On suicidal punishment among *Acromyrmex versicolor* cofoundresses:

Comparative stability of suicide and self preservation

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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 out-performs 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, population viscosity, self preservation, stochastic stability, strategic success, subgame perfection, suicidal punishment

> *Even though it may be localized,*
> *it is not local ... since it does not*
> *abide anywhere, where can you*
> *look for it?*
>
> **Kao-Ch'eng (n.d.)**
> **(Cleary 1998:24)**

Cofounding queens of the desert leaf-cutter ant *Acromyrmex versicolor* have a straightforward, if unexpected, solution to a classical commons dilemma (*sensu* Hardin 1982). Several *Acromyrmex* spp. are semi-claustral, queens supplying their obligate fungus with fresh leaves prior to worker eclosion (Rissing et al., 1989; Fowler 1992; Diehl-Fleig and de Araújo 1996; Fernández-Marín et al., 2003; cf Brown and Bonhoeffer 2003, generally). Most species known are haplometrotic, each queen founding a nest independently. *Acromyrmex versicolor*, however, is pleometrotic, with several queens (cofoundresses) often establishing nests in common (Rissing et al., 1986). In foraging there is risk, yet procured leaves feed a fungus essential to (communal) colony survival. One might expect the dangerous task to be either shared equitably or contested, perhaps competitive inferiors forced to risk for the group. Neither is the case. Usually a single queen assumes all risk, foraging for her cofoundresses (Rissing et al., 1989; cofoundresses of the ant *Pachycondyla villosa* also exhibit forager specialists, Trunzer et al. 1998). Risk is allocated without observed contention, ritualistic or overt (Rissing et al., 1996). Yet one event early in nest construction strongly predicts later (exclusive) forager assignment: as initial nest construction proceeds, one queen, the *surface excavator*, removes soil from the nest, her cofoundresses digging internally. Some time after nest construction, this prior surface excavator becomes the sole forager for fungus garden substrate (Rissing et al., 1989).

Surface excavation is allocated randomly during the first hours of nest construction, once sufficient space exists for other queens to dig while one removes soil to the surface (Rissing and Pollock 1986; Rissing et al., 1996; cf Fewell and Page 1999; Anderson and Ratnieks 2000). Risk and benefit associated with initial nest excavation are shared communally, the goal being to escape predation common to all by burrowing safely underground; partitioning excavation enhances immediate efficiency without allocating risk inequitably (Rissing and Pollock 1986; Rissing et al. 1986; Pollock and Rissing 1995). Surface specialization allocates equally beneficial, complementary roles; yet this specialization is later employed to allocate unique risk by assigning the surface excavator as forager. Randomization during nest excavation enables a later *correlated strategy* (the term comes from economic game theory; Aumann 1974; Rosenthal 1974; Myerson 1991; Pollock 1994b, 1995a, 1996 considers the economic definition in a simple evolutionary context) which allocates foraging risk without contention (Pollock and Rissing 1995; Pollock et al., 2004). Assigning the forager role to the prior surface excavator is the *coordination mechanism* allocating roles within the correlated strategy.

A correlated strategy is a randomized strategy; that is, no individual is either genotypically or competitively destined to become, in our focus, the forager. But, unlike standard randomization in evolutionary game theory (Maynard Smith 1982), randomized outcomes are *not* independent across individuals. If a fair coin tosses “tails,” that outcome does not affect the probability that another, tossing the coin, will receive “heads.” In randomization under a correlated strategy, one’s reception of “tails” may force “heads” upon another. In our forager focus, only one coin toss occurs, determining, truly randomly, who is the surface excavator. Unlike individually independent randomization, that single toss also assigns complementary roles on others in the group: not being the surface excavator, the others do not later forage. Competition is avoided, *as if* exploitation within the group were impossible (Pollock 1994b).

A correlated strategy produces group efficient outcomes by forcing complementary roles on game partners. There must be group efficient consequence from the task allocation, with deviation from the allocation removed via selection (Pollock 1994b, 1995a, 1996). Correlated strategies form a *group* phenotype, shifting competition to groups, avoiding intragroup exploitation through selection on group efficient outcomes (Pollock 1995a). A correlated strategy “refuses” to recognize exploitation by plummeting the group *as a whole* into failure upon deviation from assigned tasks (cf Radner 1980). Exploitation is denied advantage at cost to all. When correlated strategies assign risk inequitably, an extreme form of group selection may be needed for their evolutionary viability (Wilson 1990; Pollock and Cabrales 2008 and below).

We documented this process experimentally in *A. versicolor* by making the assigned forager appear to be a cheater shirking her risky role (Rissing et al., 1996; herein “cheater” and “shirker” [on surface excavator to forager coordination] are used interchangeably, such originating as mutants). Whenever the prior surface excavator tried to forage, we blocked her exit; 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 refusing foraging assignment. While we cannot make a true shirker, these latter cofoundresses encountered a world identical with shirking. The experiment manipulated not so much the assigned forager, but her cofoundresses' perception of her. In the parlance of economic game theory, we altered the *information sets* of cofoundresses to produce a game state associated with shirking (Myerson 1991). In the parlance of insect sociobiology, we created a *pseudomutant* colony which reveals a possible but rare group phenotype (Wilson 1980, 1985). The game state with apparent shirker is the rare group phenotype.

While cofoundresses clearly can forage in lieu of a cheater "refusing" her assigned task, they either (mostly) refuse 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 at survival (*self preservation*), cofoundresses die. In contrast, removal of the assigned forager, as if lost to predation while above ground, always lead to timely forager replacement by a previously nonforaging cofoundress (Rissing et al., 1996). Cofoundresses distinguish between a lost forager and one (apparently) refusing such risk, replacing only the former. Their commitment to the surface excavator/forager coordination mechanism is so great that they will punish deviation through common death. We term this *suicidal punishment* (Pollock et al., 2004). This experiment motivates a *forager game* where the surface excavator is assigned the foraging task but may refuse assignment. If she refuses, her cofoundresses replace her or not. Figure 1 presents the decision game tree, showing how our experiment reveals an otherwise latent branch.

Suicidal punishment seems so extreme as to be evolutionarily implausible. Assuming the surface excavator/forager coordination mechanism, when faced with a shirker refusing forager assignment, one certainly does better by replacing her, helping both cheater and self; true, one can hope another cofoundress will replace (as in a war of attrition in waiting times; Bishop and Cannings 1978; Maynard Smith 1982), but this just shifts the self preservation imperative onto others. And, indeed, in the evolutionary short term of several hundred generations, simulations reveal cheater replacement can persist, even increasing in frequency (Pollock et al., 2004). Yet replacing helps the cheater more than self, for the replacer may die while foraging. The offspring of cheaters increase locally relative to those of replacers, leading to stochastic "catastrophes" within a finite population where group efficient resource production (via a foraging specialist) is lost; these group inefficient locales can then be invaded by group efficient coordinators possessing latent suicidal punishment (Pollock et al., 2004; cf Pollock 1989a, 1995b).

We say "increase locally" since *A. versicolor* foundresses are viscous, dispersing locally rather than mixing widely, irrespective of parental origin (Rissing et al., 1986; Figure 2 and **Simulation design**, below). Our prior simulations mimicked *A. versicolor* natural history (expanding the parameter range thereafter) to compare the *long term* evolutionary success of strategies either suicidally punishing or replacing cheaters on coordination (self preserving). Beginning with "fair contest" populations, half latent suicidal punisher, half latent self preserving replacer, we examined the long term (100,000 year) trajectories of these morphs when exposed to shirkers (initially arising through recurrent mutation) on the coordination mechanism exhibited by *A. versicolor*. We found that personally best replacement almost never out performed suicidal punishment; either both were lost, (rarely) survived equally, or suicidal punishment predominated (Pollock et al., 2004).

Suicidal punishment fares well by eliminating the offspring of cheaters from future generations (cf Pollock 1988). The catastrophic loss of coordination which replacement engenders by incubating, locally, greater concentrations of cheaters is thereby avoided (Pollock et al., 2004). In *Acromyrmex versicolor* structured populations, local clusters consisting predominately of latent suicidal punishers remove cheaters as these (phenotypically) appear. In contrast, locales predominately composed of replacers are consumed by the cheaters which their response incubates. A replacer locale becomes a cheater locale which, when encountering a suicidal punisher cluster at their common boundary, is often reduced, then eliminated, through punishment by the latter (Pollock 1989a, 1995b; Pollock et al., 2004; cf Figure 4, below).

Our prior design focused exclusively on the relative performance of suicidal punishment and replacement in a common population. Here we examine the evolutionary stability of each separately, beginning runs with one morph saturated, thereafter exposed to cheaters. Under observed *A. versicolor* viscous dispersal (Pollock et al., 2004 and Figure 2 below) we find that suicide is indeed stable over a greater parameter range than replacement; but, *absent suicide*, the replacing morph can be stable as well. When self preserving replacement is stable so too is suicidal punishment, but not conversely.

Extended simulation runs find replacement weakly stable relative to suicidal punishment. In our finite populations, both morphs can be merely stochastically stable (defined below), enduring long, then quickly lost. If we allow the two morphs to mutate into one another, employing a simple view of mutation where mutants are *close variants* on present types (Dawkins 1980; Maynard Smith 1984; detailed below), suicidal punishment *always* supplants replacement, retaining high frequency with stochastic cycles of shocked reduction and recovery; else, ultimately, only (group inefficient) cheaters remain. In such cases initial seeding of the population as either all latent suicidal or all latent replacer is crucial. Loss of *both* morphs (with both appearing via reciprocal mutation) can be three times as great when beginning with replacers rather than latent suicidals; this is partly because replacers, under our closest variant mutation rule, induce a more "virulent" mutant cheater than do latent suicidals, as detailed below.

