

# Arms races and the evolution of big fierce societies

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The causes of biological gigantism have received much attention, but only for individual organisms. What selection pressures might favour the evolution of gigantic societies? Here we consider the largest single-queen insect societies, those of the Old World army ant *Dorylus*, single colonies of which can have 20 million workers. We propose that colony gigantism in *Dorylus* arises as a result of an arms race and test this prediction by developing a size-structured mathematical model. We use this model for exploring and potentially explaining differences in colony size, colony aggression and colony propagation strategies in populations of New World army ants *Eciton* and Old World army ants *Dorylus*. The model shows that, by determining evolutionarily stable strategies (ESSs), differences in the trophic levels at which these army ants live feed forwards into differences in their densities and collision rates and, hence, into different strategies of growth, aggression and propagation. The model predicts large colony size and the occurrence of battles and a colony-propagation strategy involving highly asymmetrical divisions in *Dorylus* and that *Eciton* colonies should be smaller, non-combative and exhibit equitable binary fission. These ESSs are in excellent agreement with field observations and demonstrate that gargantuan societies can arise through arms races.

**Keywords:** arms race, mathematical model; *Dorylus*; *Eciton*; evolutionarily stable strategies; gigantism

## 1. INTRODUCTION

Paradoxically, the study of extreme forms and unusual cases has often provided generic insights in biology (Darwin 1859). These range, for example, from the biochemistry of extremophiles (Wiegel & Adams 1998) through the neurobiology of the giant axon of squid (Hodgkin 1964) to the evolution of extreme sex ratios and exaggerated sexual dimorphism. The last two, for example, have provided major tests for inclusive fitness theory and sexual selection theory, respectively (Andersson 1994; Hamilton 1996). Extreme or giant forms may highlight important general issues in evolutionary biology (Alexander 1998).

Giant forms may evolve for a number of different reasons (McMahon & Bonner 1983). For example, very large animals may evolve in order to outgrow their potential predators. Thus, elephants are too big to be at risk from carnivores. Alternatively, a large body size may capitalize on reduced transport costs. Bigger vehicles typically have smaller transport costs, which are defined as the amount of energy consumed in moving a unit mass a unit distance (Jensen & Holm-Jensen 1980; Schmidt-Nielsen 1984). Thus, individual blue whales can enjoy ocean-wide home ranges (Mate *et al.* 1999) and are able to dive deep into the benthic abyss (Lagerquist *et al.* 2000).

In certain cases, large size may buffer an animal from environmental extremes. Polar bears are the biggest of all the *Ursidae* (Gould & McKay 1998) and their reduced surface area to volume ratios may help them keep warm amongst the snowy wastes. Alternatively, huge size may be the outcome of competition. It can be argued that giant *Sequoias* have to be so tall simply because other

*Sequoias* are also lofty and each must grow relentlessly in order to avoid the shadows of conspecifics. Male–male competition in the arena of sexual selection may also favour gigantism: consider, for example, the huge mandibles and body size of stag beetles (*Lucanus cervus*) (Halliday 1980).

All the examples above consider single organisms: what about societies of organisms? As Maynard Smith & Szathmáry (1997) have pointed out, the evolution of animal groups is one of the major transitions in the history of life. Which are the giant societies and what selection pressures may have promoted their evolution?

The largest single-family societies are those of the African army ant *Dorylus*. Colonies of *Dorylus wilverthi*, for example, have a single queen and up to *ca.* 20 million workers (Raignier & Van Boven 1955). These societies are several times larger than the biggest leaf-cutter ant colonies (*Atta vollenweideri*, for example, may have only *ca.* 7 million workers) (Jonkman 1978) and the largest colonies of fungus-growing termites (*Macrotermes bellicosus* and its close relatives may have less than *ca.* 2 or 3 million workers) (Collins 1981; Darlington 1990; Darlington *et al.* 1992). There are so-called super-colonies in certain populations of ants that are huge (e.g. *Formica yessensis* with 307 million workers) (Hagashi & Yamauchi 1979; see also Hölldobler & Wilson 1990). In such super-colonies vast numbers of nests, each housing large numbers of workers and queens, bud off from one another but remain linked by trails along which worker populations freely exchange (Hölldobler & Wilson 1990). Super-colonies resemble a vast amorphous fungal mycelium (Rayner & Franks 1987). They are the antithesis of the highly cohesive single-mother families that are army ant colonies.

