

13 Abstract:

14 Army ants are top arthropod predators in tropical forests around the world. The colonies of many army
15 ant species undergo stereotypical behavioral and reproductive cycles, alternating between brood care
16 and reproductive phases. In the brood care phase, colonies contain a cohort of larvae that are
17 synchronized in their development and have to be fed. In the reproductive phase larvae are absent and
18 oviposition takes place. Despite these colony cycles being a striking feature of army ant biology, their
19 adaptive significance is unclear. Here we use a modelling approach to show that cyclic reproduction is
20 favored under conditions where per capita foraging costs decrease with the number of larvae in a colony
21 (“High Cost of Entry” scenario), while continuous reproduction is favored under conditions where per
22 capita foraging costs increase with the number of larvae (“Resource Exhaustion” scenario). We argue
23 that the former scenario specifically applies to army ants, because large raiding parties are required to
24 overpower prey colonies. However, once raiding is successful it provides abundant food for a large
25 cohort of larvae. The latter scenario, on the other hand, will apply to non-army ants, because in those
26 species local resource depletion will force workers to forage over larger distances to feed large larval
27 cohorts. Our model provides the first quantitative framework for understanding the adaptive value of
28 phasic colony cycles in ants.

29 1. Introduction

30 Army ants are top arthropod predators in tropical rain forests around the world (Schneirla 1971;
31 Gotwald 1995; Kronauer 2009). Their colonies can measure hundreds of thousands or even millions of
32 individuals in size, and their live prey is overwhelmed by the mass onslaught of large raiding parties,
33 making army ants the ultimate group hunters. Army ant colonies emigrate frequently, a behavior that is
34 thought to be related to the necessity of regularly exploring new hunting grounds after depleting local
35 prey patches (Gotwald 1995; Kronauer 2009; Schöning 2005). While most social insect colonies are
36 founded by a single female (the queen) and then slowly grow to mature size, army ant colonies multiply
37 by a process called colony fission, during which a large colony splits into two roughly equally sized
38 daughter colonies (Schneirla 1971; Gotwald 1995; Kronauer 2009). This unusual mode of reproduction is
39 arguably related to the fact that only large army ant colonies can mount successful raids, while small
40 incipient colonies would be unviable.

41 The colonies of many army ant species undergo stereotypical behavioral and reproductive cycles, during
42 which colonies alternate between brood care and reproductive phases (Figure 1; Schneirla 1971;
43 Gotwald 1995; Kronauer 2009; Oxley et al. 2014). Colony emigrations are usually restricted to the brood
44 care phase, and foraging activity is highly intensified during that phase. The brood care phase has
45 therefore also been referred to as the “nomadic” or “foraging” phase, and the reproductive phase has
46 been referred to as the “statar” phase (“statar” meaning “settled”) by previous authors (Schneirla
47 1971; Ravary & Jaisson 2002). This phasic lifestyle has evolved repeatedly across the ant phylogeny, and
48 it can therefore be found in distantly related species. While not all army ants are phasic, all known
49 phasic species have army ant-like biology. Examples of phasic species in the subfamily Dorylinae, which
50 encompasses the vast majority of army ants, include the well-studied Neotropical army ants *Eciton*
51 *burchellii* and *E. hamatum*, the North American *Neivamyrmex nigrescens*, as well as the Asian *Aenictus*
52 *laeviceps* (reviewed in Schneirla 1971; Gotwald 1995). Several additional species in the doryline genera
53 *Aenictus*, *Cerapachys*, *Cheliomyrmex*, *Eciton*, *Neivamyrmex*, *Nomamyrmex*, and *Sphinctomyrmex* appear
54 to be phasic (Rettenmeyer 1963; Schneirla 1971; Hölldobler 1982; Buschinger et al. 1989; Gotwald
55 1995). The only ant species in which phasic colony cycles can readily be manipulated experimentally, the
56 clonal raider ant *Ooceraea biroi* (formerly *Cerapachys biroi*), also belongs to this subfamily (Ravary &
57 Jaisson 2002; Ravary et al. 2006; Teseo et al. 2013; Oxley et al. 2014; Libbrecht et al. 2016; Ulrich et al.
58 2016). Outside of the Dorylinae, phasic species with army ant-like biology can be found in the

59 subfamilies Ponerinae (genus *Simopelta*; Gotwald & Brown 1966; Kronauer et al. 2011), Leptanillinae
60 (genus *Leptanilla*; Masuko 1990), and Amblyoponinae (genus *Onychomyrmex*; Miyata et al. 2003).