Simulations reveal population loss of surface excavator/forager coordination, hence loss of commons efficiency, to be a stochastic event. Either replacement or suicide may predominate for thousands of years (suicide for hundreds of thousands), then undergo rapid elimination in a few hundred. To capture this process, our simulations run for 500,000 years each; recognizing that loss is stochastic, we duplicate these 100 times, measuring stability as probabilistic loss. We begin by detailing simulation design as motivated by *A. versicolor* natural history and experiment.

Simulation design

Cofoundress colonies, territoriality, and coordination

Simulation design follows Pollock et al. (2004), with *Acromyrmex versicolor*'s natural history cycle (Figure 3) iterated 500,000 generations per run. We envision 100 adult colonies, distributed uniformly on a circle (to avoid end point effects; e.g., Lehmann et al. 2008). In the Sonoran Desert (near Phoenix, AZ) adult *A. versicolor* colonies are somewhat linearly and uniformly spaced as one colony per large tree in desert ravines (Rissing et al. 1986; Pollock et al. 2004). In our simulation, each year adult colonies die (independently) with probability .05, giving an expected life span of 20 years (with one proviso noted shortly), slightly on the high side for *A. versicolor*, but not impossible (Rissing, pers. obs.). Extant adult colonies are territorial, destroying starting colonies whenever encountered; while foundresses will alight under any tree, only trees vacant of an adult colony provide any chance of survival. Herein we treat foundresses as haploid and asexual (*Foraging game strategies*, below); there are no males. Natural adult colonies release sexuals after desert monsoon rains; these mate locally, with mated foundresses then dispersing viscously from the vicinity of their parental adult colony. We capture this viscosity by restricting (haploid) foundress dispersal to the trees adjacent to their parental colony on the circle (Figure 2); once alight under a tree, foundresses associate therein randomly. Again, such dispersal yields death if the adjacent tree is already adult occupied.

Forming starting colonies. When the tree is adult vacant, five starting colonies with three cofoundresses each are formed; these will vie for sole possession of the tree as they mature. Three cofoundresses is the minimal n-person environment allowing full expression of strategies in the (potentially) two-stage foraging game, as noted shortly. Cofoundresses establish a surface excavator which frames the later foraging game; one of the three cofoundresses, of whatever genotype, is assigned surface excavation and always so performs. If the surface excavator accepts coordination for later foraging, she then forages for her group, enduring a simulation specific mortality probability which measures her assumed foraging risk. Foraging is idealized as a single event. If the forager dies, she nonetheless returns with food; we thus avoid micro simulation of repeated foraging trips with interim death and replacement. Forager death is the sole cause of queen specific mortality *within* colonies. *Acromyrmex versicolor* queens coexist for years without aggression in laboratory colonies. Herein, all queens in a victorious starting colony (via *brood raiding*, below) reproduce equally, save for the event of forager death.

Brood raiding. If the surface excavator refuses foraging assignment, the other queens may replace her or not, depending on their strategy type (*Foraging game strategies*, below). In either case, surface excavator refusal reduces starting colony fitness. The surface excavator, having previously oriented herself above ground, should be more efficient at initial exploration, an effect increasing with experience (e.g., 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). This reduction in colony foraging efficiency is likely amplified by a competitive dynamic among starting colonies. Adult colonies are exclusively territorial, so clumped starting colonies must ultimately fight one another for exclusive possession of the (adult) vacant tree. They do so by raiding one another for brood once workers eclose, ultimately leading to a single victor which becomes the new territorial adult (Rising and Pollock 1987; Pollock and Rissing 1989; cf Pollock et al., 2004 for further citations). Colonies with more workers are better at raiding (Rissing and Pollock 1987, 1991; Tschinkel

1992, 2006); first brood increases with early fungus health (Rissing et al., 1996) and queen (cofoundress) number (Rissing and Pollock 1987). Later exclusive adult territoriality thus amplifies small differences in foraging efficiency among clumped starting colonies by forcing a zero sum outcome (Figure 3).

We assign a starting colony whose prior surface excavator accepts her foraging role without contention or delay a fitness of 1000. Colonies where the excavator refuses to forage but is replaced by another are assigned *forager replacement* colony fitnesses of either 200 or 900 per simulation set; the lower the assigned colony fitness, the greater the loss of foraging efficiency through loss of the surface excavator's above ground orientation, coupled with any replacement delay. Assigning colonies enduring forager replacement a fitness of 200 represents *strong brood raiding*, while a fitness of 900 represents *weak brood raiding*. Brood raiding is a form of group selection by combat. When forager replacement fitness is low, 200, group selection is strong when exposed to a coordinated colony with 1000 fitness (Wilson 1990; Pollock and Cabrales 2008; D. S. Wilson, pers. com.). Our simulations herein show that coordination under the *A. versicolor* forager game requires strong brood raiding, i.e., strong zero sum group selection under contention for exclusive possession of the tree. Coordination is more likely lost with a replacement colony fitness of 900 relative to one of 200 (**Results**, below; Pollock et al. 2004).

If all refuse to forage, as may happen depending on cofoundress strategy types, the colony should die. This might produce trees remaining vacant across years, as all cofoundresses under a vacant tree might refuse in their respective starting colonies. We avoid this to streamline programming, assigning a very small colony fitness of 1 to such colonies, as though even then some queen will forage after some long delay; no matter what, some starting colony under a vacant tree will become the adult under that tree. Once starting colony fitnesses are calculated, placement as the new adult colony is random, weighted by competing starting colony relative fitnesses. Thus a nonforaging colony fitness of 1 is negligible when confronted with the simulated minimal reduced replacer colony fitness of 200.

Foraging game strategies

We consider four haploid, single locus strategies in a potentially two-stage forager game (Table 1). In the first stage, the surface excavator decides whether to accept her lot as forager. If she does, the game is over (Figure 1). Otherwise the two remaining cofoundresses decide whether to replace her. If both are potential replacers, one (randomly chosen) becomes the forager. The behavioral pairs {accept forager assignment/refuse}, { replace/not} produce four strategies:

P, a *punisher* which accepts original foraging assignment but never replaces one shirking such assignment. Our experiment with laboratory *A. versicolor* starting colonies suggests each composed of all **P**, with one queen accepting her foraging role, the others refusing to replace when the forager appeared to refuse assignment (Rissing et al. 1996). **P** is a latent suicidal punisher.

Q, a *quitter* which neither accepts original forager assignment nor replaces another shirking such assignment. **Q** unilaterally refuses to forage, so "quits" the game, so is an absolute cheater on coordination.

R, a *replacer*, which accepts original foraging assignment as does **P**, but will replace another shirking such assignment; **R** plays a personally best, self preserving response (making the best of a bad lot) when exposed to a shirker on foraging assignment. We have no natural or experimental evidence that **R** exists; yet this strategy seems intuitively the final product of individual selection. Our simulations provide **R** much as our pseudomutant experiment (*sensu* Wilson 1980, 1985) provides an apparent cheater (Rissing et al. 1996 and above). Indeed, our simulations were constructed to force the appearance of **R** even though there is no empirical evidence for self preservation.

C, a *sophisticated cheater/replacer*, which refuses original forager assignment (like **Q**) but *will* replace another shirking such assignment. **C** hopes to exploit a replacer by refusing assignment, but will preserve itself by replacing when itself exposed to a cheater. **C** fills out the strategy space consequent of the two binary properties {accept assignment/not} and {replace/not}. While intuitively artificial, **C** will often have a significant transition role in populations moving from coordination to all cheating.

C is a "cheating" variant on **R** in the same sense that **Q** is a cheating variant on **P** (Table 1 and Figure 1). **P, R** will accept original forager assignment while **Q, C** will not; **P, R** accept the coordination mechanism, **Q, C** refuse the coordination game. Neither **P, Q** will replace a shirker on assignment; **R, C** will, employing a personally best, *self preserving* response to failed coordination by another. **Q**, ever refusing to forage, de facto punishes a shirker on original coordination as does **P**, but unlike **P**, **Q** will never forage. **Q**'s refusal is a means of shifting foraging onto others; **P**'s refusal to replace a shirker is rather fidelity to the coordination mechanism over personal survival. **Q**'s refusal to forage is not contingently strategic while **P**'s is; a behavioral outcome (refusing replacement) may be motivated by distinct strategies. Whether a punishing **P** is *suicidal* depends on whether a replacer is or is not also present in the colony. Suicide is not an immediate consequence of punishment (some other queen might replace); but commitment to endure suicide as consequence is absolute.

Cofoundress assortment

Acromyrmex versicolor queens likely mate locally and disperse viscously (Rissing et al., 1986, 1989; Hagen et al. 1988; Rissing, pers. obs.). We capture this by having foundresses disperse from their parental colony to adjacent trees on the circle (Figure 2 and above), mixing randomly once there. This *viscous* dispersal will be contrasted with population wide random assortment, where all extant adult colonies contribute to a common pool from which cofoundresses are chosen randomly. In either case (adult colony) foundress production is assumed so great as to approach sampling with replacement. Under viscous dispersal a tree location would remain empty if three adult colonies in a row happened to die. We preclude this possibility to streamline simulations, so the .05 adult colony death rate is slightly higher than simulation reality, as adjacent adult deaths may prevent death of a focal adult colony; identical caveat was employed in Pollock et al. (2004). While this rule is unnecessary under random foundress assortment, where foundresses from any adult colony are able to alight under any tree, we retain it to standardize adult colony death across the two forms of dispersal.