The huge size of certain *Dorylus* colonies is highlighted by two other considerations. First, these army ant colonies are carnivores and yet they are several times larger

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than the largest colonies of leaf-cutter ants and fungus-growing termites. This is enigmatic. Both leaf-cutter ants and these termites farm fungi grown on the vegetation they harvest. Given the lower trophic level and more abundant and more reliable food supplies of these farmers, one might imagine them being able to grow larger than colonies of carnivores, although this might be moderated by the economics of food retrieval to a fixed nest site and the costs of fungus maintenance. Their different reproductive strategies may also be important and, although we do not consider the strategy of mass sexual production in this paper, we do consider the difference that different fission strategies make to colony size. Second, certain African army ants of the genus *Dorylus* have a whole suite of convergently evolved traits in common with the New World army ants of the genus *Eciton*, in particular *Eciton burchelli* (Franks *et al.* 1999; Franks 2001), yet their worker populations are 40 times bigger and colony biomasses an order of magnitude greater (see Franks *et al.* (1999) for data on the dry weights of *Eciton* and *Dorylus* workers).

These Old World (*Dorylus*) and New World (*Eciton*) army ants both swarm raid through diverse tropical communities. They are arguably two of the most polyphagous predators on earth (Franks 2001). Both have highly polymorphic worker populations that range over a remarkably similar spectrum of sizes (Franks *et al.* 1999). Both form super-efficient foraging teams and retrieve almost exactly the same sizes of prey items (Franks *et al.* 1999). Both types of colony are highly mobile: whole colonies frequently emigrate lock, stock and barrel to new nesting and foraging sites (Scheneirla 1971; Gotwald 1995; Franks 1989*a*, 2001). Both have wingless queens and both types of colony propagate by colony fission (Franks & Hölldobler 1987). That is, in both cases, colonies split in two. Either the resulting daughter colonies both have new queens or one of the 'new' colonies retains the old queen (Franks 1985; Franks & Hölldobler 1987). Before splitting, reproductive colonies produce vast numbers of winged males that fly off to other conspecific colonies, shed their wings and gain access in order to inseminate new (and possibly also old) queens. Nevertheless, despite this catalogue of similarities, *Dorylus wilverthi* colonies have worker populations 40 times larger than *E. burchelli* colonies (Raignier & Van Boven 1955; Franks 1985). Why?

Intriguingly, all but two of the explanations offered above for the evolution of gigantism invoke arms races (Dawkins & Krebs 1979), e.g. outgrowing predators or competitors. The two exceptions, which implicate either reduced transport costs (e.g. blue whales) or environmental buffering (e.g. polar bears), are unlikely to apply to *Dorylus* colonies. First, larger societies will not have reduced transport costs (as defined above) because they are not larger vehicles. For example, the average size of the workers that do all the running to and fro is actually smaller in *Dorylus* than *Eciton* (Franks *et al.* 1999). Indeed, in general, larger societies face greater overall costs of transport associated with central place foraging (Stephens & Krebs 1986). Better environmental buffering also seems an unlikely explanation here. *Eciton burchelli* colonies form bivouac nests above ground, yet they can elevate substantially and regulate the internal temperatures of such nests accurately (Franks 1989*b*). *Dorylus* colonies form nests underground (Gotwald 1995) and should be better

buffered from temperature and desiccation extremes for this reason alone.

The goal of this study is to provide testable explanations for this paradox of colonial gigantism. More specifically, we will examine the possibility that the colonial gigantism of *Dorylus* societies is also the result of arms races. These arms races may be either intra- or interspecific (see, for example, Gotwald & Cunningham-Van Someren (1990) and Gotwald (1995) who report on battles among *Dorylus* colonies and Gotwald (1995) (and references therein) who reports on battles between *Dorylus* and *Typhlopone* army ant colonies), but in the current study we consider intraspecific battles alone.

The above hypothesis is investigated through a generic mathematical model which is described in §2. Two different environments are considered, one representing the New World habitat of *Eciton* and the other the Old World habitat of *Dorylus*. We determine the evolutionarily stable strategies (ESSs) for each environment in §3. In particular, we examine whether battles between colonies may arise and consider optimal life history and reproductive strategies by allowing colony fission to occur at different sizes and in different ratios. It will be shown that the model's predictions are in very good agreement with the field data and, in particular, the model accurately predicts the absence or presence of battles and corresponding reproductive strategy in both *Eciton* and *Dorylus*.