61 The fact that phasic colony cycles have evolved repeatedly in species with army ant-like biology suggests
62 that they represent specific adaptations to the army ant lifestyle. While we are beginning to understand
63 the proximate mechanisms underlying phasic colony cycles in great detail using the clonal raider ant as a
64 laboratory model system (Ravary & Jaisson 2002; Ravary et al. 2006; Teseo et al. 2013; Oxley et al. 2014;
65 Libbrecht et al. 2016; Ulrich et al. 2016), the ultimate adaptive significance of phasic cycles has remained
66 elusive. Arguably the most general hypothesis that has been put forward is that in at least some species
67 with an army ant-like biology phasic colony cycles minimize the overall cost of foraging by temporally
68 restricting the presence of food-demanding larvae (Kronauer 2009). Here we assess the plausibility of
69 this hypothesis by developing an explicit model that integrates alternative reproductive strategies
70 (phasic vs. non-phasic) with the costs associated with different foraging scenarios. In particular, we
71 investigate three possible foraging scenarios: (1) the cost of foraging scales proportionally with the
72 number of larvae to be fed; (2) the cost of foraging increases proportionally faster for smaller numbers
73 of larvae than for larger ones (army ant-like foraging scenario); (3) the cost of foraging increases
74 proportionally slower for smaller numbers of larvae than for larger ones (non-army ant-like foraging
75 scenario). We find that a phasic lifestyle indeed minimizes the likely costs associated with group
76 predation (scenario 2), while a non-phasic lifestyle minimizes the costs associated with other forms of
77 foraging (scenario 3), thereby providing a convincing adaptive scenario for the evolution of army ant
78 colony cycles.

79

80 2. Methods

81 2.1. Modelling colony reproductive strategy

82 The relative number of larvae l in the colony at time t is modeled as a function of the form:

$$l(t) = (1 - A) \left(M - M \left(\frac{(\sqrt{10^{2e}} + 1) \sin\left(\frac{2\pi t}{P}\right)}{\sqrt{10^{2e} \sin^2\left(\frac{2\pi t}{P}\right) + 1}} + 1 \right) \right) + M \left(\frac{(\sqrt{10^{2e}} + 1) \sin\left(\frac{2\pi t}{P}\right)}{\sqrt{10^{2e} \sin^2\left(\frac{2\pi t}{P}\right) + 1}} + 1 \right)$$

83 where M represents the average of the periodical wave, P its period, and A its amplitude. The amplitude
84 A is relative to the average M of the periodical wave. When $A = 1$ the minimum value of the wave is 0
85 and the maximum is $2M$. When $A = 0$ the wave is flat (i.e. its minimum and maximum values are both
86 equal to the average of the wave). The exponent e controls the degree of "squarity" of the wave.
87 Positive values of e return a more square-like wave while negative values return a more sine-like wave.
88 This allows us to control how smooth the reproductive cycle is, in other words, how gradual or abrupt
89 the transitions between brood care and reproductive phases are.

90 For the remainder of this study, we will arbitrarily set the value of P , i.e. the length of the reproductive
91 cycle, to 1. We will also set the value of M , i.e. the average relative number of larvae in the colony, to
92 0.5. As a consequence, both the absolute length of the reproductive cycle and the absolute number of
93 larvae a colony raises per reproductive cycle are constant across all comparisons. With $P = 1$ and
94 $M = 0.5$ we can then simplify the previous equation as follows:

$$l(t) = \frac{A(\sqrt{100^e + 1})\sin(2\pi t) + \sqrt{100^e \sin^2(2\pi t) + 1}}{2(\sqrt{100^e \sin^2(2\pi t) + 1})}$$

95 Figure 2 shows the effect of varying either the amplitude A , or the "squarity exponent" e on the
96 temporal dynamics of the relative number of larvae present in the colony across the reproductive cycle.