Mutation

We consider three mutation regimes. As our focus is on the long term stability of surface excavator/forager specialist coordination, either as the correlated strategies (latent) suicidal **P** or replacing **R**, in all cases we preclude mutation from cheaters to coordinators (i.e., **Q,C → P,R**). Our prior "fair contest" work focused on cheater only mutation as either **P,R → Q** or **P,R → C,Q** with, in the latter case, **C ↔ Q**. **Q**, refusing to forage under all circumstance, is the simplest form of shirker. Resistance to emergent **Q** is the weakest form of stability for forager coordination. When the sophisticated cheater **C** is possible, we felt compelled to allow its mutation to **Q**, as quitter **Q**, never foraging, exploits a replacing **C** just as it exploits a replacing **R**; **Q → C** was in this case allowed as well to retain cheater diversity, our focus being on the stability of coordination persistently exposed to cheaters (Pollock et al., 2004). Herein we perform sample stability runs (of 500,000 years each) under these two cheater mutation regimes (**Q** only; **C,Q**) employing, as in our previous work, a uniform mutation rate of .001 to robustly test for stability against recurrent cheaters. We begin with either **P** or **R** saturated in the population, adult colonies containing only the chosen saturated type, under both **Q** only and **C,Q** mutation. Of course, queens in adult colonies do not play the foraging game, but the foundresses they produce will. After examining the stability of **R** absent **P** and conversely, we examine relative success between them by allowing **P ↔ R** mutation, again with either morph initially saturated, with a slightly different mutation to cheater rule, or third mutation regime, detailed next.

Adult colonies live many years. Mutants arise not as queens in an already established adult colony, but among their offspring. So a **P** generally breeds true, but occasionally produces an offspring of another genotype, still to breed again mostly or totally true the next year, until colony demise.

Mutation restricted to closest variants

A mutant is a variant of a pre-existing genotype; present types, as the material basis of mutation, shape their derived mutants (Dawkins 1980; Maynard Smith 1984; cf Darwin 1859 on the origin of new variation). Our four strategies **P,R,Q,C** are defined by two properties: accept assignment/not and replace a present shirker/not. Since we are everywhere excluding mutation *from* shirkers **Q,C** *to* correlated (forager assigning) strategies **P,R**, our strategy set can be represented as a simple lattice where adjacency is deviation by a single behavioral property (Table 1; cf Figure 1):

$$\begin{tikzcd}
\mathbf{P} \arrow[r, leftrightarrow] \arrow[d] & \mathbf{R} \arrow[d] \\
\mathbf{Q} \arrow[r, leftrightarrow] & \mathbf{C}
\end{tikzcd}$$

Mutant deviation of a single property is more likely than simultaneous deviation on both properties. The foregoing lattice, then, provides the most likely deviation path(s) from a present type to mutation derived by altering the *physical program* of that present type. The mutation paths **P → C** and **R → Q**, requiring gain/loss of two behaviors in separate stages of the game (Table 1; Figure 1), should be much less likely than, e.g., **P → Q**, a single change mutation path. In this our third mutation regime, we preclude two property gain/loss paths completely, assuming them several orders of magnitude less likely than one step mutants (so here mutation pathways are always to *closest variants* in the behaviorally defined strategy space; Pollock 1995b employs one step, closest variants in some finitely repeated games).

Restricting mutation to closest variants has consequence. Under viscosity, when local adult colonies are composed mostly of **P**'s, their low dispersing offspring are unlikely to encounter a **C** as cofoundress, as **C** mutates from **R**, not **P** (Table 1 and above). But, as we shall see, the sophisticated cheater/replacer **C**, directly derived from **R** but not from **P** (Table 1), is more damaging than is quitter **Q** (directly derived from **P**; Table 1) to either coordinator, **R** or **P** (Pollock et al., 2004; and below). Thus, restricting mutation to closest variants, self preserving replacer **R** engenders *a more harmful mutant to its own type* than does suicidal punisher **P**. While this effect is especially pronounced under viscosity, where a mutant cheater disproportionately encounters its "parent" type, we find it under random assortment as well; e.g., a predominantly **R** population will disproportionately encounter **C** rather than **Q** mutants relative to a predominantly **P** population, and **C** mutants more likely jeopardize the stability of either coordinator **P**, **R**. A strategy's (relative) stability is derived not just by its design, but by those strategies which, mechanistically, are most likely produced as mutation from it. One strategy (**R**) may produce its worst enemy as mutation, while another (**P**) does not.

We employ a mutation rate of .001 for the loss of a behavioral property (e.g., **R** → **P**, where the prior replacer **R** loses the ability to assess and reply to a cheating event, while retaining fidelity to coordination when the assigned forager, thus mutating to **P**). Assuming losses mechanistically easier than gains, gain mutations (e.g., **P** → **R**) occur at one order of magnitude less, .0001. A replacer must assess her environment and decide to replace; a punisher, in the presence of a designated forager, does neither. There are likely several ways to lose such assessment/decision, while gaining the mix plausibly requires a more specific mechanism. Essentially, genetic errors in a "program" outnumber creative genetic deviations. We feel a gain rate of .0001 generous, recognizing, however, that a higher loss rate *seems* to bias simulations toward suicidal **P** and against replacing **R**; as **P** → **R** mutation is ten times less likely than **R** → **P**. We shall see, however, that a higher **P** → **R** rate would likely enhance loss of *both* coordinators. Otherwise, both **P** and **R** are exposed to the same rate of mutant cheaters (albeit of different types; **P** to **Q**, **R** to **C**). Thus under mutation restricted to closest variants, loss paths **R** → **P, P** → **Q, C** → **Q** occur at probability .001 with the gain paths **P** → **R, Q** → **C** at .0001 (cf Table 1, Figure 1).

We employ high mutation rates to bias results against coordination. Even so, we find measuring the loss of coordination elusive. For instance, coordination (as either **R** or **P**) under one parameter set (200 replacement fitness, .8 forager death, under viscosity) is lost in 12 of 100 simulations, suicidal **P** retaining overall high frequency otherwise (Table 4). Each trial runs for 500,000 years, considerably longer than the inferred duration of the Sonoran Desert in which *A. versicolor* resides (being no more than 10,000 years old; Axelrod 1979). Measuring retention over a more historical time frame would inflate suicidal **P**'s stability; a longer frame than that chosen, holding simulation replicates constant, would deflate it. Such is the price of measuring a stochastic process. While we cannot claim our measured rates of (mostly) **P**'s stability are even proportionately constant across parameter sets under different mutation rates or simulation durations, *all* results point to the robust superiority of latent suicidal **P** over self preserving **R**. As in our prior work, we denote, say, a simulation with 200 replacement fitness, .8 probability of forager death, under viscosity, as {200, .8, **v**}; under global, random cofoundress assortment as {200, .8, **r**}. We denote a colony's cofoundress composition by **XYZ** where the first position, **X**, designates the surface excavator, coordination assigned, forager, whether or not she assumes the task.

Results

We begin with mutation unrestricted to closest variants, seeing how **R**, **P** fare against recurrent **Q**, then add the more strategically sophisticated **C**. Focusing on the stability of coordination, mutation from a cheater (**Q, C**) to a coordinator (**P, R**) is always precluded. First we consider **R** and **P** isolated from one another; later we allow **P** ↔ **R** with mutation restricted to closest variants to see if **R, P** may supplant one another over time frames of 500,000 years. We first restrict ourselves to *Acromyrmex versicolor* viscosity, considering population wide random foundress assortment (as well as viscosity) only under closest variant mutation.

R *absent* ***P***

Q *only mutation*. Table 2 summarizes sample stability runs of 500,000 years under viscosity, beginning with an all replacer **R** population, excluding punisher **P** entirely; then an all punisher **P** population, excluding replacer **R** entirely. Replacer **R** is stable only under low (.2) forager mortality, where its incubation of cheaters (foraging in lieu of a shirker refusing assignment) is diluted by high forager survival. Yet the logic of replacement is invariant to simulated forager mortalities; even at .8 forager mortality and strong brood raiding (200 replacement fitness), it is better to replace than share 1/3 of the fitness of a (3 queen) non-foraging colony (with trivial fitness 1). Self preservation's stability fails to conform to the intuition of individual selection even when excluding **P**.

Where **R** is stable at .2 forager mortality (under viscosity), it is not as a polymorphism with cheaters. Under **Q** only mutation, quitter **Q** briefly obtains +20% of the population occasionally over 500,000 years; otherwise **R** is almost always over 90% (Table 2). **Q** is harmed through viscous association with itself in **QQQ** colonies without foragers, these having abysmal colony fitness of 1. **Q**'s spatially local frequency is thus pushed downward repeatedly; in the quite small competitive populations induced by viscosity and the limited availability of vacant trees (Figure 2), **Q** undergoes repeated stochastic local loss. At high (.8) forager death, though, **R** exhibits significant loss through its high (cheater incubating) mortality, offsetting **Q**'s self clustering limitation under viscosity, yielding all **Q** populations rather quickly (4,200 - 4,500 years; Table 2).

C,Q *mutation.* Cheater/replacer **C** predominates under weak brood raiding (with 900 replacement fitness) and low (.2) forager death (Table 2). While **C** refuses original foraging assignment, it also replaces one shirking such assignment (Table 1; Figure 1); a **CCC** group does produce a forager, albeit of limited efficiency, while a **QQQ** group produces no forager at all. **C** is thus harmed less through the viscous creation of **CCC** groups than is quitter **Q** via creation of **QQQ** groups. At 900 replacement fitness, the 10% reduction in coordination fitness in **CCC**

groups is offset by the exploitation of **R** replacement in **CRR** groups (where, again, **X** denotes the assigned forager in **XYZ**; recall neither **Q** nor **C** will forage *when so assigned*), while **C, R** exploit one another equally in the mixed groups **CCR**, **CRC**, either **C, R** replacing half the time. Here, under viscosity, **R** enjoys mild (10%) advantage only in pure **RRR** groups. Once **C** wins placement in an adult colony, viscous foundress pools to which it contributes (coming from at most two adult colonies) occasionally create five starting colonies under a vacant tree where each has at least one potential cheater **C**; over repeated trials across thousands of years, this process tends to shift **C**'s frequency within adult colonies upward.