## 2. MODEL

All army ant colonies emigrate frequently (Gotwald 1995). Certain New World army ant colonies alternate regularly between a starchy phase and a nomadic phase (Scheneirla 1971). During the starchy phase, a colony establishes a (temporary) nest site and sends raids into the surrounding environment so that the raiding trails radiate out like the spokes of a wheel. After a certain amount of time has elapsed, the colony enters the nomadic phase; raids occur daily and result in the migration of the colony towards the end of the raiding trail (Scheneirla 1971). Old World *Dorylus* army ant colonies also alternate between staying at nest sites and moving to new ones but they are far less regular (Gotwald 1995). For simplicity, in the following model, we will consider all colonies to have starchy and nomadic phases. It is clear that, by adopting such a lifestyle, the density of 'recent' army ant raiding trails is much higher around colonies in their starchy phase than around colonies in their nomadic phase (Franks 1989*a*; Hölldobler & Wilson 1990). We neglect the intensity of raiding, which has been shown to differ between colonies in starchy and nomadic phases (see Hölldobler & Wilson 1990). Consequently, the environment resembles a mosaic of habitat patches in different stages of ecological succession where each patch corresponds to the area raided during a single starchy phase. Our model, which is derived from Britton *et al.* (1996), therefore considers the environment to consist of an infinite array of habitat patches where each patch corresponds to the area typically raided by a colony during its starchy phase and we assume that the effect of raids conducted during a colony's nomadic phase is minimal. We assume that each patch has either plentiful or exhausted resources, which in this instance are prey items

such as other insects, in particular social insects and other arthropods. We assume that the status of each patch is determined by the time since it was last raided, so that recently raided patches are exhausted of the resource (e.g. Franks 1982*b*).

One major difference between *Eciton* and *Dorylus* concerns the trophic levels at which these predators operate. Approximately 50% of the prey items of *E. burchelli* colonies on Barro Colorado Island, Panama, are from the nests of other ants (the other half of its diet is from non-social insects). Thus, *Eciton* is in part a predator of other social insect predators (Franks 1982*b*, 1989*a*; Franks & Bossert 1983). In contrast, many *Dorylus* colonies mostly eat the juvenile stages of a wide variety of non-social insects, most of which are herbivores or detritivores (Gotwald 1995). Franks (1982*b*) showed that the non-social insect prey of *Eciton* takes approximately one week to recover from army ant raiding while the social insect prey takes *ca.* 200 days. In the absence of data on prey recovery rates for *Dorylus*, we make the reasonable assumption that its prey (being mainly non-social insects) recovers faster than *Eciton* prey. The differences in prey recovery may be because *Dorylus* operates, for the most part, at a lower trophic level than *Eciton*.

Colony size plays a crucial role in the population dynamics of army ants. For example, if a colony becomes too small it dies, while if it grows sufficiently large it divides (either symmetrically or asymmetrically) into two smaller colonies. Thus, we introduce the vector  $\mathbf{N}$  where the components  $N_i$  denote the proportion of patches occupied by colonies of size  $i = 1, 2, \dots, n$ , with  $n$  denoting the number of size classes. Typically, we regard one population unit as representing several thousand worker ants and we define  $\hat{N} = \sum_{i=1}^n N_i$  to be the total proportion of patches occupied by colonies.

In this study, we are especially interested in the evolution of life histories and, therefore, we need to compare how different reproductive strategies (as may arise through mutation) fare when they compete against one another. Hence, we distinguish between a wild-type population and a mutant-type population. We suppose the wild-type population is described by the vector  $\mathbf{N}$  defined above and introduce the vector  $\mathbf{M}$  where the components  $M_j$  denote the proportion of patches occupied by mutant colonies of size  $j = 1, 2, \dots, m$ , where  $m$  denotes the number of mutant size classes. As above, we define  $\hat{M} = \sum_{j=1}^m M_j$  to be the total proportion of patches occupied by mutant colonies.

It is reasonable to model time discretely so that one time-step corresponds to the mean duration of a starchy phase plus the mean duration of a nomadic phase. We now calculate transition probabilities so that a Leslie-type matrix model (Leslie 1945) may be formed which enables the populations at time  $t + 1$  to be calculated from those at time  $t$ .

At the cessation of the nomadic phase, a colony embarks on a new starchy phase in a new environment, the quality of which is unknown beforehand. The availability of prey items determines how the colony fares during this phase: if there is an abundance of prey items the colony will increase in size while if there is a shortage the colony will decrease in size. A metapopulation-like mean field approximation is used for modelling successive

starchy nest sites (see also Britton *et al.* 1996). Such an approximation is reasonable because of two key results. First, army ant colonies migrate over large distances during the nomadic phase (e.g. >500 m in *E. burchelli*) (Willis 1967). Second, Durrett & Leven (1994) presented an analytical result demonstrating that a mean field approximation is good as long as dispersal distances are sufficiently large. Indeed, only minor differences arise in a comparison between the mean field approximation and a spatially explicit stochastic cellular automata model (see Britton *et al.* 1996). Thus, we model the starchy phase by assuming that, at every time-step, each colony moves at random to a new patch and either increases or decreases one population unit in size depending on whether the patches are plentiful or exhausted, respectively.

