

Suicidal Punishment in the Ant
Acromyrmex versicolor

Gregory B. Pollock
KALX, LLC
suzuki.court@live.com

Antonio Cabrales
Departamento de Economía
Universidad Carlos III de Madrid
Madrid 28903, SPAIN
Acabrale@eco.uc3m.es

Steven W. Rissing
Department of Evolution,
Ecology, and Organismal Biology
The Ohio State University
Columbus, OH 43210
Rissing.2@osu.edu

Kenneth G. Binmore
Department of Economics
University College London
London WC1E 6BT, UK
k.binmore@ucl.ac.uk

Abstract

Question: Foundress associations of the desert leaf-cutter ant *Acromyrmex versicolor* exhibit a single forager-foundress prior to worker eclosion. A prior specialized task, removing soil from the nest during excavation, allocates later forager risk. Experiment reveals that a queen refusing such prior assignment is not replaced by her cofoundresses; rather, these latter suicidally punish the shirker, leading to the colony's demise (Rissing *et al.* 1996). Why do cofoundresses fail to replace a shirker when failure implies reproductive death?

Method: We model cofoundress options as a game in asexual haploid strategies where self-preserving replacement of a shirking foundress exists as an alternative (Pollock *et al.* 2004). Embedding this game in the natural history of *A. versicolor*, we simulate populations for 500,000 years, with 100 replicates under various parameter sets, some deviating significantly from *A. versicolor*. Shirkers appear through mutation, with suicidal punishers and self preservers mutating one to the other.

Results: Self preservation never outperforms suicidal punishment, although it can recur and drift upwards for some time. Whenever forager assignment is retained, suicidal punishment dominates. But stability is stochastic: forager assignment may endure in many-to-most runs, yet be lost in others. Generally, the greater the frequency of self preservers, the more likely assignment will be lost entirely in the long run. Task coordination endures through suicidal punishment.

Keywords

Acromyrmex versicolor, coordination mechanism, correlated strategy, group selection, personal success, pleiotropy, population viscosity, self preservation, stochastic stability, strategic success, subgame perfection, suicidal punishment

Suicidal Punishment in the Ant *Acromyrmex versicolor*

by G. Pollock, A. Cabrales,
S. Rissing, and K. Binmore

1 Introduction

Most leaf-cutting ants are tropical, but the species *Acromyrmex versicolor* is unusual in making its home in the Sonoran Desert of Arizona, where it builds volcano-shaped nests in the shade of trees that grow along ravines. Like other leaf-cutting ants, it eats a fungus that grows on the leaves that the ants prepare for this purpose in underground gardens.

Acromyrmex versicolor is also unusual in being pleometrotic, which means that several queens (cofoundresses) often establish nests in common (Rissing *et al.* 1986). As in several other *Acromyrmex* species, the cofoundresses of *Acromyrmex versicolor* forage for leaves before workers emerge to take on this task (Rissing *et al.* 1989; Fowler 1992; Diehl-Fleig and de Arajo 1996; Fernndez-Marn *et al.* 2003; cf Brown and Bonhoeffer 2003, for the general case). Such foraging is risky, yet is essential if the colony is to survive.

One might expect the dangerous task of foraging to be shared equitably, or that competitive inferiors might be forced to take it on, but a single queen usually assumes all the risk in foraging without any observed contention, ritualistic or overt (Rissing *et al.* 1986, 1996). An early event in nest construction strongly predicts which queen will later take on the role of forager. During the construction of a nest, one queen removes soil from the nest, while her cofoundresses dig internally. Some time after nest construction, this prior surface excavator usually becomes the sole forager for fungus garden substrate (Rissing *et al.* 1989).

If the foraging queen falls victim to predation, then she is replaced. But what would happen if the queen assigned the role of forager were to refuse the task? A laboratory experiment involving an exit that is always closed when the foraging queen tries to leave (but always open to any other cofoundress) shows that the foraging queen is then not replaced (Rissing *et al.* 1996). Nobody forages and the colony dies out. Such an extreme punishment certainly provides a disincentive for the queen nominated as forager to neglect her duties, but how is such suicidal behavior on the part of her cofoundresses to be explained?

Continuing earlier work (Pollock *et al.* 2004), we look for an explanation using evolutionary computer simulations. We find that suicidal punishment can survive for long periods of time if the parameters of the model are suitably chosen, but that the rival outcome in which a recalcitrant foraging queen would get replaced is always waiting in the wings. In seeking to understand these results, we apply the methods of evolutionary game theory to a simple model of the underlying problem that we call *After You*. Our analysis points to the importance of another feature

of the fascinating natural history of the species *Acromyrmex versicolor*. Brood raiding among nests founded under the same tree leads to fierce competition that biases the outcome in favor of the suicidal alternative.

This paper has been much compressed for the purposes of publication. A much more discursive version that also reports other simulations is available at

<http://www.eco.uc3m.es/~acabrales/research/EER2586revised.pdf>

2 Natural History

The life cycle of *Acromyrmex versicolor* is summarized in Figure 1.

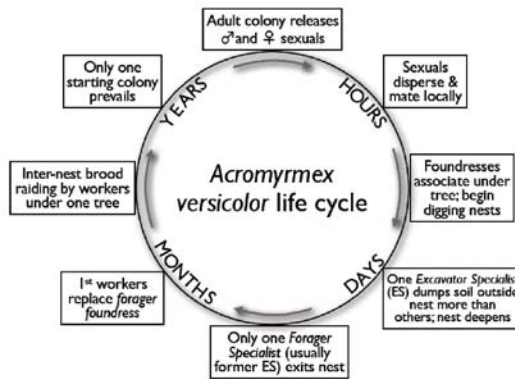


Figure 1: Life cycle of *Acromyrmex versicolor*.

Viscous dispersal. Established colonies of *Acromyrmex versicolor* release sexuals after desert monsoon rains. After mating locally, the fertilized queens disperse viscously from the vicinity of their parental colony. The dispersal is viscous (Pollock *et al.* ??) because the trees under which nests are made typically occur in linear ravines so that widespread dispersal is not viable. Extant adult colonies are fiercely territorial, destroying starting colonies whenever encountered. While foundresses will alight under any tree, their new colony will survive only if the tree they choose has no current adult colony.

Brood raiding. Multiple starting colonies under the same vacant tree are typical. (Several hundred have been observed under the same tree.) Such starting colonies must ultimately fight one another for exclusive possession of the tree. They do so by raiding one another for brood once workers eclose. A single colony ultimately triumphs, which then defends its territory against all comers (Rissing and Pollock 1987; Pollock and Rissing 1989; *cf* Pollock *et al.* 2004 for further citations). Such

zero-sum brood raiding can be seen as a form of group selection by combat (Wilson 1990; Pollock and Cabrales 2008; D.S. Wilson, personal communication).

