1 # The adaptive significance of phasic colony cycles in army ants

2

3 Simon Garnier[1] & Daniel J. C. Kronauer[2]

4

5 [1]Department of Biological Sciences, New Jersey Institute of Technology, Newark, NJ 07102, USA;

6 garnier@njit.edu

7 [2]Laboratory of Social Evolution and Behavior, The Rockefeller University, New York, NY 10065, USA;

8 dkronauer@rockefeller.edu

9

12

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 "statary" phase ("statary" 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:

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

4

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:

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

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:

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

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

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

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/ClHwDz.

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).

7

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

8

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

229   Acknowledgements:

230   We thank Yuko Ulrich and Jonathan Saragosti for discussing the ideas underlying this study with us.

231

10

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 *Cerapchys 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.
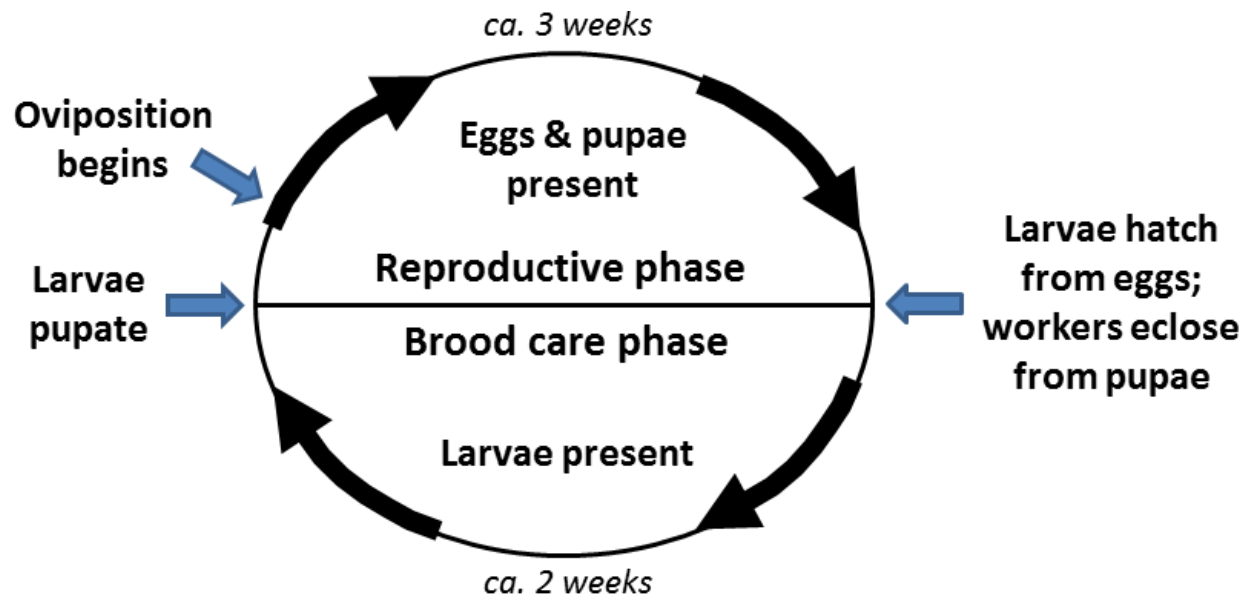
273

274   Figures and figure legends:
275
276
277

278
279
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,

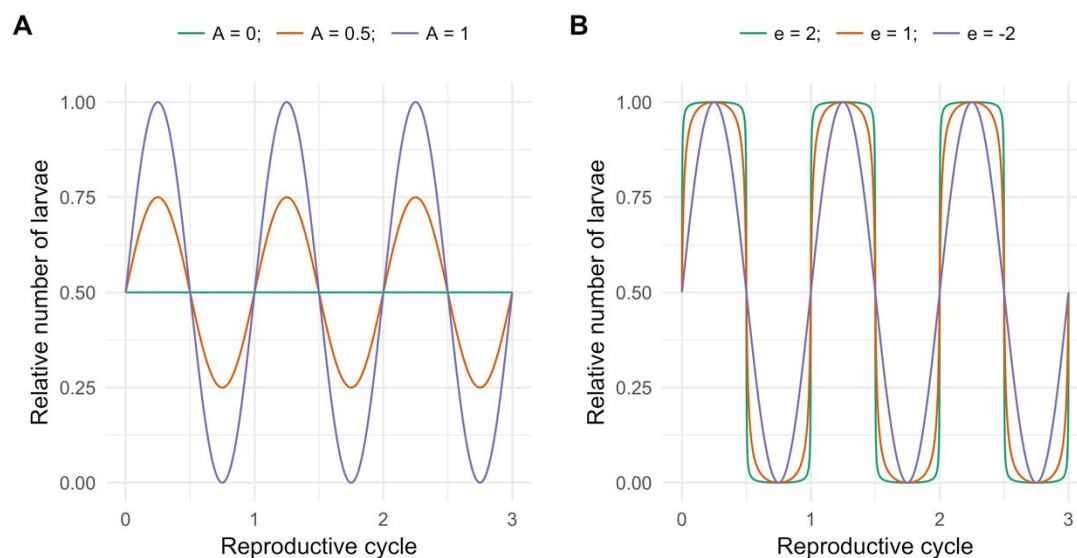288   respectively (Schneirla 1971; Ravary & Jaisson 2002).