C, however, must also resist is own cheater, quitting **Q**, who will never replace a forager. At .2 forager mortality with weak brood raiding, **C** foraging is offset by **Q**'s abysmal self clustered fitness, exactly as with self preserving coordinator **R** under **Q** only mutation, above; **C** saturates, resisting later **Q** mutants. High (.8) forager mortality, however, shifts the population to quitter **Q**, **C** now usually sacrificing itself in *self preserving* foraging, enhancing its incubation of **Q**. So only **C** will replace in **CQC** or **CCQ** groups, the replacer often dying at .8 forager mortality; **Q** exploits **C** much as it exploits **R** under .8 forager mortality. **Q** won 196 of 200 fair contest trials under this parameter set ({900, .8, **v**}), supplanting **P**, **R**, and **C** (Pollock et al., 2004). At {900, .8, **v**}, **R** stability runs exhibit a trajectory where **R** is replaced, locally, by the sophisticated cheater **C**, which is then replaced, locally, by quitter **Q** (Table 2; cf Figure 4). These quitter locales grow at their fringe upon encounter of either **C** or **R**, as **R** similarly incubates **Q** under high forager mortality (above), albeit at a lesser rate than **C** (**RRR** colonies having slightly greater fitness than **CCC** colonies under high replacement colony fitness of 900).

P's relatively greater stability (below) lies in its refusal to incubate shirkers, even though personally advantageous to do so (Table 2). Yet the sophisticated cheater **C**'s ability to replace can ultimately eliminate **P** as well, *providing the sole instance of evolutionary superiority for self preservation,* to which we now turn.

P absent R

***Q** only mutation.* Table 2 also summarizes sample stability runs beginning with an all punisher **P** population under the same parameter sets as for replacer **R**. When **R** is stable, so is suicidal **P**. Additionally, **P** is stable against quitter **Q** only mutation at high (.8) forager death while replacer **R** is not (at {900, .8, **v**}), even though self preservation mandates replacement foraging. **P**, when dying as the assigned forager, does, of course, incubate phenotypically hidden **Q** (in **PQP, PQQ** colonies). Under high (.8) forager mortality and weak brood raiding ({900, .8, **v**}), **P**'s frequency over 500,000 years dips to about 50%, but only occasionally; quitter **Q** surpasses 40% about 1.3% of the time, while **P** remains at least 90% over 92% of the time (Table 2). Under random assortment, **Q** supplants **P** under the same parameters (results deferred); but under viscosity **Q**'s high local frequency is again self damaging though the creation of **QQQ** groups.

***C,Q** mutation.* While our sample **P** stability run confirms prior fair contest results at high (.8) forager death with **Q** only mutation (Table 2 and Pollock et al., 2004), a similar stability run under **C,Q** mutation diverges from fair contest expectation, at least at first blush. Suicidal **P** won

81% of 200 fair contest trials under {200, .8, **v**} with **C,Q** mutation (Pollock et al., 2004), but fails its 500,000 year stability run (Table 2). Remarkably, **P** exhibits high frequency for most of some 455,000 years, with occasional clustered peaks of the sophisticated cheater **C**, which transform into quitter **Q** clusters, these then beaten back by clustered **P** at their common boundary (cf Pollock 1989a, 1995b). Suicidal **P**'s ultimate demise around year 455,000 is rather rapid, occasioned by the simultaneous, somewhat stochastic growth of several large **C** clusters before these can be internally transformed into **Q** clusters (also noted in Pollock et al., 2004; compare Figure 4, below). Visually, the stochastic growth of **C** clusters ultimately allows **C** to consume clustered **P** before **C** itself is consumed by quitter **Q**; about year 455,000, only quitter **Q** remains.

Fair contests hint at this process (Pollock et al., 2004). All but one of the 19% of fair contest **P** losses at {200, .8, **v**} are won by **Q** (the other a **P,Q** "tie" terminated after 100,000 years; Pollock et al, 2004). The preponderance of **P** fair contest wins reflects the cyclic recovery of **P** in the stability run, while **Q** wins reflect **P**'s potential demise through repeated (cheater/replacer **C** mediated) stochastic reductions in its frequency. Under recurrent mutation to cheaters **C,Q**, a sufficiently long simulation will remove coordinator **P**. Stability in our finite population is qualitative rather than absolute.

While the sophisticated cheater/replacer **C** flares but briefly in the {200, .8, **v**} run, its role in punisher **P**'s demise is crucial (Pollock et al., 2004). **C** will replace a clonal assigned forager shirker, limiting the self detrimental clustering effect of cheating. Under strong brood raiding (200 replacement fitness, a reduction of 80% from coordination optimum), **C** usually fares poorly against clustered, coordinating **P**; so, e.g., **P** is stable against **C** at low (.2) forager death (Table 2). High (.8) forager death, however, causes the assigned forager **P** to often sacrifice itself to phenotypically "hidden" cheaters in **PPC** and **PCC** groups. These, when placed as an adult colony, produce a high realized frequency of **C** in viscously formed foundress pools, occasionally ratcheting **C**'s frequency upward in realized starting colonies. In **R** stability runs, **R** replacing a **C** cheater on assignment, dying while foraging, amplifies the effect further (above); thus **R** under {200, .8, **v**} is eliminated 100 times faster than is **P** under the same parameter set with **C,Q** mutation (Table 2).

Clustered **C**'s resistance to clustered punisher **P** is directly related to its own resistance to quitter **Q**; so, e.g., a 900 replacement fitness makes **CCC** colonies most resistant to a coordinated (1000 fitness) colony, and most resistant to **QQQ** colonies with fitness 1. As **P**'s stochastic resistance to **C** improves (replacement fitness declines), **C**'s stochastic resistance to **Q** declines. **Q**, however, fares poorly against clustered **P**. Under strong brood raiding (200 replacement colony fitness) a prolonged balance of stochastic vulnerabilities, **P** to **C**, **C** to **Q**, results, producing local population cycles of **P ⇒ C ⇒ Q ⇒ P**. Yet the duration of these cycles, being variable and possibly present in several parts of the circle of adult colonies, can overwhelm suicidal **P**. That **P** cannot withstand **C** in {200, .8, **v**} in our 500,000 year horizon is mildly disconcerting, as this parameter set rather generously fits the population structure inferred for *A. versicolor* (Pollock et al., 2004 and **Simulation design**, above). Stochastic stability, however, will always lead to population loss of coordination under cheater only mutation; a time horizon conforming to the probable duration of present Sonoran ecology hosting *A. versicolor* (about

10,000 years; Axelrod 1979) would likely have "revealed" **P**, but not **R**, stable under {200, .8, **v**}, as the latter was lost in some 4,500 years in our trial while **P** endured for far longer than 10,000 years (Table 2).

There is a stronger sense in which suicidal **P** is superior to self preserving replacer **R**. Cheater/replacer **C** is the mirror image of punisher **P** in the two property strategy space {accept/ reject assignment}, {replace/not replace a shirker} (Table 1 , Figure 1, and **Simulation design**, above). Under viscosity, **P** should then be less exposed to mutant **C** relative to **C**'s exposure to its own one step mutant, quitter **Q** (Table 1). So, under viscosity, **P** should exhibit mostly short **P ⇒ Q ⇒ P** cycles, with high duration in **P**, as in **Q** only mutation (Table 2), retarding the local **P ⇒ C** transition just described. **P** cannot locally shift to **C** if **C** is not encountered.

Rather than conjecture a lower **P** → **C** mutation rate, we restrict mutation to closest, one step variants (defined above) to both simultaneously consider the stability of replacer **R** and suicidal punisher **P** in the same population while plausibly reducing **P**'s (viscous) encounter of **C** relative to either **P,C**'s encounter of their closest variant mutant **Q**. We find **P** robustly stable relative to the now potentially co-present **R** (derived from **P** as a mutant close variant; **Simulation Design**, above), even under {200, .8, **v**}, where, previously, **P** → **C,Q** mutation leads to **P**'s downfall (near 500,000 years, above). There is, however, a cost. Weak brood raiding (900 replacement fitness) now fails to support coordination as either suicidal **P** or replacing **R** (contra Table 2 with **Q** only mutation on **P**), as the close variant mutation sequence **P** → **R** → **C** produces, recurrently, sufficient **C** to undermine the *long term* stability of both coordinators.

While close variant mutation supports suicidal punishment uniquely (against rival self preserving replacement) in the four strategy space, stronger brood raiding, relative to **Q** only mutation simulations, is necessary to retain coordination. But this is exactly what the strong brood raiding and adult territoriality of *A. versicolor* provide. Our simulations end by telling us that the forager assignment exhibited by *A. versicolor* requires *A. versicolor*'s natural history.

Mutation restricted to closest variants

***P** predominance over **R**.* Close variant mutation restricts mutants to gain/loss of one behavioral property (Table 1, Figure 1, and **Simulation design**, above), excluding mutation from cheaters to coordinators (e.g., **C** → **R** is prohibited while **Q** → **C** is allowed). Properties are lost with probability .001, gained with .0001, so **R** → **P** is ten times as likely as **P** → **R** (rationale provided above). Table 3 summarizes 500,000 year sample stability runs under this mutation regime, beginning with either an all suicidal punisher **P** or all replacer **R** population. Under either low (.2) or high (.8) forager mortality, an all **R** population switches to all **P** in 60,000 years (or much less); thus our sample **R** stability runs become **P** stability runs (Table 3). The two all **P** runs never switch to all **R**. Bias toward **P**, while facilitated by relatively greater **R** → **P** mutation (above), is actually more a consequence of **R** → **C** mutation. Replacer **R** mutates to the more virulent cheater/replacer **C** while **P** does not, depressing **R**'s frequency under viscosity, per cheater mutation event, relative to **P**, which more readily eliminates its own cheater mutant **Q**.

Figure 4 sketches this process in idealized form. **R** → **P** mutation produces phenotypically neutral drift between the two coordinators absent cheaters, creating clumped suicidal **P** even in initial all replacer **R** runs. **R** → **C** mutation then produces local population transitions **R** ⇒ **C** ⇒ **Q** ⇒ **P**, this last when clumped quitter **Q** encounters clumped suicidal **P** at their common boundary. The effect is pronounced in the .8 forager death trial, where the sophisticated cheater **C** occasionally reaches almost 50% or the population, quitter **Q** 40% ({200, .8, **v**}, Table 3). Here replacer **R** incubates more cheaters via foraging death, producing larger cheater/replacer **C** clumps relative to low (.2) forager mortality, where neither **C** nor **Q** ever surpass 10% of the population ({200, .2, **v**}, Table 3).