The fact that only one colony under any given tree survives to adulthood necessarily amplifies small differences in fitness among clumped starting colonies, because colonies with more workers are better at raiding (Rissing and Pollock 1987, 1991; Tschinkel 1992, 2006). The number of first brood increases both with early fungus health (Rissing *et al.* 1996), and with the number of queens that found the colony together (Rissing and Pollock 1987) but the issue that matters in this paper is the amplification of differences in foraging efficiency of different starting colonies.

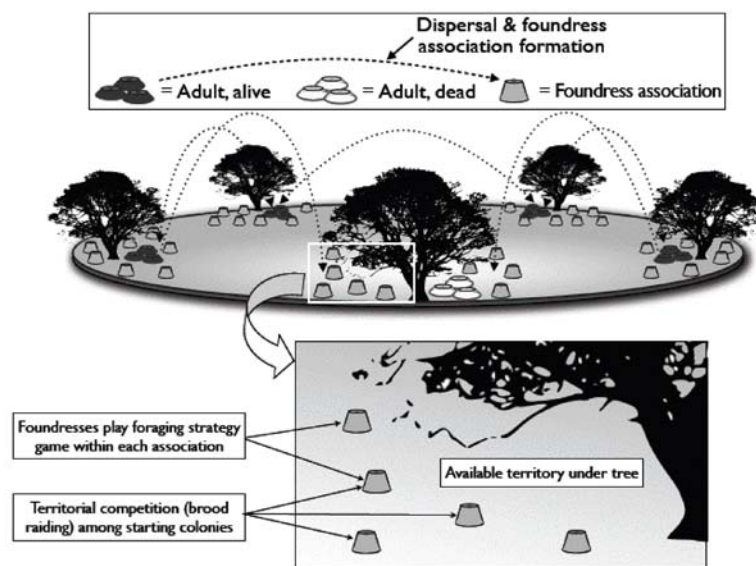


Figure 2: Viscous dispersal. Foundresses exit their parent colony, alighting only under nearby trees. (In our simulations, the available trees are placed in a circle and dispersal is restricted to immediately neighboring trees.) Foundresses that find their way to the same tree readily associate with each other irrespective of parental origin. When trees already have a resident adult colony, new starting colonies are ultimately destroyed. When a tree has no living adult colony, multiple starting colonies may get going in its territory. However, these starting colonies eventually compete with each other via brood raiding for exclusive possession of the territory. In the end, only one adult colony survives, as indicated in Figure 1.

Multiple queens. As already noted, *Acromyrmex versicolor* is pleometrotic. Several queens coordinate their behavior in building a nest together. In many species of social insects, the cofoundresses of such an association are sisters, but the need for *Acromyrmex versicolor* to get underground quickly and start producing brood

has apparently resulted in unrelated queens getting together very readily. The associations then continue with little or no internal strife.

When there is sufficient space in the nest being built for all but one queen to dig while the remaining queen removes soil to the surface, a unique queen—the queen we are calling the surface excavator—adopts the latter role until replaced by workers. This allocation of roles is seemingly made at random (Rissing and Pollock 1986; Rissing *et al.* 1996; *cf.* Fewell and Page 1999; Anderson and Ratnieks 2000). Although specialization at the surface allocates equally beneficial, complementary roles to all the cofoundresses, this same specialization therefore later determines which queen will take on all the risk of predation in her role as surface excavator and then forager.

Shirking forager? Laboratory observation reveals that if the queen assigned the foraging role fails to return to the nest as a result of predation, another queen takes on her role without excessive delay (Rissing *et al.* 1996). So the ground would seem favorable for a mutation that makes a queen assigned the role of forager into a shirker or cheat. Such a deviant would refuse the above-ground task of foraging, with its inherent risks of predation and exposure to abiotic extremes, leaving it to one of the other queens to take on this role. But no such behavior is observed.

We therefore ran an experiment in which the assigned forager was made to appear to be a cheater shirking her risky role (Rissing *et al.* 1996). Whenever the prior surface excavator tried to forage, we blocked her exit. However, her cofoundresses, when examining the exit, found it clear. Only one foundress could examine the exit at a time. The assigned forager would try to leave, but could not. Her cofoundresses perceived an open exit with a prior surface excavator apparently refusing her foraging assignment. We cannot make a true shirker, but these latter cofoundresses encountered a world identical with shirking. The experiment manipulated not so much the assigned forager, but her cofoundresses' perception of her.

While cofoundresses clearly can forage when a cheater refuses her assigned task, they either (mostly) choose not to do so, or delay so long that the irreplaceable, essential fungus perishes (Pollock and Rissing 1995; Rissing *et al.* 1996; Pollock *et al.* 2004). Rather than replace the assigned but cheating forager, thereby assuring themselves some chance of survival, all the cofoundresses then die. In contrast, removal of the assigned forager in the experiment (as if lost to predation while above ground) always leads to timely forager replacement by a previously nonforaging cofoundress. Cofoundresses therefore distinguish between a lost forager and one apparently refusing her risky task, replacing only the former.

So it seems that the cofounding queens are so strongly locked into the coordination mechanism that assigns the role of surface excavator and forager that they effectively punish deviation with behavior that leads to a common death. Such suicidal punishment (Pollock *et al.* 2004) seems so extreme that one is led to question its evolutionary stability.

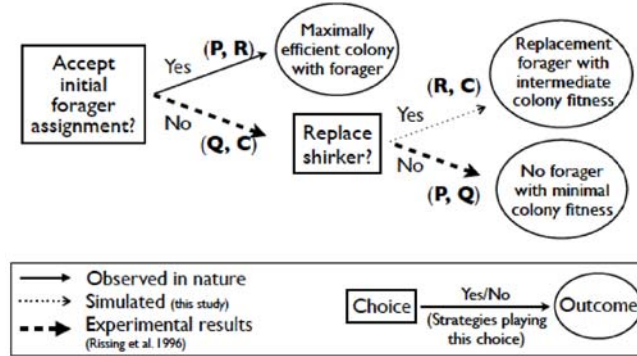


Figure 3: Schema for the foundress foraging game. The labels attached to the arrows refer to various strategies admitted in our simulations (Section 3).

3 Simulation Design

Figure 3 shows the decision tree faced by an association of queens before any workers emerge. The surface excavator must first decide whether to accept the role of forager. Laboratory observation shows that she usually accepts this assignment, but in exploring questions of evolutionary stability, it is necessary to ask what would happen if she were to refuse. Experiment in the laboratory shows that the other cofoundresses would then not replace her in a timely fashion, with the result that the colony would die out. Extending earlier work (Pollock *et al.* 2004), this paper focuses on the evolutionary stability of the latter behavior, for which purpose we need to ask what would happen if a shirking surface excavator were to be replaced. This section outlines the computer simulations we use for this purpose.

Dispersal. The simulation design follows Pollock *et al.* 2004, with *Acromyrmex versicolor*'s natural history cycle of Figure 1 iterated for 500,000 generations per run—which is a long time given that the Sonoran desert itself is estimated as being only 10,000 years old (Axelrod, 1979). In our simulation, adult colonies independently die off each year with probability 0.05, giving an expected life span of 20 years. This is slightly on the high side for *Acromyrmex versicolor*, but not impossible (Rissing: personal observation).