Recall that colonies becoming too small die while those reaching a sufficient size divide in order to produce daughter colonies. Subsequently, we assume in the model that colonies decaying to size class 0 have died while those colonies reaching size  $n + 1$  (or  $m + 1$  for the mutant population) immediately divide into two smaller colonies of sizes  $p_1^{(n)}(n + 1)$  and  $p_2^{(n)}(n + 1)$ , where the proportions  $p_1^{(n)}$  and  $p_2^{(n)}$  sum to unity. For notational purposes we shall denote this reproductive strategy by  $[p_1^{(n)}(n + 1), p_2^{(n)}(n + 1)]$  and, thus, for example, binary fission at size  $n + 1$  is denoted by  $[(n + 1)/2, (n + 1)/2]$ . We assume that the mutant-type population satisfies similar dynamics.

Habitat that escapes army ant raiding for a sufficient time will boast high prey densities while recently raided habitat will support low prey densities. Since our field data are insufficient to justify the addition of further parameters, we assume that the patch recovery time is independent of the size of the exploiting colony. We therefore introduce the parameter  $r$ , the mean time to patch recovery, which is independent of colony size (see also Britton *et al.* 1996). We define exhausted patches to be those that have been occupied during the last  $r$  time-steps, while those patches remaining unoccupied during the last  $r$  time-steps are classed as plentiful. We assume that colonies move to patches at random and, therefore, the probability that a patch escapes occupation over a single time-step is given by  $1 - \hat{N} - \hat{M}$ . Hence, at equilibrium, a proportion  $(1 - \hat{N} - \hat{M})^r$  of patches are plentiful of prey items, while the rest are exhausted. Thus, we assume that the probability of a colony landing on a plentiful patch, thereby increasing in size, is given by

$$\mathbb{P}(\text{plentiful patch}) = (1 - \hat{N} - \hat{M})^r. \quad (2.1)$$

In particular, equation (1) assumes that the populations do not change significantly over the previous  $r$  time-steps (a reasonable assumption, see Britton *et al.* 1999).

As they raid and move around, army ant colonies might collide. Intriguingly, collisions between healthy *E. burchelli* colonies have not been observed (Franks & Bossert 1983; Franks & Fletcher 1983) but in certain *Dorylus* species both intraspecific collisions and battles do occur (Leroux 1979; Gotwald 1995). Our model uses spatially averaged dynamics and, therefore, the probability that one colony collides with another is given by the proportion of occupied patches. We now introduce a quantity  $\gamma$ , which is independent of colony size and which

denotes the probability of fighting upon a collision, enabling the probability of a battle in each time-step to be determined. The probability of a wild-type colony fighting during the current time-step is given by the chance of colony collision multiplied by the probability that either party wishes to battle:

$$\begin{aligned} & \mathbb{P}(\text{wild-type fights in time-step}) \\ &= \underbrace{\hat{N}}_{\mathbb{P}(\text{collide with } V)} \times \underbrace{[1 - (1 - \gamma_V)(1 - \gamma_V)]}_{\mathbb{P}(\text{fight occurs})} \\ &+ \underbrace{\hat{M}}_{\mathbb{P}(\text{collide with } M)} \times \underbrace{[1 - (1 - \gamma_V)(1 - \gamma_M)]}_{\mathbb{P}(\text{fight occurs})}. \end{aligned} \tag{2.2}$$

Notice that a battles commences if either party so desires; this is fundamentally different from the classic hawk–dove games (e.g. Maynard Smith & Szathmary 1997) where a battle occurs only if both armies opt to fight. The probability of a mutant-type colony fighting is given by a similar formula.

The outcome of fighting is a change in colony size, yet the precise mechanism of battles between rival colonies is unknown. It has been suggested previously that army ant colonies exploit Lanchester’s square law in order to fight with and capture their prey items (Franks & Partridge 1993). However, when applied to two warring armies, this law always results in the death of the smaller army. Since intraspecific army ant battles rarely end in colony death, the use of Lanchester’s square law for battles between army ant colonies is much less appropriate than for battles between army ants and their prey. Therefore, we model colony battles by the following simple rule: when two colonies fight we assume that the larger colony increases by one population unit in size while the smaller colony decreases by two population units in size and, should two colonies of the same size fight, we assume that one colony wins and grows by one unit while the other loses and decreases by two population units, the toss of an unbiased coin deciding the victor and the loser. An increase in colony size is a reasonable outcome of battle success since the victor has won the bodies of all the dead soldiers which, through cannibalism, may be channelled into the production of more worker ants. Notice that this simple rule accounts for an imperfect conversion of dead soldiers into new worker ants. Thus, a colony of size  $i$  wins all its battles (thereby increasing by one population unit in size) against colonies of sizes  $1, 2, \dots, i - 1$ , loses all its battles (and decreases in size) against colonies of sizes  $i + 1, \dots, \max(n, m)$  and wins half its battles against colonies of the same size.