At .2 forager death, suicidal **P**'s frequency falls occasionally under 20%, replacer **R** reaching occasionally over 80% (Table 3). Variance in **P,R** is here mostly due to drift, biased away from **R** when the sophisticated cheater **C** appears in one of **R**'s clusters. The net effect is tolerance for brief flares of **R** with **P** otherwise prevalent, as witnessed by a complete population shift from initial all **R** to all **P** in 56,000 years ({200, .2, **v**}, Table 3). High (.8) forager death depresses flares of high **R** by creating flares of **C**. If these latter are not eliminated by quitter **Q** mutants (see above), suicidal **P** may encounter its most virulent rival (**C**) at rather high frequency. Repeated trials might then engender loss of both **P,R** coordinators; such is the case (Table 4).

Stochastic stability revealed through repeated trials. Table 4 summarizes 100 initial all suicidal **P**, 100 initial all replacer **R** trials of 500,000 years each under closest variant mutation. At {200, .8, **v**}, initially all **P**, coordinators **P,R** are both lost in 12 cases, ultimately leading in these cases to an all quitter **Q** population. **P**'s demise is again due more to cheater/replacer **C** than to quitter **Q**; either **C** eliminates **P** and is then eliminated in turn by **Q**, or **P**, while eliminating **C**, is at such low frequency as to succumb stochastically to quitter **Q**. At .8 forager death **P** is never eliminated unless **R** is as well. By contrast, under moderate (.5) to low (.2) forager death **P** can be lost yet *always* recovers, reemerging via **R** → **P** mutation, usually again with over 90% of the population at terminal year 500,000 (Table 4).

Evolutionary stability as a measure across a metapopulation. Paradoxically, under closest variant mutation, suicidal **P**'s statistical *long term* persistence is enhanced by allowing its short term loss through drift to **R** (at lower forager deaths; Table 4 and immediately above). High (.8) forager death biases the population toward higher **P** frequency states, but at the cost of its stochastic catastrophic loss (Table 4); as **R** is then lost as well, the population remains in an all shirker state, here as all **Q**. Once **R** and **P** are both lost, they cannot be recovered, as we preclude coordinator mutation from cheaters. Replacing **R** incubates coordination shirking **C** at a high rate under .8 forager mortality, dying as it forages, creating stochastically dangerous cheater **C** clusters which **P** must later encounter. At lower forager deaths both the rate of **R**'s decline and the size of later (**P** encountered) **C** clusters is lower. These allow greater play for **P, R** mutual drift, leading sometimes to **P**'s loss to **R**; here **P** loses to **R** through neutral drift, *not* because of any phenotypic advantage to **R**. Admissible **R** → **P** closest variant mutation, however, then recovers **P** under the very long 500,000 year time frame; and, as generally **P** outperforms **R** under closest variant mutation, **P** eventually predominates again (Table 4).

Admittedly, this effect is sensitive to mutation rates. Lower rates would create 500,000 year runs where **P** is lost "permanently" at low/moderate forager death. Note, though, that our "mutation" might also include migration; an immigration rate of .001 for **P** (artificially disallowing **P** migration into cheater clusters) would recover the paradoxical "metapopulation" result: to avoid losing **P** in the long term, lose it in the short term, allowing recovery through mutation from **R** or migration before quitter **Q** saturates. This is a result not of populations, but a metapopulation--that is, the same process repeated in multiple, distinct populations--with "stability" a probabilistic measure across the repetitions. Under *A. versicolor* social (brood raiding, forager risk game) and population (viscosity, adult colony [tree] distribution) structure, *persistence*, measured as the probability of encountering a focal morph after a prolonged period, may not be adequately captured solely by an immediate fitness advantage, partly because variable mixes of strategies alter stochastic vulnerability of a focal morph in long horizons. One must then shift measured stability to persistence across many populations of long simulations; persistence, or evolutionary stability, becomes a measure on a metapopulation--what will happen in a long running population most, or much, of the time.

Stability and initial conditions. Since **R** both uniquely creates the sophisticated cheater/replacer **C** under closest variant mutation and incubates it through self preserving replacement once present, beginning trials with an all **R** population might enhance the loss of both coordinators, producing populations vulnerable to stochastic, high fluctuations of cheater/shirkers. Such is the case. When the population begins all **R**, coordination is lost, leaving an all quitter **Q** population, in 43 trials at {200, .8, **v**}; *coordination loss is enhanced by a factor of 3.5 (43 vs 12 losses) simply by beginning a trial with all replacer* ***R*** *rather than all* ***P*** *when mutation is restricted to close variants (Table 4).* Unlike suicidal **P** in initial all **P** runs, replacing

R is always lost in initial all **R** trials (Tables 3,4); and, as in the case of initial all **P** trials, in populations where coordination has not been lost to quitter **Q**, **P** predominates at terminal year 500,000 (Table 4). Under viscosity, self preserving replacer **R** *nowhere* exhibits superiority to suicidal punishment when both can occur.

Stability under random assortment with closest variant mutants

We have focused on *Acromyrmex versicolor* like viscosity, as such dispersal augments the evolutionary long term costs of self preserving replacement, associating the descendants of cheaters with the descendants of replacers (Pollock et al., 2004). We expect coordination (either as **R** or **P**) to fare worse under random assortment, and so it does. Somewhat surprisingly, however, the process we have identified under viscosity operates under random assortment as well, providing a reduced range of stability for (mostly) suicidal **P**. Table 5 summarizes 100 (closest variant mutation) trials of initial all **P** populations under random assortment with strong (200 replacement fitness) brood raiding. **P** is lost in 86 trials each under both low (.2) and moderate (.5) forager death, yet regained in each instance; in 80% of these cases, **P** is at least 90% of the population at the 500,000 year terminus. Apart from greater fluctuations in morph frequencies overall, the major difference between these results and those under viscosity (Table 4) lies in the 3 to 6 fold increase in loss *and recovery* of suicidal **P** under random assortment.

At high (.8) forager mortality, however, coordination is lost in 93 of 100 trials, compared to only 12 under viscosity (Tables 4,5). Here the incubation of cheaters under high forager mortality is no longer partially curtailed through viscosity. As under viscosity, high cheater frequency is initially usually as cheater/replacer **C**. But under random assortment the offspring of a successful **C** exploit **P** and **R** identically. Suicidal **P** experiences the same encounter rate as replacer **R**; nor is **P** able to localize its competition with **C** at a cluster boundary (contra Figure 4). In consequence, recurring shocks of high frequency **C** lead ultimately to the catastrophic loss of coordination (both **R** and **P**).

In the few cases where coordination survives under random assortment at .8 forager mortality, it survives as suicidal **P**. In 6 of 7 cases where coordination lasts for 500,000 years, **P** is never lost. In the remaining case it is regained through **R** → **P** mutation, recovering to +98% of the population at terminal 500,000 (Table 5). Under closest variant mutation, high frequency **P** population states produce mostly quitter **Q** as mutant cheaters. These are more readily eliminated than cheater/replacer **C** (e.g., **QQP** groups are inferior to **CCP** groups, as the latter enjoy intermediate, replacement forager colony fitness through a replacing **C**) allowing the population to hover longer at high **P** frequency, once there, relative to a population at high **R** frequency, which will produce mostly **C** mutants (see *Wins against selection* in Pollock et al., 2004). In consequence, trial trajectories bifurcate: a few retaining long periods of high **P** frequency, with **P** at least 50% of the population over 99% of the time (Table 5), while most slide into the long term average basin of quitter **Q** through **P** ⇒ **R** drift, then rapid **R** ⇒ **C** ⇒ **Q** transitions.

The weak range of evolutionary persistent coordination under random assortment revealed in Table 5 cannot be said to be a stable polymorphism in coordinators and cheaters. Generally, self preserving replacer **R** is repeatedly supplanted by suicidal **P**, **R** later again flaring to high frequency; **P**, usually if not invariably lost mid sequence, is regained as **R** → **P** mutation, drifting upward via pure coordinator groups (e.g., **RRP, PRP**, etc.). While replacement foraging (as either **R,C**) is always personally advantageous in our parameter space, the consequences of replacement are often lost in vacant tree arenas containing a coordinated colony; the latter, most likely placed as the adult colony under strong brood raiding, mute the contested forager game(s). Neutral **P,R** drift is consequently amplified. When coupled with closest variant mutation which focuses virulent cheater/replacer **C** in high frequency **R** populations (above), projected infinite population polymorphism in cheaters and coordinators is usually unrealized, as witnessed by the periodic recovery and preponderance of suicidal **P**. Unexpectedly, what drives **P**'s stability/ preponderance under viscosity provides a weaker form of stability under random assortment.

Conclusion

Strategic randomization and unavoidable failure

As correlated strategies, both latent suicidal **P** and replacing **R** focus foraging risk onto a single cofoundress. The surface excavator/forager coordination mechanism allocates risk without contention, employing above ground experience to enhance colony efficiency. The experienced surface excavator forages for leaves more efficiently, enhancing growth of the fungus garden, in turn enhancing the future cohort of brood raiding workers (Pollock and Rissing 1995; Rissing et al. 1996; Pollock et al., 2004). Her experience lessens her personal predation risk, which again enhances garden growth, and may reduce outside exposure to fly parasites (e.g., Feener and Moss 1990) and microbial pathogens (e.g., Hughes and Boomsma 2004). Her lesser risk should also preserve her contribution to brood production, also enhancing the brood raiding force.