In the Sonoran Desert, adult *Acromyrmex versicolor* colonies are somewhat linearly and uniformly spaced at one colony per large tree in desert ravines (Rissing *et al.* 1986; Pollock *et al.* 2004). In our simulation, we employ 100 adult colonies, distributed uniformly on a circle to avoid end-point effects (Lehmann *et al.* 2008).

We treat queens as haploid and asexual, so that there are no males in our simulation. Each year, new foundresses depart simultaneously from their parental colonies and seek a new tree under which to form an association with other foundresses. The

members of each association under a particular tree are equally likely to be drawn from any of the parental colonies that send foundresses to that tree. If the tree happens to be occupied already by an adult colony, such a new association dies.

The cases of unrestricted and viscous dispersal of foundresses from the parental colony were treated in separate simulations, although we only report the latter simulations here. Under unrestricted dispersal, all extant adult colonies send an adequate number of new queens to all trees. The more realistic case of viscous dispersal (Rissing *et al.* 1986, 1989; Hagen *et al.* 1988; Rissing, personal observation) is captured by restricting the spread of new queens to trees adjacent to their parental colony on the circle shown in Figure 2.

Coordination. When a tree is not already occupied by an adult colony, the simulation assumes that 5 starting colonies with 3 cofoundresses each will form. Except in the event of the death of a forager, all queens reproduce equally in the starting colony that emerges victorious from a later brood-raiding phase that determines which of the 5 colonies ends up in sole possession of the tree.

In each starting colony, a surface excavator is first chosen at random independently of her genotype. She performs the excavating task without fail, but may or may not honor the coordination mechanism that subsequently assigns her the role of forager. Which way she goes depends on the strategy written into her genotype.

If the surface excavator honors the coordination mechanism, then she forages for her group, thereby facing a death probability d that measures her assumed foraging risk in the simulation. Different simulations use the values $d = 0.2$, $d = 0.5$, and $d = 0.8$. Foraging is idealized as a single event in which the forager returns with substrate even if she dies. Otherwise it would be necessary to simulate multiple foraging trips, with deaths from predation resulting in associations with less than three queens when replacement occurs. (Associations with up to 16 cofoundresses have been observed but our informal estimate of the average number is 2.5.) Death of the forager is the sole cause of queen-specific mortality in the simulation, reflecting the fact that *Acromyrmex versicolor* queens coexist for years without aggression in laboratory colonies.

If the surface excavator refuses the foraging assignment, she may or may not be replaced, depending on the strategies written into the genotypes of the other queens. In either case, a refusal by the surface excavator is assumed to reduce the fitness of a starting colony. The reason is that, even if there is no significant delay, the effectiveness of a forager should improve with the experience that the surface excavator gained while orienting herself above ground during the initial construction of the nest (Schmid-Hempel and Schmid-Hempel, 1984; Hölldobler and Wilson, 1990; Dukas and Visscher, 1994; Schatz *et al.* 1995; Ratnieks and Anderson, 1999; Robson and Traniello 2002; Bisch-Knaden and Wehner, 2003).

Brood raiding. Any reduction in colony foraging efficiency will be amplified by the brood-raiding competition among starting colonies illustrated in Figure 2.

To model such a zero-sum game with only one winner, our simulation assigns a fitness of $A = 1,000$ to a starting colony whose prior surface excavator accepts her foraging role. Colonies whose excavator refuses to forage but is replaced by another queen are assigned replacement fitnesses of either $B = 200$ or $B = 900$, depending on the particular simulation being run. A lower fitness in these circumstances corresponds to more foraging inefficiency through loss of the surface excavator's experience coupled with any replacement delay.

Once starting colony fitnesses are calculated, the simulation chooses the new adult colony at random from the competing starting colonies with probabilities that are proportional to their relative fitnesses. An association with a fitness of $B = 200$ will therefore suffer severely from brood raiding, while an association with a fitness of $B = 900$ will be relatively free from brood raiding.

We avoid assigning a fitness of 0 to a non-foraging colony to guarantee that trees cannot remain vacant for years on end. A fitness of $B = 1$ is therefore assigned to a colony whose queens all refuse to forage. This choice corresponds to assuming that a forager is actually always replaced, but only after a nearly fatal delay. The very small fitness of 1 assigned to a non-foraging colony is negligible when compared with the fitness of at least 200 assigned to a replacing colony—but Table 1 shows that it nevertheless significant when the predation rate d is high.

Strategies. At the first decision node of Figure 3, the surface excavator decides whether to accept her assignment as the forager. If she refuses, the two remaining cofoundresses in the simulation decide at the second decision node whether or not to offer themselves as replacements. If both make the offer, the actual choice of a replacement is made at random.

A queen might need to make a decision at either of the two nodes of Figure 3. Its genome must therefore determine a strategy that tells the queen what to do if she finds herself at either of the two nodes. We simplify by considering only haploid genomes at which the relevant strategies are determined at a single locus.

The tree of Figure 3 has two decision nodes at each of which two choices are available. So the simulation requires $4 = 2 \times 2$ strategies corresponding to the decisions $\mathbf{R} = (yes, yes)$, $\mathbf{P} = (yes, no)$, $\mathbf{C} = (no, yes)$, $\mathbf{Q} = (no, no)$ in Figure 3. These strategies are described more discursively below:

P is a punisher that agrees to forage when occupying the role of surface excavator, but never replaces a surface excavator that shirks. So **P** is the suicidal punisher revealed by our experiment (Rissing *et al.* 1996).

Q is a quitter that always refuses to forage in either role. After refusing to forage when occupying the role of surface excavator, a quitter will be punished by any queen in the association using **P**.

R is a replacer that always agrees to forage in either role. A replacer therefore plays according to the established coordination mechanism when occupying the role of surface excavator, but “makes the best of a bad lot” by planning to play her individual best reply when exposed to a surface excavator that shirks.

C is a (sophisticated) cheater that refuses to forage when occupying the role of surface excavator, but always offers to replace a surface excavator that shirks. Such a cheater can exploit queens in the association using **R**. We have no natural or experimental evidence that **C** currently exists.

To assess how these four strategies interact, it may be helpful to study Figure 4, which anticipates results from Section 4 by outlining a typical evolutionary simulation that ends in the population state **PPP** in which all three cofoundresses use the suicidal punishment strategy **P**. However, it should not be thought that all our simulations yield such a tidy history of events. Much depends on the parameter values in use and the mutation assumptions to be made next.