289

13

290
291

292
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.
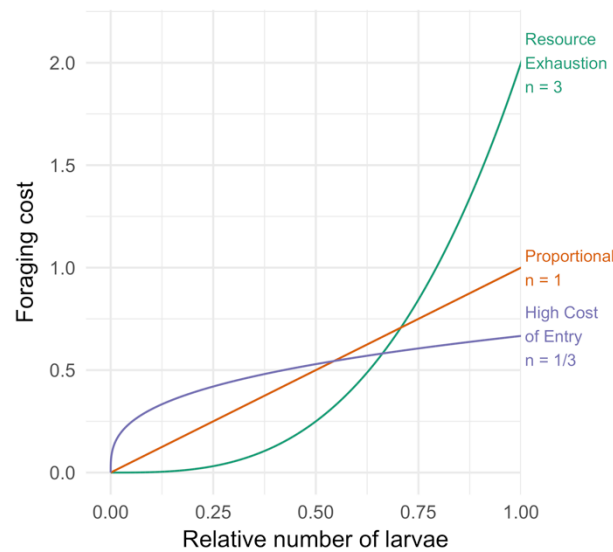
295

296

Figure 3. Effect of varying the scaling parameter n on the shape of the foraging cost function. The "Proportional" scenario is obtained with $n = 1$. The "High Cost of Entry" scenario is obtained with $0 \leq n < 1$ ($n = 1/3$ is shown here as an example). Finally, the "Resource Exhaustion" scenario is obtained with $n > 1$ ($n = 3$ is shown here as an example).
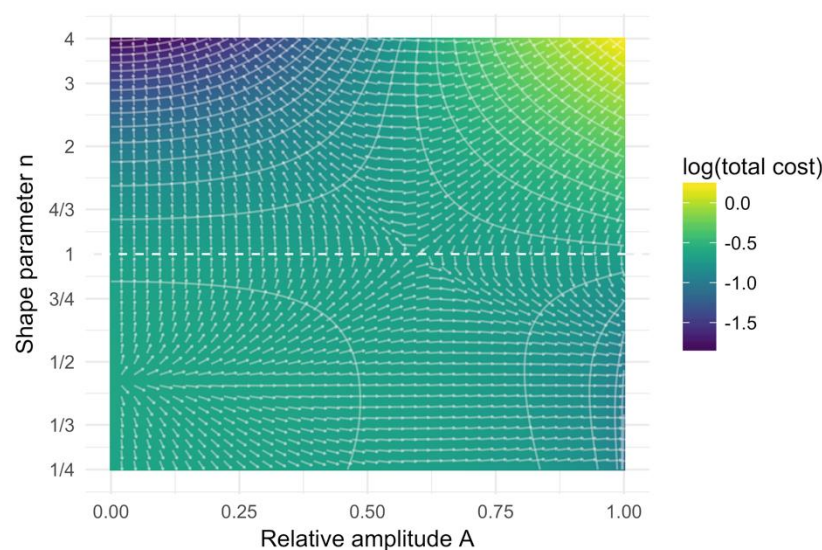
301

Figure 4. Total foraging cost over a reproductive cycle for various combinations of the relative amplitude A of the reproductive cycle and the shape parameter n of the foraging cost function. Values of n above the dashed line (which indicates the "Proportional" scenario) correspond to "Resource Exhaustion" scenarios, while values below the dashed line correspond to "High Cost of Entry" scenarios. Isolines (white contour lines) represent points in the parameter space with constant value, and gradient vectors (white arrows) represent the direction, but not the intensity of the local gradient.
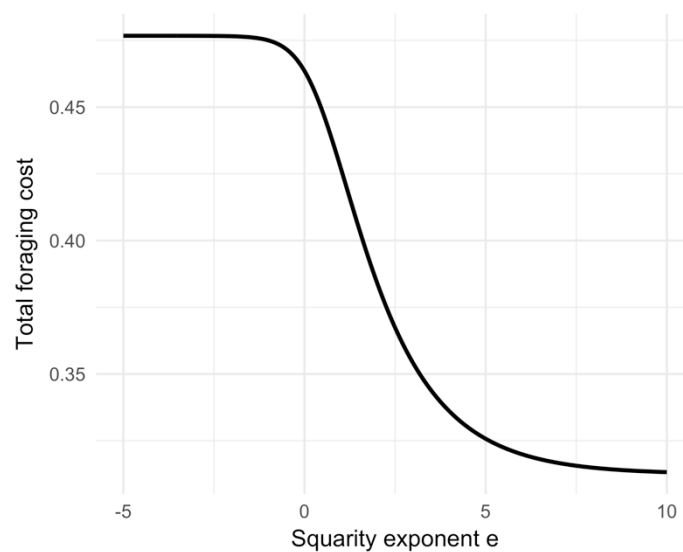
16

312

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.

315

316