508

509