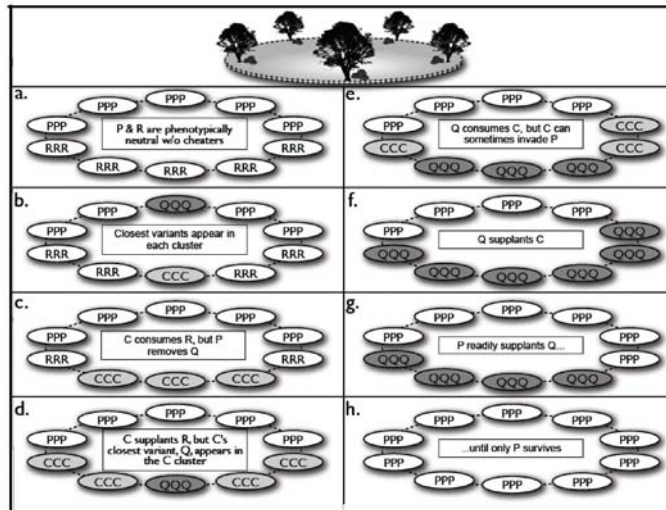


Figure 4: How does suicidal punishment get established? The figure shows an idealized sequence of cofoundress associations in simulated adult colonies under viscosity with closest variant mutation (regime 3). The succession from Figure 4a to Figure 4h shows the strategy **P** eventually supplanting **R** via a sequence of intermediate states that reflect the differing reactions of **P** and **R** to **Q** and **C**. Associations are shown as all using the same strategy for clarity—associations like **QPP**, **CRR**, **CPP**, and **CCP** should properly intervene as long temporal sequences of transitional states between the pure states of the figure. In Figures 4b and 4c, **P** eliminates **Q** when it appears at a predominantly **P** location. In Figures 4b and 4c, **R** incubates its closest mutant variant **C**. In Figure 4d, **C** incubates its closest mutant variant **Q**, until **C** is eliminated in Figure 4f. In Figures 4g and 4h, **P** eliminates **Q** encountered at its boundary, until only **P** remains.

Mutation. Adult colonies live many years. Mutants arise not as queens in an already established adult colony, but among their offspring. So a genotype generally

breeds true, but will occasionally produce an offspring of another genotype.

Since our focus is on the survival of cooperative behavior when challenged by quitters and cheaters, we never allow mutations from the latter kind of strategy (**Q** and **C**) to the former (**P** and **R**). Within this constraint, our simulations explored three different mutation regimes. The first and second of these mutation regimes were studied previously in Pollock *et al.* 2004. We note here only that our results with these regimes in the more elaborate setting of the current paper are consistent with the earlier work. We therefore restrict attention to the third mutation regime, which we feel to be more realistic. Unless something is said to the contrary, mutation should therefore always be assumed to follow the following rules.

The simulations always begin with the population saturated with either the strategy **P** or the strategy **R**. We call these population states **all P** and **all R**. We allow mutations from **P** to **Q** and from **R** to **C**; also mutations back and forward between **Q** and **C**, and between **P** and **R**.

Hopeful monsters? Our mutation assumptions take account of the fact that some of our strategies are more complex than others by ruling out the equivalent of very unlikely “hopeful monsters” (Dawkins, 1980; Maynard Smith, 1984; Darwin, 1859 on the origin of new variation). Only mutations that change one planned piece of behavior at a time are therefore allowed. The arrows of Figure 5(a) show all the mutations possible under this restriction.

We employ a mutation probability of 0.001 for the loss of a behavioral property and a mutation probability of 0.0001 (one order of magnitude smaller) for the gain of a behavioral property. That is to say, we make the probability attached to an arrow in Figure 5a that corresponds to a *no* mutating into a *yes* much lower than the probability attached to an arrow in the reverse direction. We thereby recognize that mutations that disable some existing piece of complex behavior are much more likely than mutations that create a new piece of complex behavior (where the complex behavior in our case consists of an ant conditioning her behavior on being the surface excavator, or conditioning her behavior on the surface excavator shirking her duty).

All our simulations also rule out mutations that convert genotypes in which the surface excavator behaves cooperatively (**P** and **R**) into one that does not (**Q** and **C**). This latter requirement biases the simulation against the evolutionary stability of the coordination mechanism observed in nature in which the surface excavator accepts the role of forager. Eliminating these possibilities from Figure 5a yields Figure 5b, which should be taken as summarizing how we model mutation in the simulations reported here.

Initial population states. The initial states in all our simulations consist of populations in which either all queens are programmed with **R** or else with **P**. How stable are such populations? If unstable, where does evolution take the system?

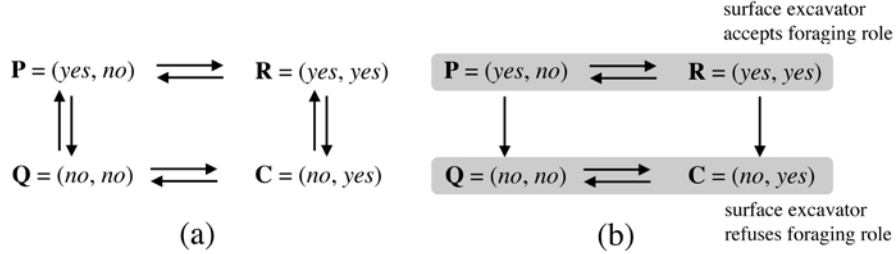


Figure 5: Restrictions on mutations. Figure 5(a) shows that mutations affecting more than one piece of behavior at a time are not allowed. Figure 5(b) incorporates the extra assumption that mutations which convert a genotype that refuses to honor the coordination mechanism into a genotype that does honor the coordination mechanism are not allowed. Arrows that point down or left are assigned a mutation rate of 0.001. Arrows that point up or right are assigned a mutation rate of 0.0001.

4 Simulation Results

Space does not permit our describing all our simulations, and so we report only what we believe to be the most significant results. In particular, we confine our attention to the more realistic case of viscous dispersal, noting only that the effects we report are significantly weaker in the case of unrestricted dispersal.

For the fixed mutation regime described in Section 3, the results depend on the values of the parameters d (the death probability of a forager) and B (the replacement fitness of a colony). Table 1, shows the strategies that are predominant in the long run with both initial states **all P** and **all R**.

	$B = 200$	$B = 900$
$d = 0.2$	P	C
$d = 0.8$	P	Q

Table 1: Strategies predominating in the long run. The table is the same whether the initial state is **all P** or **all R**. The simulations were run for 500,000 years, but the table would be the same with a time period of 60,000 years or less. It should not be thought that the predominating strategy is never challenged. In practice, there is a fair amount of churning. In particular, **R** recurs persistently when $B = 200$.

The evolutionary success of **C** and **Q** when $B = 900$ (and so brood raiding is a relatively weak phenomenon) is discussed in the next section. (The surprising appearance of **Q** arises because we set the replacement fitness of a colony consisting of all **Q** to $B = 1$ rather than $B = 0$.)

We focus here on what the simulations tell us about the evolutionary success of the suicidal punishment built into **P** when $B = 200$ (and so brood raiding is

a relatively strong phenomenon). We note that the level of the forager’s death probability seems unimportant for the latter result since it is sustained with both $d = 0.2$ and $d = 0.8$ (and also with $d = 0.5$).

When the initial state is **all R**, the tendency to move toward **P** when $B = 200$ is facilitated by the fact that mutations from **R** to **P** are ten times more likely than mutations in the reverse direction. However, a detailed examination of the history of the simulations (100 runs when $B = 200$) shows that mutations from **R** to its “cheater” variant **C** are much more important. The probability of mutation from **P** to its own “cheater” variant **Q** is the same, but **Ps** more readily eliminate **Qs** than **Rs** eliminate **Cs**.