97 2.2. Modelling colony foraging cost

98 We consider three possible scenarios for the distribution of foraging costs as a function of the number of
99 larvae that have to be fed:

- 100 1. "Proportional": In this scenario, the cost of foraging grows linearly with the number of larvae. This
101 scenario is biologically unlikely but will serve as a baseline comparison for the performance of the
102 other two scenarios.
- 103 2. "High Cost of Entry": In this scenario, the cost of foraging increases proportionally faster for smaller
104 numbers of larvae than for larger ones. This corresponds to cases where a minimum number of
105 workers are required before foraging yields significant benefits (for instance where ants have to
106 overpower large prey items or other social insect colonies). This is the scenario likely faced by
107 many ant species with army ant-like biology.

108 3. "Resource Exhaustion": In this scenario, the cost of foraging increases proportionally slower for
109 smaller numbers of larvae than for larger ones. This corresponds to cases where local resources
110 are exploited faster than they are replenished, which forces workers to cover increasingly larger
111 foraging distances as the number of larvae increases. This is the scenario that is likely faced by ant
112 species that mainly forage as scavengers, herbivores, or individual predators, i.e. all ant species
113 except those with army ant-like biology.

114 For all three scenarios, we can model the change in foraging cost c as a function of the relative number
115 of larvae l with a function of the form:

$$c(l) = \frac{1}{2}(n+1)k^{1-n}l^n$$

116 where k is the maximum number of larvae that a colony can have at any given time, and n is a
117 parameter that determines how the cost of foraging scales with the number of larvae to be fed. When
118 $n = 1$, the cost of foraging scales linearly with the number of larvae ("Proportional" scenario). When
119 $n > 1$, the cost of foraging grows slower for smaller than for larger numbers of larvae ("Resource
120 Exhaustion" scenario). When $0 \leq n < 1$, the cost of foraging grows faster for smaller than for larger
121 numbers of larvae ("High Cost of Entry" scenario).

122 Note that this function is designed to ensure that its integral between 0 and k is the same regardless of
123 the value of n , hence normalizing the foraging cost between all possible values of n .

124 For the remainder of this study, we will set $k = 1$, which allows us to simplify the previous equation as
125 follows:

$$c(l) = \frac{1}{2}(n+1)l^n$$

126 Figure 3 shows the effect of varying n on the shape of the foraging cost function.

127 2.3. Integrating reproductive strategy and foraging cost

128 To evaluate the performance of a given reproductive strategy under different foraging cost distributions,
129 we calculate the total foraging cost (i.e. we integrate the composite function $c(l(t))$) across one entire
130 colony cycle for different values of the relative amplitude A of the reproductive cycle, the "squarity
131 exponent" e of the reproductive cycle, and the foraging cost scaling parameter n . The general shape of
132 the integral function is as follows:

$$\int c(l(t)) = \frac{1}{2}(n+1)k^{1-n} \int \left((1-A) \left(M - M \left(\frac{(\sqrt{10^{2e}} + 1) \sin\left(\frac{2\pi t}{P}\right)}{\sqrt{10^{2e} \sin^2\left(\frac{2\pi t}{P}\right)} + 1} \right) + 1 \right) + M \left(\frac{(\sqrt{10^{2e}} + 1) \sin\left(\frac{2\pi t}{P}\right)}{\sqrt{10^{2e} \sin^2\left(\frac{2\pi t}{P}\right)} + 1} \right) + 1 \right)^n dt$$

133 With $P = 1$, $M = 0.5$ and $k = 1$, we can simplify this equation as follows:

$$\int c(l(t)) = 2^{-n-1}(n+1) \int \left(\frac{A(\sqrt{100^e} + 1) \sin(2\pi t) + \sqrt{100^e \sin^2(2\pi t)} + 1}{\sqrt{100^e \sin^2(2\pi t)} + 1} \right)^n dt$$

134 2.4. Software

135 We used Mathematica 11.0.1.0 to simplify the equations and generate the integral of the function
136 combining the reproductive strategy with the foraging cost: $\int c(l(t))$.

137 We used the “integrate” function in the “stats” package (version 3.3.2) in R (version 3.3.2) to calculate
138 the value of the integral $\int c(l(t))$ over various values of the parameters A , e , and n .

139 All figures were generated in R using the ggplot2 (version 2.2.0) and cowplot (version 0.7.0) packages.

140 All code used in this manuscript can be found at <https://goo.gl/CIHwDz>.

141

142 3. Results

143 3.1. Cost of foraging under different foraging scenarios and reproductive strategies

144 Using the integral function described above, we compute the total cost of foraging over a colony cycle
145 for various combinations of the relative amplitude A of the reproductive cycle and the shape parameter
146 n of the foraging cost function. Since we are not interested here in the effect of the shape of the
147 reproductive cycle, which will be treated in Section 3.2, we set its shape to a near-square wave ($e = 10$).
148 Note, however, that the results are qualitatively equivalent with a sine wave. Figure 4 summarizes the
149 results.