Group efficiency, however, does not ensure evolutionary stability. One might expect the surface excavator to avoid her future assignment (depending on the colony efficiency/foraging risk trade off) if another cofoundress, worrying for self, will assume the risk. Self preservation as replacement would then become free floating, a "hot potato" tossed among cofoundresses, until one "decides" to forage, as in a war of attrition (Bishop and Cannings 1978; Maynard Smith 1982). Such competition in replacement waiting times would create starting colonies of inferior brood raiding ability when cofoundresses with extended waiting times chance to associate; these would be more likely eliminated in inter-colony brood raiding, exactly as is a cheater/shirker exposed to suicidal punishers under coordination. Both latent suicide and individual competition in replacement times lead to unavoidable personal (through group) failure, albeit along different strategy paths. "Self preservation" can be a misleading label in the individual case, often rather being personally disastrous as experienced. Commitment to an extended replacement waiting time can be as *situationally* personally detrimental as is *expressed* suicidal punishment.

Personally disastrous outcomes will occur even in the restricted strategy space of replacer **R** and quitter **Q**. Under random assortment this space can yield a polymorphism (at {900, .5, **r**}; Pollock et al., 2004), insuring the continual creation of **QQQ** groups, generally doomed to competitive failure. Stepping back, we can view this polymorphism in pure strategies **R**,**Q** as a mixed strategy playing **R,Q** in appropriate probability (Maynard Smith 1982; Myerson 1991). This mixed strategy is *subgame perfect sensu* Selten (1975), playing a best response to any mutant strategy deviating from the equilibrium mix of probabilities (Selten 1975; Myerson 1991).

This best response is *strategic* rather than *personally experienced* (Aumann and Maschler 1972; Pollock 1994a). The *average* outcome of the strategy remains best when encountering a deviant strategy; one cannot say that the strategy always generates personally best outcomes (here, cofoundress group environments) since, even in equilibrium, abysmal **QQQ** groups are guaranteed.

This is also true of suicidal **P** when encountering rare, shirking **Q**. When predominate, **P** does *on average* quite well, almost always enjoying maximal colony fitness through forager coordination. When exposed to a cheating **Q**, however, it does as poorly as the subgame perfect mixed strategy in **R**,**Q** when yielding, as outcome, **QQQ**. In both cases *personal failure* is an unavoidable random outcome in strategy play, as encounter of a rare **Q** mutation in the former, as regularly recurring event under randomized play in the latter. Subgame perfect randomization involves a commitment as complete, and as potentially disastrous, as does suicidal punishment (Aumann and Maschler 1972; Pollock 1994a). Suppose two individuals have randomized to play (nonforaging) **Q** as outcome. The last cofoundress should then refuse to play **Q** even if her randomization mechanism allocates **Q** as outcome; her *personally best response* is to play replacing **R**. She faces the same quandary as **P** faced with a surface excavator determined to refuse foraging assignment under coordination. Here *subgame perfection requires the same degree of personal sacrifice as does suicidal **P***. Subgame perfection hides this sacrifice by defining best response as average success at the strategic level, even though actual individuals may experience only one outcome of a randomized strategy, as among *Acromyrmex versicolor* cofoundresses (cf Pollock 1994a).

Suicidal **P** and our mixed strategy example differ only in their randomization mechanisms. Standard mixed strategies randomize independently per phenotype. Correlated strategies like **P** allocate roles randomly but exhaustively; while the first role is truly random, future assignments are sequentially contingent on prior allocation. Consequently, correlated strategies produce group efficient outcomes at greater frequency than mixed strategies, allowing the former to often invade, sometimes supplant, the latter (Pollock 1995a). Mixed strategies *seem* autonomous, as randomization occurs independently (Aumann and Maschler 1972; Pollock 1994a), but as the **QQQ** outcome in randomized **R,Q** play shows, independent randomization is as binding as suicide. The *A. versicolor* experiment revealing suicidal punishment (Rissing et al., 1996) was motivated by the prior laboratory discovery of the surface excavator/forager coordination mechanism (Rissing et al., 1989). We conducted the experiment precisely because we thought the revealed coordination mechanism intuitively implausible. We thought “best response” meant *personally* best response, which would forbid suicide. Even in game theory absent correlated strategies, however, strategic best response need not imply personal best response (Aumann and Maschler 1972).

Our confusion lay in a false semantic identity between individual and strategy (or, in evolutionary thought, genotype), one long recognized by G. C. Williams (1992:43):

> The term *individual* in abstract discussions of population genetics usually refers to a genotype, produced by a sampling of genomes from a gene pool... In other contexts it means a physiologically independent material entity, an interactor developed from genotypic instructions. For many of the organisms of greatest interest, genotypic and physical individuality coincide. [emphasis in original]

Actually, this identity is never present when randomization is employed. An uncorrelated randomized strategy always devolves relative disaster on some. Luce and Raiffa (1957:76) stressed the point at the foundation of game theory. Consider a general who must allocate fighting tactics to pilots in a squadron. Some will be "on point," most vulnerable to attack, others placed in supportive, safer roles:

> Compare the role of [the general] who selects pilots ... with the pilots themselves. The conflict in point of view becomes apparent if we suppose an unhappy pilot [allocated on point] with whom the [general] is friendly. From the strategic point of view the [allocation] is profitable. From the individual point of view it does not seem so.

The general is the strategy or genotype; his pilots realized play of the strategy. Forcing him to empathize with each allocation, or phenotypic realization, creates strategic disaster. Only by sacrificing some (here, empathized) instances of itself can the abstract genotype/strategy do well. Independent randomization creates personal self sacrifice in the same way suicidal punishment in *A. versicolor* does; indeed, *more* such sacrifice will occur under randomization than under suicidal punishment because suicide removes the offending (instanced) cheater genotype from future generations.

When fitnesses are socially mediated, mandating personally best responses invites exploitation. Within the group, personally best responses, maximizing *situational fitness sensu* Myles (1988; cf West Eberhard 1981) seem unavoidable as selection

> identif[ies] situations and then consider[s] the fitness improvements possible by responses involving facultative switches. The term "situation" is used here ... to refer to intermittently recurring contingencies that may strongly affect the fitness

> outlook of individuals but to which not all individuals are subjected ... situational adaptations ... expand the genome's overall phenotypic capability and may not have to be selected at the expense of present adaptational capabilities. [Myles 1988:413]

But social situations may be forced, as coordination shirking **Q,C** do to replacing **R**. **Q/C**'s success lies in forcing **R**'s personally best response. The logic of maximizing situational fitness can fail when situations are themselves created as a strategic response (cf Hand 1986; Pollock and Rissing 1988; Lewis 2002). Suicidal **P** denies this situational power to shirkers by sacrificing itself. Thus while **R** survives for only some 4,500 years at {200, .8, **v**} in the strategy space **R,C,Q** (Table 2), **P** endures for 455,000 years before succumbing in the parallel space **P,C,Q** (Table 2). Most telling, when **R** endures unique mutation to the cheater/replacer **C** as its closest variant mutant, the space **P,R,C,Q** yields predominate suicidal **P** under the same parameter set (Table 3). Suicidal **P** predominates over replacing **R** by refusing shirkers de facto control over the production of social environments.

Self preservation as epiphenomenon

Even when a pure strategy plays a personally best response when exposed to exploitation, its evolutionary stability may actually be unrelated to the *personal* success thereby enjoyed. Consider the following example under the iterated Prisoners' Dilemma (from Pollock 1988). Suppose a space restricted to two haploid pure strategies, **ALL D**, which always defects in game play, and **MASSIVE RETALIATION (MR)**, which begins iterated play by cooperating, continuing so unless defected upon, thereafter unilaterally defecting in (unending) punishment (Axelrod 1980). Under appropriate parameters (Pollock 1988), **MR** resists invasion by **ALL D**.

That is, designating V(**X**|**Y**) as the payoff strategy **X** receives against strategy **Y**, V(**MR**|**MR**) > V(**ALL D**|**MR**); **MR**, predominate in the (large) population, experiences mostly play against itself, while rare mutant **ALL D** perforce encounters **MR**. Rare **ALL D**, performing worse than the population average, is eliminated. Now the Prisoners' Dilemma yields V (**ALL D**|**MR**) > V (**MR**|**ALL D**); **ALL D** exploits an **MR** partner, always doing relatively better than that partner. This leads to the curious result that if rare **ALL D** is eliminated, *so too is the **MR** it happens to exploit*. If the exploited **MR** did not punish its **ALL D** exploiter (i.e., if **MR** continued to cooperate), invading **ALL D** would be viable. Yet this punishment *as instanced*, so necessary for the *strategy* **MR**'s stability, does not save the exploited **MR** from elimination; colored by his vulnerability, he vanishes with his exploiter (Pollock 1988).

MR's punishment of **ALL D** sustains unexploited **MR**'s within the population. Similarly, instanced **P**'s suicide when exposed to a cheater is personally disastrous, although the strategy **P** thereby predominates, overall, in the population. In both cases the punisher is removed with his exploiter. It so happens that punishment is *apparently* self preserving in our Prisoners' Dilemma example, as a punishing **MR** limits its loss. Yet the role of punishment in the two cases is identical: to depress the fitness of the exploiter (shirker in the foraging game), removing it from the population (Pollock 1988; Boyd and Richerson 1992; Pollock and Rissing 1995; Boyd et al. 2003). Playing a personally best response (or being subgame perfect; Selten 1975) happens to be the mechanism for effective punishment in our restricted strategy space Prisoners' Dilemma example. But focusing on self preservation as the underlying mechanism would suggest replacer **R** is (at least) relatively more stable in the forager game, which is not the case (e.g., Tables 3, 4, 5). The actual mechanism underlying punishment, depressing the fitness of groups containing exploiters, thereby enhancing the relative standing of groups in cooperative harmony (Wilson 1983, 1990; Pollock 1988; Wilson and Dugatkin 1997), is identical in the two cases. **MR**'s self preserving action is an epiphenomenon, unrelated, in isolate, to its evolutionary stability.