Figure 4 is an idealized description of an observed progression to **all P** that is most marked when $d = 0.8$ and $B = 200$. We think it important to stress that such a progression depends on dispersal being viscous. It begins in Figure 4a with a mixture of strategies **R** and **C** that are phenotypically indistinguishable except in the presence of the cheater variants **C** and **Q**. Figure 4b illustrates the appearance of **Q** in a colony previously held by **P**, and the appearance of **C** in a colony previously held by **R**. Figure 4c shows the **P** colony that converted to **Q** reverting to **P** after invasions from its **P** neighbors. It also shows the **R** colony that converted to **C** not only remaining a **C** colony but taking over its neighbors. Figure 4c shows the strategy **C** spreading further but also being contaminated by the appearance of **Q**. Figure 4e shows **Q** spreading at the expense of **C** until **C** is lost in Figure 4e. But then **P** eliminates **Q** in Figure 4d, finally leaving **all P** in Figure 4f.

5 Game Theory

This section seeks to make sense of our simulations with the help of the game of Figure 6a that we call *After You* because it captures the idea that the queen who accepts the task of foraging is put at a disadvantage. Our simulations represent a substantial simplification on what happens in nature and *After You* simplifies even further. For example, the game has only two players.

5.1 After You

The extensive form of the game *After You* starts at the decision node labeled 1 in Figure 6a. At this node, the surface excavator decides whether or not to accept the role of forager. If she accepts (Y), the game ends at a box where the colony’s fitness is A ($A = 1,000$ in the simulation). Both queens would then get a payoff of $\frac{1}{2}A$ (because only half the brood will be offspring of a particular queen) if it were not for the fact that the forager faces a probability d of predation. The forager’s average payoff therefore needs to be adjusted to As , where $s = 1 - d$ is the probability that the forager survives. If the forager fails to survive, the simulation assumes that the colony nevertheless persists with overall fitness A but all offspring derive from the surviving queen, whose average payoff is therefore $\frac{1}{2}As + Ad = \frac{1}{2}A(2 - s)$. Here and

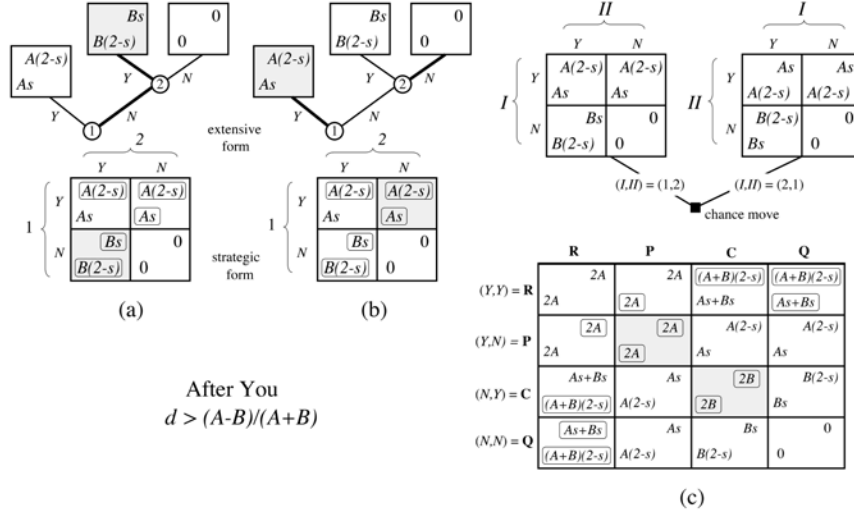


Figure 6: The game *After You*. Only the case with $d > (A-B)/(A+B)$ is illustrated, and so the analysis does not apply when $B = 200$ and $d = 0.5$ or $d = 0.8$. (Recall that $d = 1 - s$.) Figure 6a shows the game with the Nash equilibrium (N, Y) highlighted. (Factors of $\frac{1}{2}$ are systematically omitted.) Figure 6b shows the same game with the Nash equilibrium (Y, N) highlighted. The equilibrium (N, Y) is subgame perfect, which reduces in this simple case to the requirement that the second mover plans to move optimally. The equilibrium (Y, N) is not subgame perfect, because the second mover would move suboptimally if her decision node were reached. This suboptimal move corresponds to the suicidal punishment studied in this paper. Figure 6c illustrates the fact that *After You* should be regarded as a subgame of a larger symmetric game that begins with a chance move which assigns the roles of 1 (surface excavator) and 2 at random to the players I and II. Note that the two symmetric Nash equilibria (P, P) and (C, C) in the symmetrized game correspond to the use of (Y, N) and (N, Y) respectively in *After You*.

elsewhere, we suppress the factor of $\frac{1}{2}$ when writing payoffs in representations of games. The surface excavator's payoff in the southwest of the box that represents her accepting the role of forager is therefore only proportional to her fitness. The same goes for the payoff to the other queen written in the northeast of the box.

If the surface excavator refuses (N) the role of forager at node 1, then the other queen decides whether or not to accept the role of forager at the node labeled 2 in Figure 6a. If she accepts (Y) , the colony's fitness is B ($B = 200$ or $B = 900$ in the simulations). If she refuses (N) , the colony's fitness is 0 (rather than 1 as in the simulation).

In evolutionary game theory, it is unorthodox to model the timing issues captured by the extensive form of a game. One usually goes immediately to the strategic (or normal) form of the game, which is a table that shows the payoffs of the players for each possible combination of strategies that the players might use. It is also unorthodox to consider an asymmetric strategic form like *After You*. Usually, only

the payoffs of the first player are written down, with the implicit assumption that the game is symmetric (looks the same to both players).

Symmetrization. Our simulation assigns the roles of first and second mover in *After You* at random. This chance move is modeled in Figure 6c.

The players in the symmetrized game are labeled I and II. Each becomes the first mover in *After You* with probability $\frac{1}{2}$. (This $\frac{1}{2}$ is suppressed when writing payoffs). A player's (pure) strategy must now say what she will do, both when chosen as 1 and when chosen as 2. The resulting four strategies are **R**, **P**, **C**, and **Q**, as already described in Section 3. The strategic form of Figure 6c constructed with these four strategies is symmetric, but we have nevertheless included the payoffs for both players (with player I's payoff in the southwest of each cell).

Equilibria. Only the strategy **C** is an evolutionary stable strategy (ESS) in Figure 6c, but this is not an adequate reason to reject the strategy **P**, because the ESS notion is fully satisfactory only in the case of symmetric 2×2 simultaneous-move games. Even in symmetric 3×3 games, the replicator dynamics—the simplest mathematical model of an evolutionary process—sometimes converges on strategies that are not ESS (Hofbauer and Sigmund [2]). In extensive-form games, matters are worse (Binmore *et al.* [?], Cressman [?]). We therefore appeal instead to the notion of a Nash equilibrium, which relaxes the requirements of an ESS by only requiring of a pair of strategies that each be a best reply to the other. When the replicator dynamics converges in a symmetric game, it necessarily converges on a symmetric Nash equilibrium.