150 When the foraging cost function corresponds to a “Resource Exhaustion” scenario ($n > 1$), the lowest
151 total foraging cost is obtained by a non-phasic reproductive strategy that distributes the number of
152 larvae produced by the colony uniformly in time (i.e. $A = 0$; see top left part of Figure 4).

153 On the contrary, when the foraging cost function corresponds to a “High Cost of Entry” scenario
154 ($0 \leq n < 1$), the total foraging cost decreases with periodical variation in the number of larvae
155 produced by the colony. Lower costs are achieved for larger oscillation amplitudes, and colonies
156 perform best under the most extreme phasic reproductive strategy in terms of oscillation amplitude (i.e.
157 $A = 1$; see bottom right part of Figure 4).

158 3.2. Effect of smoothness of phase transitions

159 Here we test the effect of abrupt phase transitions in which all larvae hatch and pupate at the exact
160 same time (i.e. a square wave cycle) versus smooth phase transitions in which larvae hatch and pupate
161 around an average time (i.e. a sine wave cycle) in a “High Cost of Entry” scenario. We do not test this
162 effect in a “Resource Exhaustion” scenario because the results in Section 3.1 show that a perfectly non-
163 phasic reproductive strategy is favored in this case.

164 Using the integral function described above, we compute the total cost of foraging over a reproductive
165 cycle for different values of the cycle’s “squarity exponent” e . We set A to 1, i.e. a cycle with maximum
166 oscillation intensity, and n to $1/4$, i.e. a “High Cost of Entry” scenario. Note that results are qualitatively
167 similar for any combination of $A > 0$ and $0 < n < 1$. Figure 5 summarizes the results.

168 The total cost of foraging decreases with the value of the “squarity exponent” e , indicating that abrupt
169 phase transitions are more beneficial than smooth phase transitions for colonies experiencing a “High
170 Cost of Entry” foraging scenario.

171

172 4. Discussion

173 Our model shows that phasic colony cycles are adaptive in species where the relative cost of foraging,
174 that is the investment required per larva, is high when few larvae have to be fed, but decreases as the
175 number of larvae increases (Figure 4). Such a “High Cost of Entry” scenario applies, for example, when a
176 substantial investment into foraging is required before foraging yields any benefits at all. This seems to
177 be the case in many army ants, because large prey items or other social insect colonies can only be
178 overpowered by large raiding parties, while individuals or small groups of foragers will not be successful.
179 In other words, for much of the parameter space an army ant colony should either mount a full-blown
180 attack or not forage at all. A phasic cycle allows army ant colonies to do exactly that: during the brood

181 care phase costly raids bring in lots of food to feed large cohorts of larvae, while little or no foraging is
182 required during the reproductive phase when no larvae have to be fed.

183 Our model further shows that, under a “High Cost of Entry” scenario, phase transitions should be as
184 abrupt as possible (Figure 5). In other words, the larvae of a given cohort should be perfectly
185 synchronized in their development. While larval development in phasic army ants is indeed tightly
186 synchronized, this synchronization is not perfect, and different larval instars overlap to some extent
187 during the brood care phase (Schneirla 1971; Ravary & Jaisson 2002). However, this overlap could simply
188 reflect a tradeoff between minimizing the period of reproductive activity to maximize developmental
189 synchronization and the incentive to produce large brood cohorts.

190 Outside of army ants, foraging strategies are extremely diverse across different ant species (Lanan
191 2014). However, in the vast majority of cases increased investment in foraging is unlikely to yield the
192 same disproportionate returns via synergistic effects of foraging in large groups. In particular, as
193 foraging intensity increases, these species should suffer from “Resource Exhaustion” as the resources in
194 the immediate vicinity of the nest become depleted and foragers have to cover larger distances to
195 encounter food. In other words, the per capita cost of feeding larvae increases with the number of
196 larvae that have to be provided for. Our model shows that these species should therefore be non-
197 phasic, and indeed no phasic species without an army ant-like biology are known.