The rules of central place foraging greatly restrict how an ant colony may operate (Stephens & Krebs 1986). Large colonies require vast amounts of food that can only be obtained by foraging at considerable distances from the colony nest. Foraging over such distances requires much energy and so there exists a critical colony size beyond which the colony is unable to support itself. For this reason, we introduce an upper limit on colony size  $D$ , which is determined solely by the environment. Thus, environments having low values of  $D$  are those that support low densities of prey items.

We finally introduce the concept of queen death. In nature, queenless colonies die if they fail to rear a replace-

ment queen or fuse with another colony (Schneirla & Brown 1950). For simplicity we assume queen death automatically leads to colony death and that this event occurs via a Poisson process. Thus, with probability  $\delta \neq 0$  we assume that each colony dies during the current time-step.

Our model divides each time-step into two phases. The first phase considers colony collisions that result in battles (and, therefore, corresponds to the nomadic phase), while the second phase accounts for the raiding of patches (and, therefore, corresponds to the statory phase). Using the above assumptions, suitable transition matrices  $P_1(\mathbf{N}, \mathbf{M})$ ,  $Q_1(\mathbf{N}, \mathbf{M}) \in \mathbb{R}^{\max(n,m) \times \max(n,m)}$  may be formed in order to describe the effect of the nomadic phase, while transition matrices  $P_2(\mathbf{N}, \mathbf{M})$ ,  $Q_2(\mathbf{N}, \mathbf{M}) \in \mathbb{R}^{\max(n,m) \times \max(n,m)}$  may be constructed in order to describe the effect of the statory phase. Thus, if the wild and mutant populations at time  $t$  are  $\mathbf{N}(t)$ , and  $\mathbf{M}(t)$ , respectively, the populations at time  $t + 1$  may be obtained by solving the following system:

$$\begin{cases} \mathbf{N}(t + 1/2) = P_1(\mathbf{N}(t), \mathbf{M}(t))\mathbf{N}(t) \\ \mathbf{M}(t + 1/2) = Q_1(\mathbf{N}(t), \mathbf{M}(t))\mathbf{M}(t) \\ \mathbf{N}(t + 1) = P_2(\mathbf{N}(t + 1/2), \mathbf{M}(t + 1/2))\mathbf{N}(t + 1/2) \\ \mathbf{M}(t + 1) = Q_2(\mathbf{N}(t + 1/2), \mathbf{M}(t + 1/2))\mathbf{M}(t + 1/2) \end{cases} \tag{2.3}$$

where  $\mathbf{N}(t + 1/2)$  and  $\mathbf{M}(t + 1/2)$  correspond to the wild and mutant populations after the completion of the nomadic phase, respectively. The transition matrices are square and have the dimension  $\max(n, m)$  since this value corresponds to the size of the largest possible colony. Moreover, with the exception of entries in the  $n$ th and  $m$ th columns, respectively,  $P_1$  and  $Q_1$  are pentadiagonal and  $P_2$  and  $Q_2$  are tridiagonal, with the rogue elements arising from colony divisions. Repeated construction and multiplication of the transition matrices enables the long-term behaviour of the competing populations to be observed.

The various strategies considered were constructed from all possible combinations of the set of reproductive strategies  $\{[1, 1], [2, 1], \dots, [D, 1], [2, 2], [3, 2], \dots, [(D + 1)/2, (D + 1)/2]\}$  (which has either  $D/2(D/2 + 1)$  or  $(D + 1/2)^2$  elements depending on whether  $D$  is even or odd, respectively) and the set of fighting probabilities  $\gamma \in \{0, 0.5, 1\}$ . Each possible strategy was considered as a wild type with the initial value taken to be the single-type equilibrium  $\mathbf{N}^*$  determined by the solution of

$$\mathbf{N}^* = P_2(P_1(\mathbf{N}^*, \mathbf{0})\mathbf{N}^*, \mathbf{0})P_1(\mathbf{N}^*, \mathbf{0})\mathbf{N}^* \tag{2.4}$$

(see equation 2.3), and a small amount of patches (typically  $10^{-4}$ ) were inhabited by a mutant population systematically selected from the above combinations. Thus, mutant types may differ in size, division ratio and aggressiveness from the wild type. An ESS is then given by a strategy that is immune to invasion by any mutant type constructed from the possible combinations.