Best replies are shown in Figure 6c by circling payoffs. For example, in the strategic form of Figure 6c, player I's payoff of $2A$ is circled twice in the column corresponding to the strategy **P**, because both **R** and **P** are best replies for player I to player II's choice of **P**. A Nash equilibrium in pure strategies arises when both payoffs in a cell are circled. So Figure 6c has four Nash equilibria in pure strategies, but we need only pay attention to the symmetric equilibria (**P**, **P**) and (**C**, **C**), because only symmetric equilibria can result when players I and II are drawn from the same population of genetically programmed potential players. The equilibrium (**P**, **P**) corresponds to both players using the asymmetric Nash equilibrium (Y, N) for *After You* highlighted in Figure 6b. The equilibrium (**C**, **C**) corresponds to the asymmetric Nash equilibrium (N, Y) for *After You* highlighted in Figure 6a.

Nash equilibria in mixed strategies—when players use their pure strategies with appropriate probabilities—are also relevant in this problem. In particular, it is a Nash equilibrium in Figure 6a if 1 plays Y for certain, and 2 plays Y with a sufficiently low probability x ($x \leq As/B(2-s)$). Such a mixed equilibrium can be realised without any active randomizing on the part of the players if the population of animals from which 2 is drawn is polymorphic, with a fraction x programmed to play Y and $1-x$ programmed to play N .

Any randomizing in a mixed equilibrium has nothing to do with the chance move

of Figure 6c, which models the coordination mechanism that determines who gets first refusal at the foraging role. Correlated equilibria arise when such coordination mechanisms exist but are not formally modeled. In mixed equilibria the players randomize independently.

The case $d > (A - B)/(A + B)$. In our simulations, $d > (A - B)/(A + B)$ whenever $B = 900$ and for $d = 0.8$ when $B = 200$. Figures 6a and 6b show that *After You* then has two Nash equilibria (N, Y) and (Y, N) in pure strategies. Always playing according to the first of these yields the Nash equilibrium (C, C) in Figure 6c. Always playing according to the latter yields the Nash equilibrium (P, P) in Figure 6c.

The **all P** equilibrium is Pareto efficient in the class of symmetric outcomes (those in which players I and II use the same (possibly mixed) strategy). This means that there is no other outcome that makes one player better off without making another player worse off. A naive group selection argument would therefore favor **all P** over **all C**. However, the strategy **C** is an ESS, whereas **P** is not. An additional reason for being doubtful about the evolutionary viability of **P** is that it is not subgame perfect.

Game theorists say that the Nash equilibrium (N, Y) of *After You* is subgame perfect because it calls for Nash equilibrium play in all subgames of *After You* (whose only proper subgame begins at node 2). The Nash equilibrium (Y, N) is not subgame perfect because it calls for the suboptimal play of N at node 2. This paper dramatizes this feature of the equilibrium (Y, N) (and hence of the strategy **P**) by saying that it specifies suicidal punishment.

The fact that **P** is neither ESS nor subgame perfect does not imply that it cannot be an attractor of the replicator dynamics. Binmore and Samuelson [?, ?] demonstrate this fact for a game that is very similar to *After You*, but the point is evident from Figure 7a, which shows trajectories of the standard replicator dynamics for the symmetrized game of Figure 6c in the case when $B = 900$ and $d = 0.8$. There is an asymptotic attractor at the ESS **C** marked by a star. There is also a whole set N of locally stable attractors that correspond to Nash equilibria that are neither ESS nor subgame perfect. These attractors are all mixed except for **P**.

Introducing low levels of mutation moves the ESS at **C** slightly, but cannot destabilize it. The same is not true of the attractors in N . If mutations tend to move the population to the right in the neighborhood of the set N , then it will eventually reach the right endpoint of N (where $p = As/B(2 - s)$), from whence it will be carried away to **C**. However, Binmore and Samuelson [?] show that introducing mutations that tend to move the system to the left in the neighborhood of N can reduce the set N to a single *asymptotic* attractor **L** whose precise location is determined by the mutation regime. The attractor **L** will primarily be a mixture of **P** and **R** but will not usually lie on the surface of our tetrahedron.

When should we expect to see such an asymptotically stable rest point **L**? The answer depends on the mutation regime and the size of the set N . Larger values

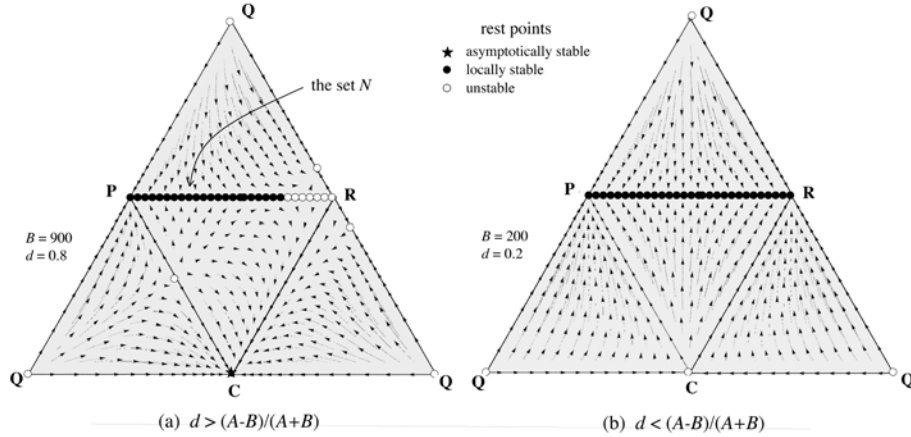


Figure 7: The standard replicator dynamics for the symmetrized version of the game *After You* (Figure 6c). The four surfaces of a tetrahedron with vertices **P**, **Q**, **R**, and **C** have been unfolded to lie flat on the page. A point (p, q, r, c) with $p+q+r+c=1$ in the tetrahedron corresponds to a state in which a fraction p of the population play **P**, a fraction q play **Q**, a fraction r play **R**, and a fraction c play **C**. Figure 7a shows the more interesting case when $d > (A-B)/(A+B)$. The particular parameter values are $A = 1,000$, $B = 900$, and $d = 0.8$. (The set N is smaller for other parameter values). There is an asymptotic attractor at **C** with a large basin of attraction. If the population is displaced slightly from **C** the dynamics return it to **C**. The set N consists of local attractors. If population is displaced slightly from a local attractor it is returned to a nearby point. Figure 7b shows the case $d < (A-B)/(A+B)$ for the parameter values $A = 1,000$, $B = 200$, and $d = 0.2$. Note that the asymptotic attractor at **C** disappears and N expands to be the whole line segment joining **P** and **R**. We are grateful to Francisco Franchetti for his help in preparing these figures.

of $As/B(2-s)$ make the set N bigger and so favor the appearance of **L**. So does our mutant regime, in which mutations from **R** to **P** are ten times more likely than mutations from **P** to **R**. More importantly, the process described in Figure 4 also has the same effect.