198 Interestingly, not all army ants are phasic. Prominent examples of non-phasic army ants include the Old
199 World genus *Dorylus* (Schneirla 1971; Schöning 2005), as well as the New World genus *Labidus*
200 (Rettenmeyer 1963). Even though colonies of non-phasic army ants still emigrate frequently, possibly in
201 response to local food depletion or predator attack, the emigrations do not follow a regular temporal
202 pattern and do not coincide with the presence of particular developmental stages (Rettenmeyer 1963;
203 Schneirla 1971; Schöning 2005). According to our model, we would predict that in these species foraging
204 is more efficient with a relatively small investment. In other words, the relationship between foraging
205 cost and the number of larvae should constitute a “Resource Exhaustion” scenario rather than a “High
206 Cost of Entry” scenario as in phasic army ants (Figure 4). In this context it is interesting to note that both
207 *Dorylus* and *Labidus* colonies are unusually large, containing from over a million to several million
208 workers, while the colonies of other army ants are at least one or two orders of magnitude smaller
209 (Rettenmeyer 1963; Schneirla 1971; Gotwald 1995). It is therefore possible that even raiding parties that
210 are large in absolute size and therefore can forage efficiently come at a small cost at the colony level in
211 these species, because they still represent only a small fraction of the total worker force. Furthermore,

212 while most army ants exclusively or predominantly prey on other social insects, social insects constitute
213 only a small proportion of the prey in *Dorylus* and *Labidus*, whose prey spectra are generally much
214 broader than those of other army ants (Rettenmeyer 1963; Gotwald 1995; Schöning et al. 2008). In fact,
215 *Dorylus* and *Labidus* are the only army ants that also forage on things other than live prey, including
216 animal carcasses, nuts, fruits, grains, and vegetable oil (Gotwald 1995). This implies that food might be
217 more readily available for *Dorylus* and *Labidus* army ants. Furthermore, less relative investment into
218 foraging could still have positive returns because it can be directed toward plant material, animal
219 carcasses, or prey that can be more easily overwhelmed than the well-fortified colonies of social insects.
220 These and possibly other factors might well place non-phasic army ants in a “Resource Exhaustion”
221 scenario. However, given the difficulty of working with army ants in the field, it will be challenging to
222 experimentally quantify the cost of foraging in relation to the number of larvae to be fed for any given
223 species.

224

225 Authors’ contributions:

226 SG and DJCK conceived the study and developed the model. SG implemented and analyzed the model.

227 SG and DJCK wrote the paper.

228

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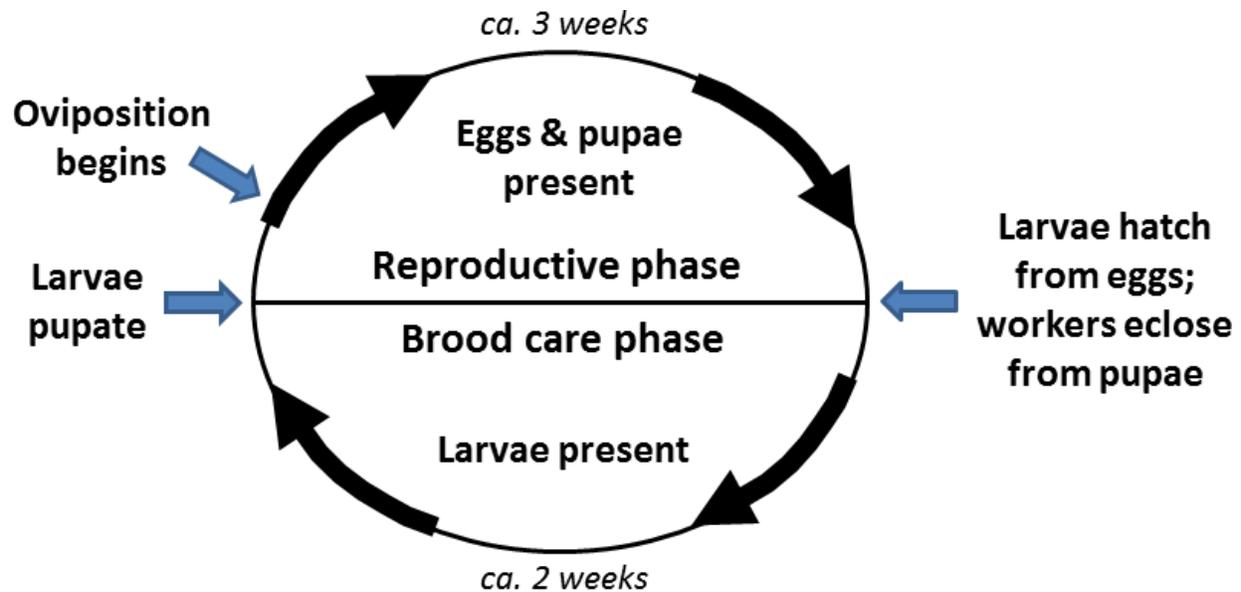
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232 References:

- 233 Buschinger, A., Peeters, C., Crozier, R.H. (1989). Life-pattern studies on an Australian *Sphinctomyrmex*
234 (Formicidae: Ponerinae: Cerapachyini): functional polygyny, brood periodicity and raiding behaviour.
235 *Psyche* 96: 287-300.
- 236 Gotwald, W.H. Jr, Brown, W.L. Jr (1966). The ant genus *Simopelta* (Hymenoptera: Formicidae). *Psyche*
237 73: 261-277.
- 238 Gotwald, W.H. Jr. (1995). Army ants: the biology of social predation. Cornell University Press.
- 239 Hölldobler, B. (1982). Communication, raiding behaviour and prey storage in *Cerapachys* (Hymenoptera:
240 Formicidae). *Psyche* 89: 3-23.
- 241 Kronauer, D.J.C. (2009). Recent advances in army ant biology (Hymenoptera: Formicidae).
242 *Myrmecological News* 12: 51-65.
- 243 Kronauer, D.J.C., O'Donnell, S., Boomsma, J.J., Pierce, N.E. (2011). Strict monandry in the ponerine army
244 ant genus *Simopelta* suggests that colony size and complexity drive mating system evolution in social
245 insects. *Molecular Ecology* 20: 420-428.
- 246 Lanan, M. (2014). Spatiotemporal resource distribution and foraging strategies of ants (Hymenoptera:
247 Formicidae). *Myrmecological News* 20: 53-70.
- 248 Libbrecht, R., Oxley, P.R., Keller, L., Kronauer, D.J.C. (2016). Robust DNA methylation in the clonal raider
249 ant brain. *Current Biology* 26: 391-395.
- 250 Masuko, K. (1990). Behavior and ecology of the enigmatic ant *Leptanilla japonica* Baroni Urbani
251 (Hymenoptera: Formicidae: Leptanillinae). *Insectes Sociaux* 37: 31-57.
- 252 Miyata, H., Shimamura, T., Hirosawa, S., Higashi, S. (2003). Morphology and phenology of the primitive
253 ponerine army ant *Onychomyrmex hedleyi* (Hymenoptera: Formicidae: Ponerinae) in a highland
254 rainforest of Australia. *Journal of Natural History* 37: 115-125.
- 255 Oxley, P.R., Ji, L., Fetter-Pruneda, I., McKenzie, S.K., Li, C., Hu, H., Zhang, G., Kronauer, D.J.C. (2014). The
256 genome of the clonal raider ant *Cerapachys biroi*. *Current Biology* 24: 451-458.
- 257 Ravary, F., Jaisson, P. (2002). The reproductive cycle of thelytokous colonies of *Cerapachys biroi* Forel
258 (Formicidae, Cerapachyinae). *Insectes Sociaux* 49: 114-119.