Notice that the model assumes that each daughter colony inherits the same characteristics as its parental colony. This is reasonable given that colonies reproduce by fission and, hence, daughter colonies inherit workers from their mother colonies. However, it does neglect the

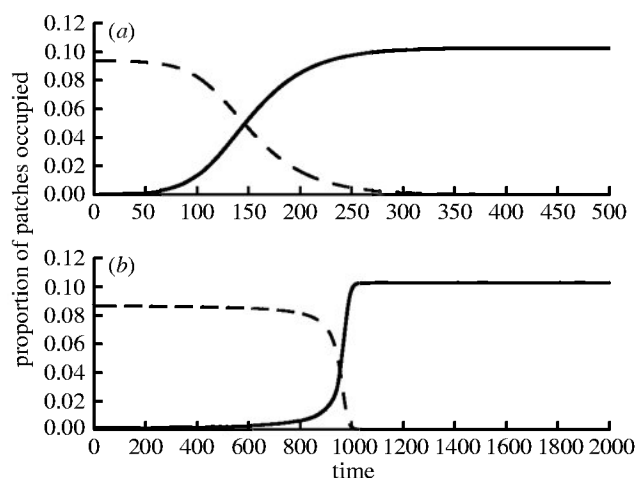


Figure 1. Mutant-type populations are introduced and invade certain wild-type populations where  $r = 6$  and  $\delta = 0.05$  and the environmentally determined maximum colony size is  $D = 5$ . (Thus, the environment represents New World habitat.) (a) The mutant-type population  $[1, 1]$  with  $\gamma_M = 0$  invades and forces the wild-type population  $[2, 2]$  with  $\gamma_N = 0$  to become extinct; thus, fast reproduction is favoured under these circumstances. This mutation is the ESS for the given habitat. (b) The mutant-type population  $[1, 1]$  with  $\gamma_M = 0$  displaces the wild-type population  $[1, 1]$  with  $\gamma_N = 1$  and clearly fighting is not favoured in this environment.

influence of genes from males flying in from other colonies. In a sense, therefore, the model overlooks sexual reproduction, but this is common when determining ESSs.

### 3. RESULTS

Although we are particularly concerned with the cause of colony gigantism of *Dorylus* army ants, it is also interesting to consider why certain other characteristics have been selected for in this Old World species but substantially different characteristics have arisen in the New World army ant *Eciton*. To this end, we consider two different environments, one mimicking the New World habitat, where prey recovery is slower, and a second environment representing the faster recovering habitat of *Dorylus*. Consistent with the data of Franks (1982b) and the model of Britton *et al.* (1996), we choose  $r = 6$  to represent the New World habitat and set the patch recovery time for the Old World to be  $r = 1$ .

#### (a) New World habitat

The slow-recovering New World habitat yields a single ESS given by  $[1, 1]$  with  $\gamma = 0$ , that is colonies that grow to size class 2, split in half and choose not to fight. This strategy is independent of  $D$ , the environmentally determined maximum colony size.

The environment selects for small colonies which reproduce rapidly and against larger but slower reproducing colonies. For example, in figure 1a we show that the ESS invades and forces a strategy given by  $[2, 2]$  with  $\gamma = 0$  to become extinct. Smaller colonies are more at risk of immediate death than larger colonies. For example, it is fatal for a colony of size class 1 to land on an exhausted

patch while it takes an unfortunate run or a queen death for larger colonies to suffer the same fate. However, the larger a colony grows before splitting, the more likely it is to suffer queen death and so smaller but faster reproducing colonies are able to displace larger but slower reproducing ones.

This slow-recovering environment selects against colonies that choose to fight. For example, in figure 1b we show that the ESS  $[1, 1]$  with  $\gamma = 0$  displaces the early-splitting fighting strategy given by  $[1, 1]$  with  $\gamma = 1$ . There are two reasons for this. First, in figure 1b all the colonies are in size class 1 and, therefore, there is a high chance of colony death through battle defeat. Subsequently, colonies that avoid fighting are favoured. Second (and specifically for a mutation where colony division occurs at a larger size class than 2), since prey recovery is slow, colony density is low (compare figures 1 and 2) and, therefore, colony collisions are infrequent. This implies that colonies that grow to a larger size (so that the outcome of a battle is not necessarily colony death) are not selected for since the advantage of being able to win battles is offset by longer reproductive times.

It is also of interest to note the predictions of the model on colony densities and on the proportion of exhausted habitat patches. The model (see figure 1a) predicts that, at equilibrium, the ESS has a proportion 0.1051 of the patches being occupied. In this instance, since  $r = 6$ , approximately half of the patches are exhausted (see equation 1), while the remaining patches are classed as plentiful.