We therefore have an evolutionary model in which the suicidal punishment built into **P** can survive as part of a mixture with **R** for certain values of our parameters, provided that the system is started at **P** or some other point within the basin of attraction of **L**. If the system is started outside this basin of attraction—say at **R**—it will converge on **C**.

The case $d < (A-B)/(A+B)$. This case arises when $B = 200$ and $d = 0.5$ or $d = 0.2$. The strategy **R** is now (weakly) dominant, which implies that it always yields at least as good a payoff as any alternative strategy. However, (\mathbf{R}, \mathbf{R}) is not the only symmetric Nash equilibrium because (\mathbf{P}, \mathbf{P}) continues to be an equilibrium.

There are also mixed Nash equilibria (\mathbf{M}, \mathbf{M}) in which \mathbf{M} is any mixture of \mathbf{R} and \mathbf{P} . Figure 7b shows that the replicator dynamics does not necessarily converge on the weakly dominant strategy \mathbf{R} . It is also necessary to recall that mutation regime 3 makes mutations from \mathbf{R} to \mathbf{P} ten times more likely than in the reverse direction, which will tend to increase the fraction of \mathbf{P} s in a population consisting of a mix of only these two strategies.

Finite population. In the case when $d > (A - B)/(A + B)$, the replicator dynamics may take the system to one of two outcomes: \mathbf{C} or a mixture \mathbf{L} of \mathbf{P} and \mathbf{R} . To investigate which of these two possibilities is more likely, we need to make the model more realistic.

The population size in our simulations is only 30. Unlike the deterministic replicator dynamics, so the underlying evolutionary dynamics has a stochastic component. One must therefore expect that the system will (very) occasionally be bounced out of the basin of attraction in which it currently resides into the basin of attraction of another attractor.

The closer an attractor is to the boundary of its basin of attraction, the easier it will be to bounce the system into a new basin. This consideration counts against a mixture of \mathbf{P} and \mathbf{R} like \mathbf{L} because it will usually be much closer to the boundary of its basin of attraction than \mathbf{C} is to the boundary of its basin of attraction (Binmore and Samuelson, [?]). Without other considerations, we must therefore expect to see attractors like \mathbf{L} appearing only with low frequency over a long period. However, there are other considerations.

5.2 Stochastic stability.

The payoffs of zero associated with the strategy pair (\mathbf{Q}, \mathbf{Q}) in Figure 6 fail to capture an aspect of the strategy \mathbf{Q} that turns out to matter. In our simulation, a very small positive payoff is assigned to such an association, which guarantees that it will almost never win a brood-raiding competition except when its competitors are equally inept at starting a colony. But what if just that situation were to arise?

Asking this question makes it clear that considering the replicator dynamics operating in a single game is an inadequate approach. We really have two games sitting on top of each other: a zero-sum brood-raiding game (in which the players are associations rather than individuals) and a reproduction game. The replicator dynamics is also deficient. It suppresses all noise and implicitly assumes random dispersal within an infinite population. It is possible to use Young's [4] theory of stochastic stability to address these issues to some extent, to which end we simplify the model of our simulation even more.

C versus Q. A population of all \mathbf{C} is said to "incubate" invading \mathbf{Q} s in Figure 4. How come?

To study this question, we present the new model with only the alleles **C** and **Q**. In the new model, there are only 3 trees (rather than 10) and associations are restricted to pairs of queens (rather than triples). Figure 8a shows the 10 configurations (or states) of associations then possible after brood-raiding has reduced the number of competing colonies at each tree to one. In each period, a colony dies out with a probability D that is small enough to make the possibility that two colonies die out simultaneously negligible ($D = 0.01$ in the simulation). Assuming viscous dispersal, we can then compute the transition probabilities between our ten states when the death probability of a foraging queen is d ($d = 0.2$, $d = 0.5$, or $d = 0.8$ in the simulation).

The new model makes the brood-raiding competition even fiercer than in our simulation by assuming that a vacant tree is immediately invaded by infinite numbers of infant queens from the neighboring trees, who then pair off at random. The winning association is then chosen from the infinity of associations that result (rather than 5 associations as in the simulation) by choosing one of the associations with highest fitness at random (rather than choosing an association with a probability proportional to its fitness).

Figure 8b shows the Markov chain that governs transitions from one of the 10 states of the new model to another when $0 < d < 1$. Firmly drawn arrows indicate positive transition probabilities in the absence of mutations. The only absorbing states in the absence of mutations are **1** (all **C**) and **10** (all **Q**). It follows immediately from Young's [4] Theorem 3.1 that these are the only stochastically stable states of the system with mutations. This means that the probabilities that the system is in a particular state converge over time to a distribution that itself converges as mutation rates become vanishingly small to a limiting distribution that assigns positive probability only to all **C** and all **Q**. The immediate point is that all **Q** always survives with positive probability.

To determine the relative probabilities with which all **C** and all **Q** survive in the long run, we can appeal to a result of Friedlin and Wentzell [?] that Young [4] quotes as Lemma 3.1. However, this is easy only in the extreme cases when $d = 0$ and $d = 1$. In case $d = 0$, the existence of the two barriers drawn in Figure 8c—which can be crossed from left to right only with the aid of a mutation—is enough to show that the long-run probability of all **Q** is zero. In the more interesting case when $d = 1$, the symmetry (including transition probabilities) of Figure 8d in the absence of mutations allows us to reduce everything to the rates with which mutations allow the system to exit from **1** and **10**. The rate ϵ ($\epsilon = 0.001$ in the simulation) at which **C** mutates to **Q** is assumed to be ten times the rate at which **Q** mutates to **C** in the simulation (Figure 5). Maintaining this assumption in the new model and confining attention to the limiting case when ϵ becomes vanishingly small, we are led to the conclusion that the long-run probability of all **Q** is ten times the long-run probability of all **C**, reflecting the fact that it is a lot easier to get out of the absorbing state all **C** than all **Q**.