- 259 Ravary, F., Jahyny, B., Jaisson, P. (2006). Brood stimulation controls the phasic reproductive cycle of the
260 parthenogenetic ant *Cerapachys biroi*. *Insectes Sociaux* 53: 20–26.
- 261 Rettenmeyer, C.W. (1963). Behavioral studies of army ants. *University of Kansas Science Bulletin* 44:
262 281-465.
- 263 Schneirla, T.C. (1971). *Army ants: a study in social organization*. W.H. Freeman & Co.
- 264 Schöning, C., Njagi, W.M., Franks, N.R. (2005). Temporal and spatial patterns in the emigrations of the
265 army ant *Dorylus (Anomma) molestus* in the montane forest of Mt Kenya. *Ecological Entomology* 30:
266 532-540.
- 267 Schöning, C., Njagi, W., Kinuthia, W. (2008). Prey spectra of two swarm-raiding army ant species in East
268 Africa. *Journal of Zoology* 274: 85-93.
- 269 Teseo, S., Kronauer, D.J.C., Jaisson, P., Châline, N. (2013). Enforcement of reproductive synchrony via
270 policing in a clonal ant. *Current Biology* 23: 328-332.
- 271 Ulrich, Y., Burns, D., Libbrecht, R., Kronauer, D.J.C. (2016). Ant larvae regulate worker foraging behavior
272 and ovarian activity in a dose-dependent manner. *Behavioral Ecology and Sociobiology* 70: 1011-1018.
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274 Figures and figure legends:
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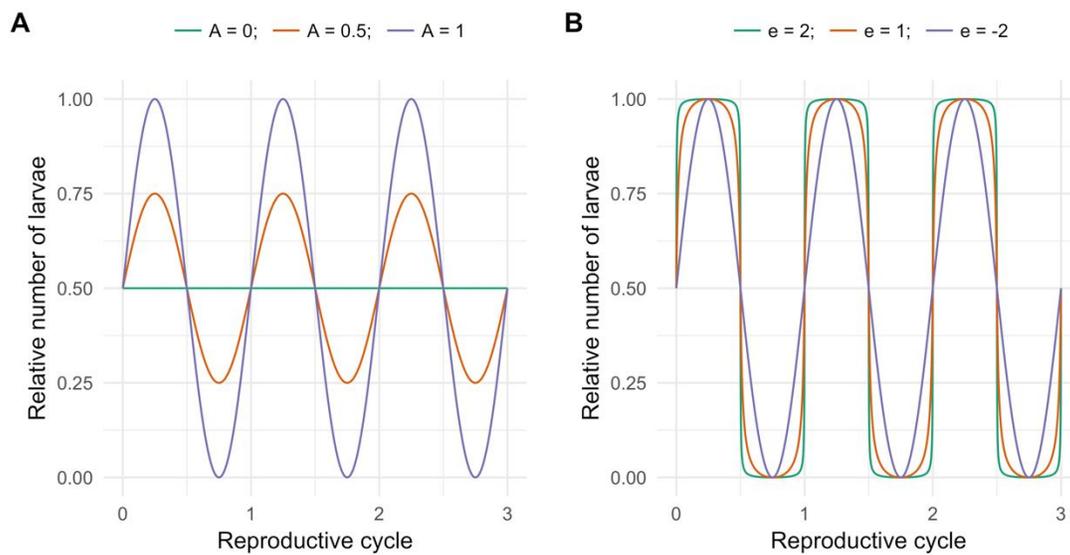


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280 **Figure 1.** Schematic of a generalized phasic army ant colony cycle. Larvae are present during the brood
281 care phase and develop in discrete cohorts. Larvae have two main effects on adults: they suppress
282 ovarian activity and oviposition, and induce brood care behavior, including nursing and foraging (Ravary
283 et al. 2006; Teseo et al. 2013; Ulrich et al. 2016). As larvae pupate toward the end of the brood care
284 phase the colony transitions to the reproductive phase. Oviposition commences a few days into the
285 reproductive phase. As larvae hatch and young workers emerge from pupae toward the end of the
286 reproductive phase the colony transitions to the next brood care phase. In *Eciton burchellii*, *E. hamatum*,
287 and *Ooceraea biroi*, the reproductive and brood care phases last for ca. three and two weeks,
288 respectively (Schneirla 1971; Ravary & Jaisson 2002).

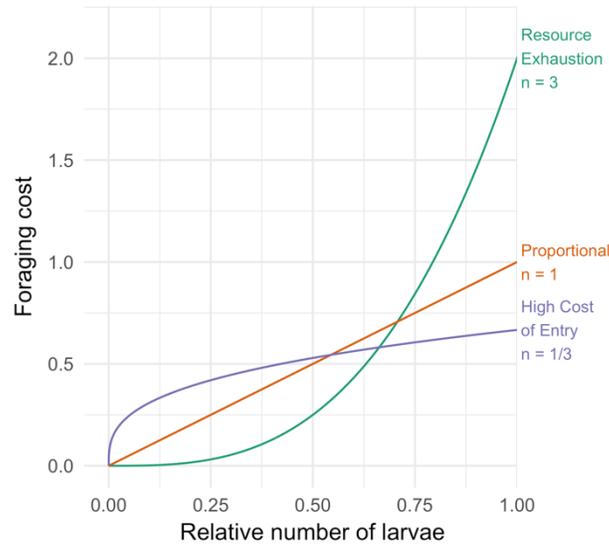
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293 **Figure 2.** Effect of varying **(A)** the amplitude A and **(B)** the "squarity exponent" e on the temporal
294 dynamics of the relative number of larvae present in the colony across the reproductive cycle.