Upon comparison of the ESS determined by the model with the field data, many similarities arise. It has been estimated that, at any moment in time, one-half of certain tropical rain forests in the New World are recovering from the effects of raiding by army ants (Franks 1982b), which is in excellent agreement with the predictions of the modelling. New World army ant colonies have never been observed to collide with one another: *Eciton* army ants colonies seem to avoid one another actively by producing and avoiding one another's long-lasting pheromone trails (Franks & Bossert 1983; Franks & Fletcher 1983). Moreover, *Eciton* colonies reproduce by binary fission (Franks 1985; Franks & Hölldobler 1987), as predicted by the modelling.

#### (b) Old World habitat

The fast-recovering Old World habitat gave rise to a single ESS described by  $[D, 1]$  with  $\gamma = 1$ . Thus, the model favours colonies that, in the event of colony collision, fight one another and reproduce by growing to the environmentally determined maximum colony size  $D$  before budding off the smallest number of workers possible which can function as a new colony.

The habitat patches recover very quickly from the effect of occupation and this, in part, means colony densities are much higher in the Old World scenario than in the New World scenario (compare figures 1a and 2a) and so colony collisions occur much more frequently. Victory in battle provides an additional food source, thereby increasing the size of the victorious colony. Thus, colonies can benefit by fighting, but only if they have a good chance of winning a battle (see, for example, figure 2b where a fighting mutation displaces a non-fighting wild

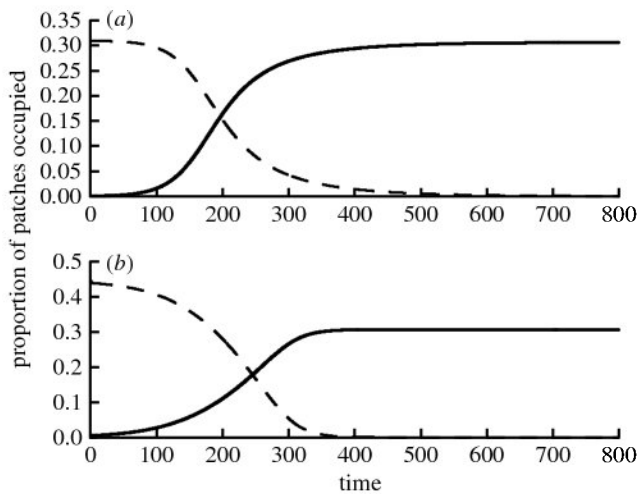


Figure 2. Mutant-type populations are introduced and invade certain wild-type populations where  $r = 1$  and  $\delta = 0.05$  and the environmentally determined maximum colony size is  $D = 5$ . (Thus, the environment represents Old World habitat.) (a) The wild-type population described by [4, 1] with  $\gamma_N = 1$  is invaded and forced to become extinct by the mutation [5, 1] with  $\gamma_M = 1$  so that large individual colony size is selected. Notice that the mutant type is the ESS for the given environment. (b) The aggressive mutant population [4, 1] with  $\gamma_M = 1$  invades and forces the wild-type population [2, 2] with  $\gamma_N = 0$  to become extinct and clearly fighting is favoured in this environment.

type). In order to maximize their chance of victory, colonies need to be larger than their opponents. For this reason the largest colony size is that determined by the environment. It remains to consider the means of colony reproduction. Binary fission, as arose in the ESS of the New World habitat, would result in two colonies of size  $(D + 1)/2$  that would frequently lose battles, since many colonies would be larger than them, resulting in their demise. Therefore, a more favourable division strategy is to bud off one small colony resulting in one very small colony and one very large colony (see figures 2a and 3a). The large colony will only very rarely lose battles and, therefore, should remain close to the environmentally determined maximum colony size, while the smaller colony will only manage to grow to its reproductive size if it is extremely fortunate in both escaping battles and avoiding exhausted patches.

It is interesting to examine the distribution of colony sizes at the equilibrium of the ESS in this Old World environment (see figure 3a). The model shows that the majority of colonies are either close to the environmentally determined maximum colony size or close to their smallest size. As a comparison, the distribution of colony sizes determined by the model for *Eciton* is also given (figure 3b). Notice that there is a marked difference in the colony distributions between the species. Hence, the model makes a testable prediction: the distribution of colony size in *Dorylus* is bimodal, with modes at the maximum and minimum colony sizes, while colony size in *Eciton* is triangularly distributed (cf. Britton *et al.* 1996).