One can choose a strategy space for the Prisoners' Dilemma where something akin to a personally best response will predominate in its own right, apart from potential punishment (Boyd and Lorberbaum 1987; Farrell and Ware 1989; Sugden 2005). Admissible strategies define the actual mechanisms underlying elimination and survival. These mechanisms may be captured by labels such as "self preserving," "subgame perfect," or "making the best of a bad lot" in one strategy space; in another, not. We would avoid privileging such categories as general rationale underlying evolutionary stability or the resolution of social conflict, focusing rather on game particulars revealing actual selection mechanisms (cf Binmore et al. 1995; Binmore 2010).

Isolation by distance

Lehmann et al. (2008) present a population structure for altruism somewhat similar to that of *A. versicolor* simulated here: a circular discrete lattice, where offspring disperse varying viscous degrees from a focal location. In Lehmann et al. (2008) each location or lattice node consists of a very large number of individuals divided into two types, a sterile aiding worker and standard reproductives. These two types are produced in various ratios by parents who, of course, are standard reproductives. Sterile workers aid all at their location, die, the reproductives then producing their programmed ratio of both types, then dying; the offspring produced stay or disperse viscously. In *A. versicolor,* offspring (cofoundresses) disperse in restricted viscosity, subdivided at each location into starting colonies. **P**, when effectively suicidal, is something of a sterile worker: she sacrifices herself and her colony, thereby aiding those in other, proximate starting nests in coming brood raids, there being one less colony to contend with. She is *strongly altruistic* (*sensu* Wilson 1979; Pollock et al. 2004), reducing her absolute fitness in aid of others at her tree location, but not in her nest. Yet our simulations suggest this altruism is *not* a straightforward consequence of inclusive fitness via viscosity.

Simply, **P** can endure at high frequency even under random assortment (Table 5) while Lehmann et al. (2008)'s sterile worker would fail in such circumstance. In 14 of 100 runs each **P** persists without loss/mutation recovery for 500,000 years in both {200, .2, **r**} and {200, .5, **r**}; while **R** briefly flares to high frequency, populations are predominately **P** (Table 5). In the 86 runs of both parameter sets where **P** is lost, **R** → **P** mutation recovers **P** about 80% of the time, **P** then once again is dominate in the population. The 14 cases of persistent **P** in both parameter sets in itself denies inclusive fitness via viscosity essential for **P**'s retention. As detailed in Results, these populations cycle as **P** ⇒ **R** drift, then rapid **R** ⇒ **C** ⇒ **Q** transitions, sometimes leading back to high frequency of **P**. The same cycle occurs under viscosity, with **R** clusters producing the cycle **R** ⇒ **C** ⇒ **Q**, clustered **Q** then encountering clustered **P**, yielding repeated local cycles **P** ⇒ **R** ⇒ **C** ⇒ **Q** ⇒ **P**. But **P** may fail recovery, yielding an all **Q** population under viscosity (Tables 3, 4). Viscosity tightens the cycle with two effects: **P** retains overall higher frequency than under random assortment, but at risk of catastrophic loss when **Q** clusters become too large through happenstance. Evolutionary stability (given our prohibition of back mutation from cheaters to coordinators) bifurcates into populations mostly of **P**, sometimes of all **Q**. No point measure of the population would capture this.

Lehmann et al. (2008) consider an altruistic trait absent a contingent move game; their sterile worker is sterile always, aiding those at her lattice node. Thus their evolutionary stability analysis produces a paradox: spatial, locally homogeneous clustering of types, seemingly a primary intuitive consequence of viscosity (e.g., J. B. Wilson 1987; Pollock 1989a,b; Wilson et al. 1992), is lost through their population point measure of stability. So they show their circular lattice model is identical in evolutionary outcome to an infinite island model which preserves offspring assortment while dispersing globally--offspring have a certain probability of staying together as they travel throughout the population (Lehmann et al. 2008). In this infinite island model, strategy type clustering as exhibited in our *A. versicolor* population simulations *cannot* occur and is absent in their circular lattice viscosity model as well, lattice viscosity just another way to have offspring stay together as they move. A viscosity coefficient of offspring (kin) assortment will not create an insular cluster were some of a morph encounter only their clones, irrespective of the morph's population wide frequency. Focusing on the offspring association common to both Lehmann et al. (2008)'s isolation by distance model (a circular lattice) and their infinite island model, the cycles of clustered strategy types often retaining coordination in the *A. versicolor* foraging game cannot be conjectured or discerned. The local clusters revealed by our simulations represent true isolation by distance; Lehmann et al's (2008) viscosity coefficient, allowing any type to retain identical minimal association with itself, does not. Viscosity may induce *cycles* of local strategy preponderance essential to the long term persistence of a focal strategy (Pollock 1989a, 1995b). The effect of viscosity is not restricted to point stability measures of inclusive fitness theory or uniform probabilities of offspring encounter.

Self-sacrificial behavior such as observed suicidal **P** may falsely motivate appeal to kin selection or inclusive fitness (cf Pollock and Cabrales 2008). As with **MR** in the Prisoner's Dilemma (above), we may be tempted to allow a label (here, "altruism") to assign explanation. Our simulations of *A. versicolor* suicidal punishment suggest that snap shots of behavior, removed from the game and population structure evoking them, can lead us astray.

Appendix: Principle propositions from simulations

The forager game has potentially two stages. If the surface excavator accepts forager assignment (accepts the coordination mechanism), the game ends at stage 1. If she refuses, her cofoundresses choose to replacer her, or not (stage 2). Forager risk is measured as probability of death while foraging. Colony efficiencies through foraging are realized via competitive brood raiding (group selection)

Coordination may be associated with latent replacement upon exposure to a shirker [**R**], or not [**P**]. Shirking assignment (refusing coordination) may be associated with latent replacement upon exposure to another shirker [**C**], or not [**Q**]. **Q** never forages; **C** will not forage if the surface excavator does but will forage if she is not the surface excavator and that surface excavator refuses. Further details in text; cf Figure 1 and Table 1.

The following propositions are contingent on parameters such as forager mortality, brood raiding, and viscosity. They are not universal, but apply in some parts of the parameter space:

1. Replacement, while self preserving, incubates shirkers for future generations. A shirker always does better than her replacing cofoundress. As forager death increases, so does shirker incubation (for the forager, with the replacing genotype, is less likely to reproduce). Replacement may evolutionarily fail even when a personally best response because of its beneficent effect on shirkers.

2. Punishers never aid shirkers, even if their refusal is effectively suicidal. Punishment removes the offspring of shirkers from future generations. Thus keeping the frequency of shirking low, latent punishment can do quite well.

3. Game play failing coordination reduces colony fitness. Under strong brood raiding, colonies in internal contention are less likely to win placement as an adult colony. Punishment augments this effect, curtailing phenotypic shirking from reproducing. Because coordinated colonies have maximal fitness, **R** and **P** drift between each other being phenotypically neutral in such colonies.

4. Under viscosity, the offspring of shirkers associate with themselves, reducing the fitness of such genotypes. Shirkers capable of replacing another shirker [**C**] can do better than

shirkers who never replace [**Q**], but this reverses as forager mortality increases.

5. Replacing shirkers can be invaded by non-replacing shirkers. These latter may come to predominate; but they are also most vulnerable to punishment.

6. Replacement with coordination [**R**] can be stable against shirking, but only if punishers are excluded. When both **R** and **P** are allowed, **P** predominates, or both are lost.

7. In the full strategy space [**P, R, C, Q**], self preservation (replacing a shirker) must be coupled with shirking [as strategy **C**] to have any chance of surviving.

8. Under viscosity, with both coordinators **R, P** possible, local population cycles of **P ⇒ R ⇒ C ⇒ Q ⇒ P** can emerge where replacement drifts to high frequency locally, then incubates shirkers when they appear until replacement is destroyed. Punishers then push back shirkers until only punishers remain (Figure 4). Replacement may recur through mutation and drift, beginning the cycle again.

9. In finite populations under viscosity, stability is stochastic. While the cycle **P ⇒ R ⇒ C ⇒ Q ⇒ P** usually prevails, shirkers may become so predominate that they stochastically eliminate coordinators completely. Stability is a probabilistic measure.

10. Being probabilistic, stability is a property of metapopulations, not populations. A

population may be stable for 100,000s years, then shift rather quickly. The longer one waits, the more likely a population will shift. Punishment elongates shifting times.

11. Measures of stability may outstrip ecological time. The Sonoran Desert hospitable to *A. versicolor* is thought to be around 10,000 years old (Axelrod 1979). But loss of punishment in our simulations can take an order of magnitude longer. Restricting simulations to ecological time, we would not encounter punishment's limits. Replacement, however, is readily lost during ecological time, as simulated.

12. Significant portions of a viscous population may be in transition state during the lifetime of an ecologist/sociobiologist. Snapshots of nature, even in the social environment of a cofoundress colony, may appear, as sampled, stable, when they are not.

13. Strategies do not encounter all possible mutants at identical rates. When prevalent, a strategy is most likely to encounter a mutant derived from itself. The mechanism of a strategy, by shaping what mutants derived from it may be, helps shape the strategy's evolutionary stability. Under viscosity, most mutants encountered will be so derived. Some strategies can readily mutate to their worst enemy, while other strategies mutate to a less virulent enemy. In the *A. versicolor* foraging game, punishment mutates to a weaker enemy than does replacement.

14. Even under random assortment, a predominate strategy will mostly encounter mutants derived from itself. Some predominate strategies will create less virulent mutants, so retain

population wide predominance longer, than other strategies. So punishment retains predominance longer than replacement, under random assortment or viscosity, with a low frequency of stability even under random assortment.

15. Standard randomized strategies produce some outcomes disastrous when experienced. Such outcomes are no different than realized suicidal punishment. Randomized strategies appear individually "free," but this is not so when an unfavorable outcome is realized. Freedom under randomization is an illusion. Correlated strategies simply shift the focus of coercion under randomization. We hide failure in the average fitness of a randomized strategy. Suicidal punishment under a correlated strategy highlights failure, but the correlated strategy is evolutionarily successful because it does well under coordination, not simply because it punishes.