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Figure 3. Effect of varying the scaling parameter n on the shape of the foraging cost function. The

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"Proportional" scenario is obtained with $n = 1$. The "High Cost of Entry" scenario is obtained with

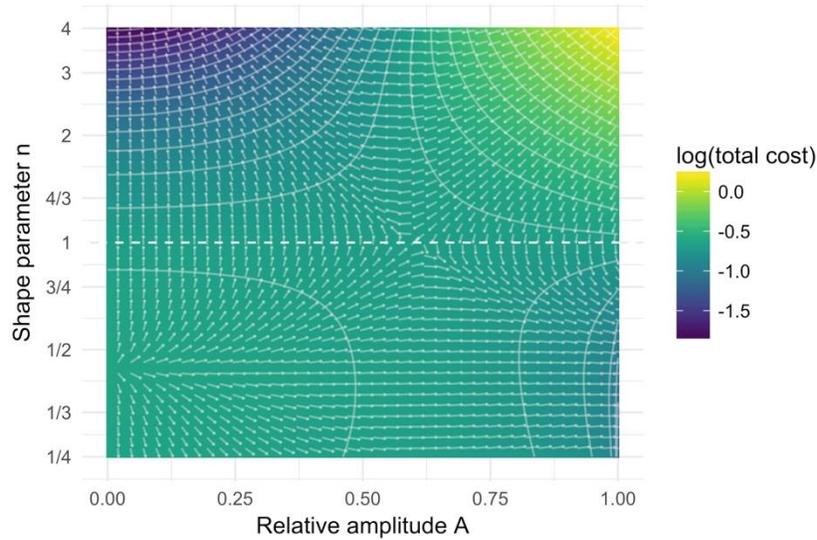
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$0 \leq n < 1$ ($n = 1/3$ is shown here as an example). Finally, the "Resource Exhaustion" scenario is

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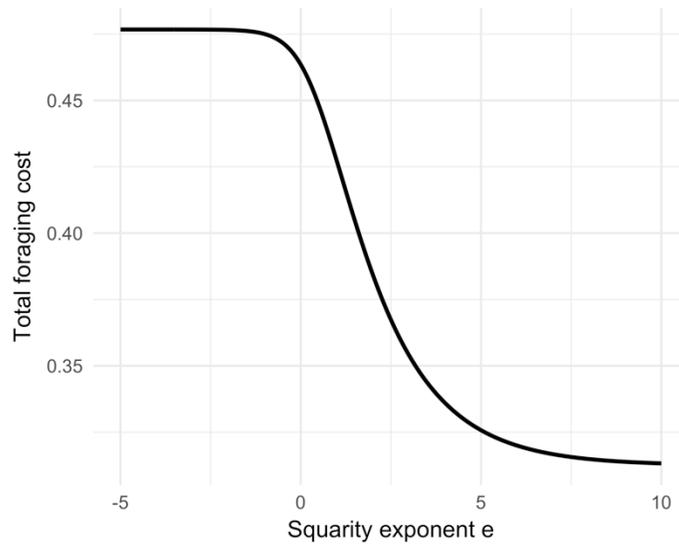
obtained with $n > 1$ ($n = 3$ is shown here as an example).

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303 **Figure 4.** Total foraging cost over a reproductive cycle for various combinations of the relative amplitude
304 A of the reproductive cycle and the shape parameter n of the foraging cost function. Values of n above
305 the dashed line (which indicates the “Proportional” scenario) correspond to “Resource Exhaustion”
306 scenarios, while values below the dashed line correspond to “High Cost of Entry” scenarios. Isolines
307 (white contour lines) represent points in the parameter space with constant value, and gradient vectors
308 (white arrows) represent the direction, but not the intensity of the local gradient.

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313 **Figure 5.** Effect of the smoothness of phase transitions (determined by the “squarity exponent” e) on
314 the total foraging cost over a reproductive cycle for colonies in a "High Cost of Entry" foraging scenario.

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