Reduced foraging investment as an adaptation to patchy food sources: A phasic army ant simulation

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A B S T R A C T

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

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1. Introduction

Within several taxa belonging to the ant subfamily Dorylinae (*sensu* Brady et al., 2014), species are considered "phasic" or "non-phasic" according to their lifestyle (Schneirla, 1971; Gotwald, 1995; Kronauer, 2009). In phasic species, broods develop synchronously in distinct cohorts of the same age, and colonies undergo virtually discrete phases of foraging and reproduction based on the presence or absence of food-demanding larvae (Schneirla, 1971; Gotwald, 1995; Ravary and Jaisson, 2002; Kronauer, 2009; Teseo et al., 2013). In non-phasic species, larvae are not synchronized in their development, and foraging and reproduction are not strictly coordinated with reproductive cycles. Within army ants, non-phasic taxa include the genera *Dorylus* and *Labidus*, whereas phasic taxa include some species within the Old World genus *Aenictus* and the New World genera *Eciton* and *Neyvamyrmex* (Kronauer, 2009). Outside army ants, phasic groups include some species in the gen-

era *Sphinctomyrmex* (Buschnger et al., 1989), *Leptanilloides* (Brandão et al., 1999; Donoso et al., 2006), *Cerapachys* (Wilson, 1958a; Ravary and Jaisson, 2002), and to some extent *Simopelta* within the Ponerinae subfamily (Gotwald and Brown, 1967) and *Leptanilla japonica* within Leptanillinae (Masuko, 1990). Found in loosely related groups, phasic colony cycles have recently been suggested to have evolved repeatedly and early in army ant evolution, and to have been secondarily lost in genera such as *Dorylus* and *Labidus* (Kronauer, 2009).

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

Although the molecular, individual and colony-level mechanisms underlying the alternation of phases are now beginning to

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be understood (Ravary and Jaisson, 2002; Ravary et al., 2006; Teseo et al., 2013; Oxley et al., 2014; Ulrich et al., 2015), the adaptive significance of the phasic lifestyle is still to some extent unknown. At present, a single study (Kronauer, 2009) has formulated explicit hypotheses about the adaptive value of the phasic lifestyle, suggesting that it likely provides several main benefits. First, in some army ant species, colonies migrate throughout the foraging phases. Migrations probably maximize the foraging success and help avoiding resource depletion at a local scale (Wilson, 1958b; Franks and Fletcher, 1983; Gotwald, 1995). Second, phasic cycles minimize the time invested in foraging, which in turn minimizes the costs involved in foraging activity and emigrations. Third, stationary reproductive phases are sometimes necessary because, in raid-conducting genera such as *Eciton* and *Neyvamyrmex* (but not in *O. biroi*), physogastric egg-laying queens are not mobile or cannot be transported by workers. Finally, doryline ants are in fact specialized predators of the brood of other social insect colonies (Brady et al., 2014; Borowiec, 2016), a food source that is difficult to find but may be overabundant when found (Kronauer, 2009). Developmentally synchronized cohorts of larvae should, in principle, consume more efficiently the large quantities of rapidly decaying prey that become unpredictably available during foraging phases compared to non-synchronized broods including eggs and pupae.

In this study, we use simple computer simulations to explore some of the hypotheses regarding the adaptive value of phasic cycles in army ants, with the goal of understanding whether these may have appeared as an adaptation to specific ecological conditions. In nature, colonies of phasic ant species only forage in the presence of developing larvae, a period corresponding approximately to half the duration of a complete reproductive cycle in *E. burchelli* or *O. biroi* (Schneirla, 1971; Ravary and Jaisson, 2002). In such species, however, colonies need to reach a certain threshold size in order to successfully split, via fission, into two viable daughter colonies. Accordingly, the main assumption of our model is that, everything else being equal, phasic colonies invest in foraging only half of their time. Therefore, due to the reduced investment in foraging, growth and reproduction in phasic colonies are restricted to around only half of their potential. From an evolutionary perspective, in a hypothetical ancestral population in which different ant colonies make quantitatively different foraging investments, colonies with a low foraging investment should grow and reproduce relatively slower and eventually become extinct; on the other hand, colonies with a high foraging investment should grow and reproduce faster, invading the population. Our model aims to understand the evolution of phasic cycles by investigating the conditions in which reducing rather than maximizing the time invested in foraging may result in a selective advantage for virtual ant colonies. In particular, we ask whether and how the cost of foraging, the probability to find food items and the size of the food items affect the population dynamics of low- and high-foraging virtual ant colonies, which we respectively refer to as "phasic" and "non-phasic". These two colony types, or species, behave exactly the same way, with the only exception that the foraging investment of phasic colonies is only half of that of non-phasic colonies.

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

2. The models

2.1. Density-dependent growth of phasic or non-phasic colonies

Our simulations are inspired by the logistic growth model and describe the population dynamics of phasic and non-phasic ant colonies in a discrete time framework. Each time iteration corresponds to an activity cycle, during which colonies grow according to their interaction with the environment. In a first set of simulations, we examine the growth curve of populations constituted of either only phasic or only non-phasic colonies, in discretized time. In each simulation, the total population is composed by a variable number of colonies represented by a vector $\bar{n}$, which we refer to as the population vector. Each element n_i within $\bar{n}$ represents the number of individuals within the ith colony. The length of $\bar{n}$ represents the number of colonies in the population, and varies with time depending on colony death and reproduction. At each time iteration (identified by the subscript t), the discrete variation of the size of each colony is computed according to the following equation:

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

where $n_{i,t}$ is the number of individuals in the ith colony at the tth time iteration, f is the "foraging" factor varying for phasic ($f = 1/2$) and non-phasic ($f = 1$) populations, $p_{i,t}$ is the food income (the value that the stochastic variable p takes for the ith colony at the tth time iteration), c is the foraging cost, l_t is the number of colonies at time t, and L is the carrying capacity for the population, expressed as the maximal number of colonies that are able to survive in the environment. Except for $n_{i,t}$, all factors constituting the second term of the equation are adimensional. The idea behind our simulations is that virtual ant colonies explore the environment in search of food, and may encounter food items of various sizes and at different probabilities. The time unit of the simulation corresponds to one colony cycle, a period in which each colony may find a food item and possibly reproduce or die, depending on its size. We decided to use this approach, and not to explicitly model the alternation of phases throughout cycles in continuous time, in order to keep simulations as simple as possible, and significantly reduce the computing effort, allowing a high number of repetitions for a given set of parameters. In our simulations, each iteration represents the sum of the activities of each colony during a full biphasic cycle. As a consequence, phasic colonies forage only half of what non-phasic colonies do (i.e. half of the time), employing a relatively more conservative strategy; in particular, they spend half of the energy spent by non-phasic colonies, and receive only half of the benefits of finding food items. In our algorithm, colonies find on average the same quantity of food, but the food distribution is parametrically controlled to allow testing and comparing differential scenarios. To keep the average food income constant among scenarios, the size of the available food items and the probability to encounter them are inversely proportional. For example, in a given scenario, food items are small and easy to find, whereas in another one they are large and difficult to find. We thus implement the food income p as a stochastic variable depending on the random number x, which is uniformly distributed in the interval [0,1], in the following way:

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

where s represents the average food income per colony, w is the parameter used to tune food distribution in the different scenarios (it regulates the probability of finding food without changing the average food income over time per colony), and s/w is the probability of finding food. The model is based on the iteration of an