In summary, if only **C** and **Q** were possible within the new model and the foraging death rate were $d = 1$, we would see all **C** 0.09 of the time and all **Q**

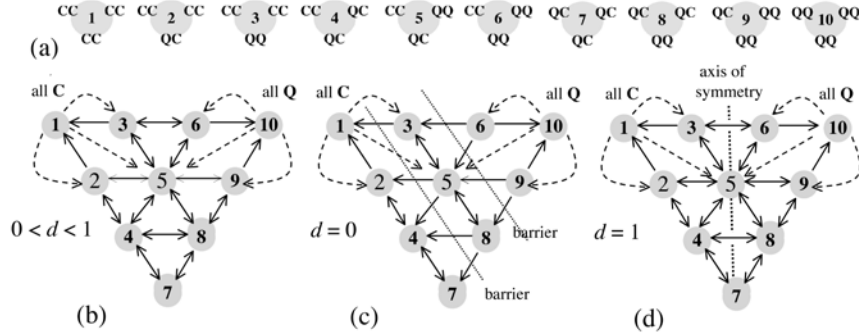


Figure 8: Stochastic stability: Figure 8a shows all possible configurations of associations possible in the new model. Figure 8b shows the Markov chain that governs transitions from one of these states to another when $0 < d < 1$. Firmly drawn arrows indicate positive transition probabilities in the absence of mutations. Broken arrows indicate possible transitions due to mutation at states 1 and 10. (Mutations at other states will also occur but are suppressed in the diagrams because their effect becomes negligible when the mutation rate is small enough—except when crossing barriers in Figure 8c.) To illustrate how transition probabilities are calculated in the absence of mutations, note that state 9 transits to state 5 with probability $\frac{1}{2}D$, to state 8 with probability $\frac{3}{2}(1-d)D$, and to state 10 with probability D . The rest of the time, the system stays in state 9. If a colony corresponding to **QQ** dies in state 9, then the winner of the ensuing brood-raiding contest under the resulting vacant tree is **CC** with probability $\frac{1}{4}$ and **QC** with probability $\frac{3}{4}$ (where writing **Q** first means that the quitter is chosen as surface excavator). It is then important to factor in the possibility that the foraging queen may be lost to a predator. If this happens to an association that would correspond to **QC** if the forager survived, then the association becomes **QQ**, because the adult colony that finally results will only have the **Q** allele but will be no smaller than colonies under other trees. Figure 8c shows the case $d = 0$ with two barriers that cannot be crossed from left to right without a mutation. Figure 8d shows the case $d = 1$, which is entirely symmetric about the vertical axis.

0.91 of the time. When $d = 0$, we would see **all C** essentially all the time.

P versus Q. The simplifications of the new model allow the conclusions of the preceding analysis to be applied to this case as well when the mutant regime is that of Figure 5a (rather than Figure 5b, which is mutant regime 3 of the simulation). The important difference is that the rate at which **P** mutates to **Q** is now *one tenth* of the rate at which **Q** mutates to **P**. If only **P** and **Q** were possible within the new model and the foraging death rate were $d = 1$, we would therefore see **all P** 0.91 of the time and **all Q** 0.09 of the time.

C versus P. The same reasoning can also be applied to this case, provided that one ignores the fact that mutations between **C** and **P** must necessarily proceed via

the other two strategies in Figure 5a. When $d = 1$, it would then be equally difficult to leave both the absorbing states **all P** and **all C**, and so each would occur half the time.

5.3 Summary

We hope that the game theory of this section removes the apparent paradox implicit in the survival of **all P**, both in nature and in our simulations. One problem is that the mutant regime 3 of Figure 5b does not allow downward mutations in Figure 5a. This assumption makes it harder for **all P** to survive in the simulations, so the fact that it does sometimes survive becomes more significant. The stochastic stability analysis suggests that **all P** would eventually be lost in the absence of such mutations over a sufficiently long time span. But the Sonoran desert is thought only to have been in existence for some 10,000 years (Axelrod 1979) and it can often take much longer periods to get out of the basin of attraction of an equilibrium when mutation rates are small.

6 Conclusion

The current paper follows Pollock *et al.* (2004) in being motivated by the experimental finding in Rissing *et al.* (2004) that if a founding queen were to refuse when assigned the foraging role, none of the other cofoundresses would replace her, with the result that the colony would die. Such apparently suicidal behavior seems paradoxical. It cannot, for example, be part of a subgame-perfect equilibrium in the game the cofoundresses play. In a subgame-perfect equilibrium, a cofoundress that refuses the foraging role will necessarily be replaced, but the final outcome is then inefficient in the sense that all the players would be better off on average if they always accepted when assigned the foraging role. Is it possible that the very fierce competition between rival colonies through brood-raiding (Rissing and Pollock 1987, Pollock and Rissing 1989) can explain why the inefficient outcome is not observed in practice?

Continuing the analysis of Pollock *et al.* (2004), this paper conducts additional simulations using a simplified version of the natural history of *Acromyrmex versicolor*. The simulation assumes that the cofoundresses of a new colony are programmed with predetermined answers to two questions: Shall I accept the role of forager when nobody has so far refused this role? Shall I accept the role when it has already been refused? The strategies (punisher (**P**), replacer **R**, quitter **Q**, and cheater **C**) describe the $4 = 2 \times 2$ possible ways these questions can be answered. We improve on the simulations of Pollock *et al.* (2004) by using a more realistic mutation regime. In particular, mutations between **P** and **R** are allowed. We also offer a game-theoretic analysis of a simplified version of the game our simulated ants play in an attempt to better understand our simulation results.

The main result is that when brood raiding is relatively strong the punisher strategy **P** is very resilient, especially if in addition the mortality risk d when foraging is large. Under those conditions, the frequency of **P** is very high at the final date of the simulations independently of the initial conditions, and it is very rarely lost. Studying the dynamics of the simulations reveals the predominant process by means of which this preeminence is achieved. The environments with clusters of **P** punishers and **R** replacers give rise to their mutant variations, which are **Q** quitters and **C** cheaters respectively. The inefficiency of **Q** makes it an easy target for **P**. Strategy **R**, in turn, is easily taken over by **C**, which itself breeds **Q**, that is finally displaced by **P**.

The analytic solution of the *After You* game offers insight into both the experimental and the simulation results. We show that there is a component of Nash equilibria with various mixtures of **P** and **R**. For some of the parameter range there is also a Nash equilibrium with the whole population playing **C**. The latter is also an ESS and subgame perfect, whereas the former is neither, which perhaps can be viewed as a formalization of the “puzzle” motivating this research. However, the equilibrium component with **P** and **R** can be an attractor of the replicator dynamics. This attractor set is fragile, since the endpoint of the attractor set need not itself be a local attractor, and if reached the population will be carried away to **C**. But Binmore and Samuelson (1997) have shown that adding suitable mutations can shrink the attractor set to a single asymptotically stable attractor, thereby eliminating the fragility problem. This goes a long way towards explaining the apparent puzzle, since even under random assortment the **P** strategy in combination with **R** can be the limit outcome provided the initial conditions are not too distant from that point.

The game-theoretic analysis of the *After You* game leaves some open questions, since the replicator dynamics assumes away both random factors and viscosity, which are important in small populations and in the simulations. We thus complement it by studying the stochastic stability of pairs of strategies in the game. Using this analysis it becomes clear that when only **Q** and **C** are present, **Q** dominates most of the time. If only **Q** and **P** are present, on the other hand, **P** dominates. This is very much in line with the dynamics observed in the simulations and provides an analytical rationale for those findings.

One advantage of introducing the game *After You* is that it highlights a phenomenon that may be much more general. It is captured in the fable of *Belling the Cat*, in which all the mice will profit if one of their number will take on the dangerous task of attaching a bell to the cat’s tail (Perry [3] 1965; see also Bilodeau and Slivinski [1] (1996) for an updated discussion of providing a public service at a personal cost). We hope that the present paper will encourage a search for examples of similar phenomena in other species other than the fascinating *Acromyrmex versicolor*.

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