There are many similarities between the ESS determined by the model and the characteristics displayed by *Dorylus* colonies. *Dorylus* army ant colonies have been observed to both collide and fight with one another and to reproduce by small colonies splitting off at irregular time-

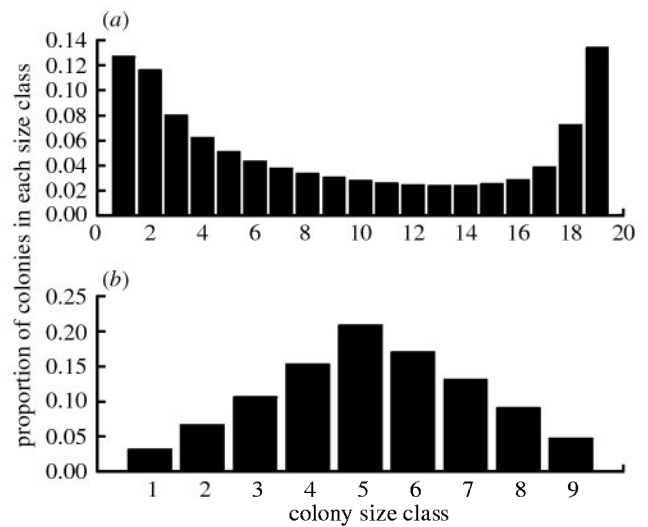


Figure 3. The distribution of colony sizes predicted by the model in Old and New World habitats. (a) The distribution of colony sizes at the equilibrium of the ESS for the Old World habitat ( $r = 1$ ). Here  $D = 19$ ,  $\delta = 0.01$  and the ESS is given by [19, 1], with  $\gamma = 1$ . The majority of colonies are either close to their maximum size class  $D$  or minimum size class 1. (b) A distribution of colony sizes at equilibrium for a typical New World strategy ( $r = 6$ ) given by [5, 5] with  $\gamma = 0$ . In this example  $D = 10$  and  $\delta = 0.01$  so that, in New World habitat, the model predicts that the distribution of colony sizes is triangular.

intervals (Leroux 1979; Gotwald 1995). Moreover, the density of *Dorylus* colonies is approximately two or three (N. R. Franks, personal observations) or even six times (Raignier & Van Boven 1955) higher than *E. burchelli* colonies in their respective environments, a figure in close agreement with that suggested by the modelling.

#### 4. DISCUSSION

Army ants have evolved separately in the Old and New Worlds, and yet *Dorylus* and *Eciton* have a suite of traits in common (Gotwald 1995; Franks *et al.* 1999; Franks 2001). However, there are important differences too, for example in their choice of prey, their colony size and their aggressiveness (Gotwald 1995). In this study we have used mathematical modelling in order to investigate how the differences in prey may lead to the other differences. *Eciton* prey mainly on other social insects (Franks 1982a, 1989a; Franks & Bossert 1983) and are thus at a higher trophic level than *Dorylus*, which prey mainly on solitary insects (Gotwald 1995). It follows that the prey of *Dorylus* recover more quickly. Faster prey recovery leads to higher colony densities, which increases colony collisions and favours intraspecific aggression. This in turn leads to an advantage in being large and a consequent asymmetric splitting strategy.

At certain sites *Dorylus* may encounter one another without (always) engaging in battle (see Raignier & Van Boven 1955), but at these and other sites virulent predatory attacks on *Dorylus* by *Typhlopone* army ant colonies may be very important (see Gotwald (1995) and references therein). (*Typhlopone* is currently considered as a subgenus of *Dorylus* (Gotwald 1995).) Thus, arms races not only among *Dorylus* colonies but also between *Dorylus*

and *Typhlopone* army ant colonies may have selected for a large colony size in *Dorylus*. We suspect that attacks by *Typhlopone* colonies may also favour large colony size and asymmetrical splitting strategies in *Dorylus*.

There are arguments based on kin selection for asymmetrical splitting in social insect colonies that propagate by fission. Such theories consider that workers might be better able to promote their inclusive fitness by staying with their mother queen rather than accompanying a queen who is their sister (see Bourke & Franks 1995; Crozier & Pamilo 1996 for reviews). However, such theories assume that workers could determine which new colony contains their mother queen and which has a queen that is their sister. There is no evidence for army ants that workers can do this. Furthermore, sometimes both new colonies will have new queens. For these reasons, this paper has only explored the ecological factors that might explain asymmetrical splitting.

In this paper in particular, we have shown that large colony size in the African army ant *Dorylus* can be explained through the use of an arms race argument. This is the first time, to the authors' knowledge, that such an argument has been applied to societies of organisms rather than just individual organisms. An important feature of this work is that two aspects of strategy are considered, a life-history aspect (reproductive strategy) and a behavioural aspect (aggressiveness). These two aspects turn out to be intimately connected (see also Petersen & Hardy 1996) and, moreover, to depend on a single difference, that of trophic level. We suggest that a search for ESSs that involve more than one aspect of strategy may lead to a deeper understanding of how different traits can be related to each other. This approach is certainly not restricted to the field of social insects.

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