16. Group selection for efficiency can favor correlated strategy randomization over standard individualistic randomization. Randomization is a property of strategies, not individuals. Punishment in the forager game is one way randomization can be policed. Indeed, under individual randomization one generally assumes one *cannot* escape random outcome, so policing is unnecessary. Suicidal punishment is simply an aspect of randomization under the surface excavator forager coordination mechanism; group selection through brood raiding is the other, essential, component.

17. By construction, a standard randomized strategy *requires* the regular production of inferior outcomes. A correlated strategy reveals inferior outcomes only under game, or mutant,

deviation. A standard randomized strategy produces inferior outcomes at significant frequency every generation. In terms of worlds actually experienced, standard randomized strategies are less pleasant than correlated strategies.

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Table 1

Admissible strategies by two-stage game properties

Strategy	Accepts original foraging assignment?	Replaces a shirker of foraging assignment?
Punisher, **P**	Yes	No
Quitter, **Q**	No	No
Replacer, **R**	Yes	Yes
Sophisticated Cheater/Replacer, **C**	No	Yes

Table 2

Sample R and P stability runs, cheater mutants only. One run of 500,000 years per parameter set; *viscous dispersal*

Strategy Saturated Initially	Mutation Regime	Forager Death Rate	Replacement group fitness[1]	
			200	900
All R	Q	.2	not necessary[2]	$f_R \geq .7$; $f_R \geq .9$ (99.14%)
		.8	$f_Q = 1$ around year 4,200	not necessary
	Q,C	.2	$f_R \geq .8$; $f_R \geq .9$ (99.9%) $f_C < .2$; $f_Q < .1$	$f_C = 1$ around year 7,500 $f_Q < .2$; $f_Q \geq .1$ (.036%)
		.8	$f_Q = 1$ around year 4,500	not necessary
All P	Q	.2	not necessary	$f_P \geq .9$
		.8	not necessary	$f_P \geq .5$ $f_P = .9967$ @ year 500,000 $f_Q \geq .4$ (.013%)
	Q,C	.2	$f_P \geq .8$; $f_P \geq .9$ 99.92% $f_Q < .1$ $f_C \geq .1$.(087%)	$f_C = 1$ around year 8,000
		.8	$f_Q = 1$ around year 455,000 before this population cycles locally: **P ⇒ C ⇒ Q ⇒ P**	not necessary

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[1] $f_x > .y$ cc% means the frequency of X is greater than .y (cc%) of the time

[2] not necessary; i.e., other row cell implies current cell is (is not) stable.

Table 3

Sample stability runs for P,R, mutation restricted to closest variants

viscous dispersal

Strategy	Replacement group fitness 200	Replacement group fitness 900
initially all P .2 forager death	$f_P \geq .1$; $f_P \geq .9$ 79.5% $f_P < .5$ 2.36% $f_P = 1$ @ 500,000 $f_R < .9$; $f_R \geq .5$ 2.35% f_Q ,f_C $< .1$	f_C =1 around year 33,000
initially all P .8 forager death	$f_P \geq .4$; $f_P \geq .9$ 84.7% $f_P = .997$ @ 500,000 $f_R < .5$; $f_R \geq .3$ 0.46% $f_Q < .4$, $f_C < .5$ occasional patches of **R** yielding **R** ⇒ **C** ⇒ **Q** ⇒ **P** cycles	$f_Q = 1$ around year 27,000
initially all R .2 forager death	$f_P = 1$ around year 56,000	$f_C = 1$ around year 13,000
initially all R .8 forager death	$f_R = 0$ around year 10,000 $f_P = 1$ around year 42,000	$f_Q = 1$ around year 4,800

Table 4.

P and R stability runs with mutation restricted to closest variants

Based on 100 runs of 500,000 years each with replacement fitness set at 200

Viscous dispersal

Forager Death Rate	Strategy saturated initially	Probability initial strategy is lost at year 500,000	Frequency of initial strategy at year 500,000
0.2	All P	0.28	$f_P > .9$ 20 of 28 runs (71.4%)[1] $f_P < .5$ 3 of 28 runs (10.7%)
	All R	1.00	$f_R > .9$ 0 of 100 runs; $f_R > .5$ 6 of 100 runs (6%) [$f_P > .9$ 70 of 100 runs (70%)]
0.5	All P	0.14	$f_P > .9$ 8 of 14 runs (57.1%) $f_P < .5$ 2 of 14 runs (14.3%)
	All R	1.00	$f_R > .9$ 0 of 100 runs; $f_R > .5$ 3 of 100 runs (3%); [$f_P > .9$ 80 of 100 runs (80%)]
0.8	All P	0.12 ($f_Q = 1$ in all runs)	**P** never recovers when lost
	All R	1.00 ($f_Q = 1$ in 43 of 100 runs)	$f_R \leq .2433$; $f_R < .1$ 96 of 100 runs (96%) [$f_P > .9$ 39 of 57 runs where $f_Q < 1$; $f_P \geq .68$ in other 18 of 57 runs, $f_Q < 1$]

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[1] $f_x > .y$ cc% means the frequency of X is greater than .y (cc%) of the time

Table 5

P stability runs under nearest mutation

100 runs of 500,000 years each

200 replacement fitness, random dispersal

Forager Death Rate	Probability P lost over 500,000 years	f_P @ year 500,000 when P lost mid- sequence	$f_R \geq .9$	Average minimal f_P
.2	.86	$f_P > .9$ 71/86 (82.6%) $f_P < .5$ 9/86 (10.5%)	5.32%	.033; $f_P < .5$ 9.21%
.5	.86	$f_P > .9$ 68/86 (79.1%) $f_P < .5$ 9/86 (10.5%)	3.11%	.032*; $f_P < .5$ 8.44%
.8	.93 ($f_Q = 1$ in all cases)	In 1 case where **P** lost and regained (through mutation from **R**), $f_P = .987$; in 6 other cases with $f_Q < 1$, **P** never lost	In 7 cases** with $f_Q < 1$, 0.102%	In 7 cases** with $f_Q < 1$, .243; $f_P < .5$ 0.595%

*In two runs, $f_P \geq .6, .7$.

**Averages include only those cases where some coordinators exist at year 500,000.

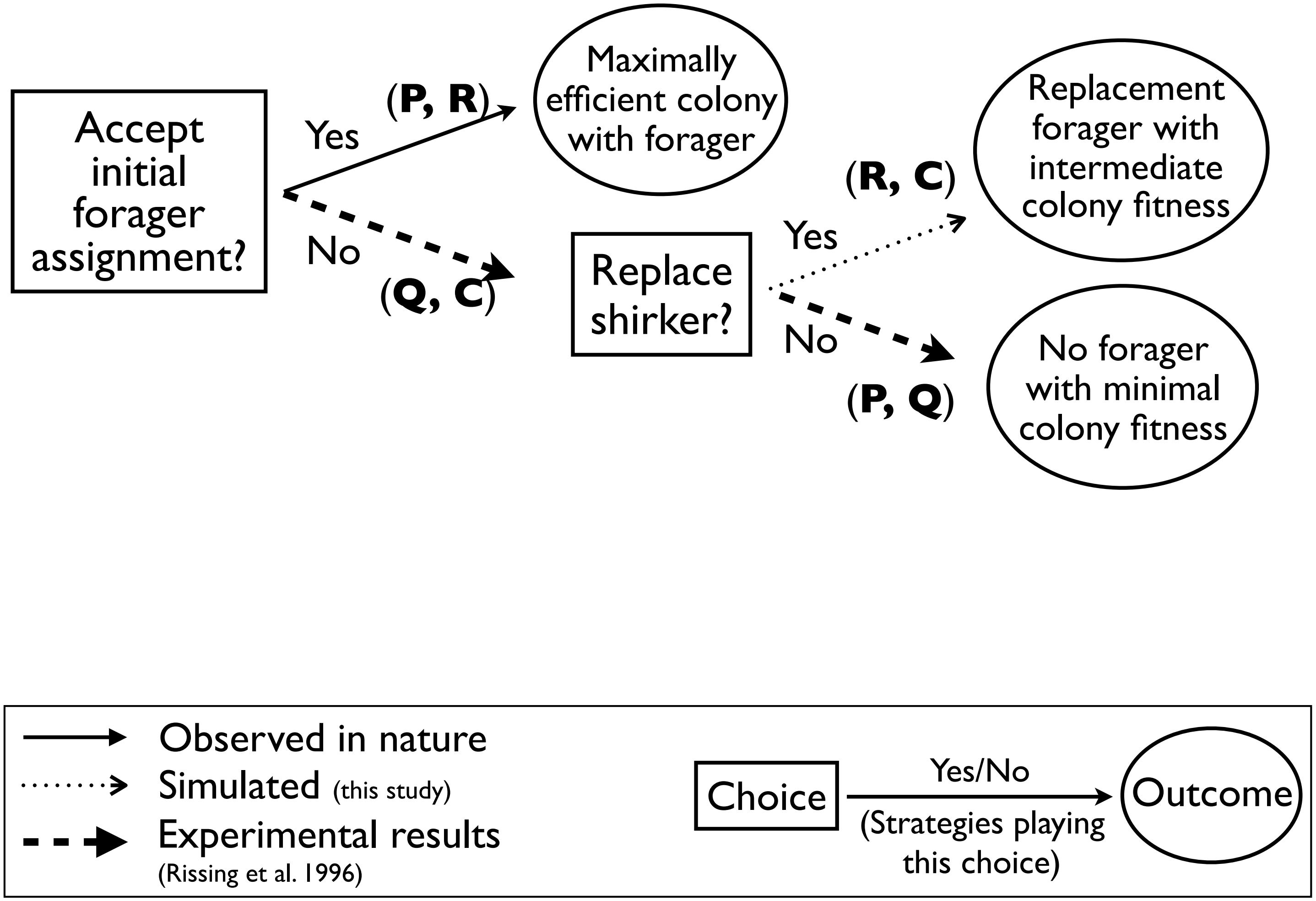


Figure 1. The *Acromymex versicolor* foundress foraging game.

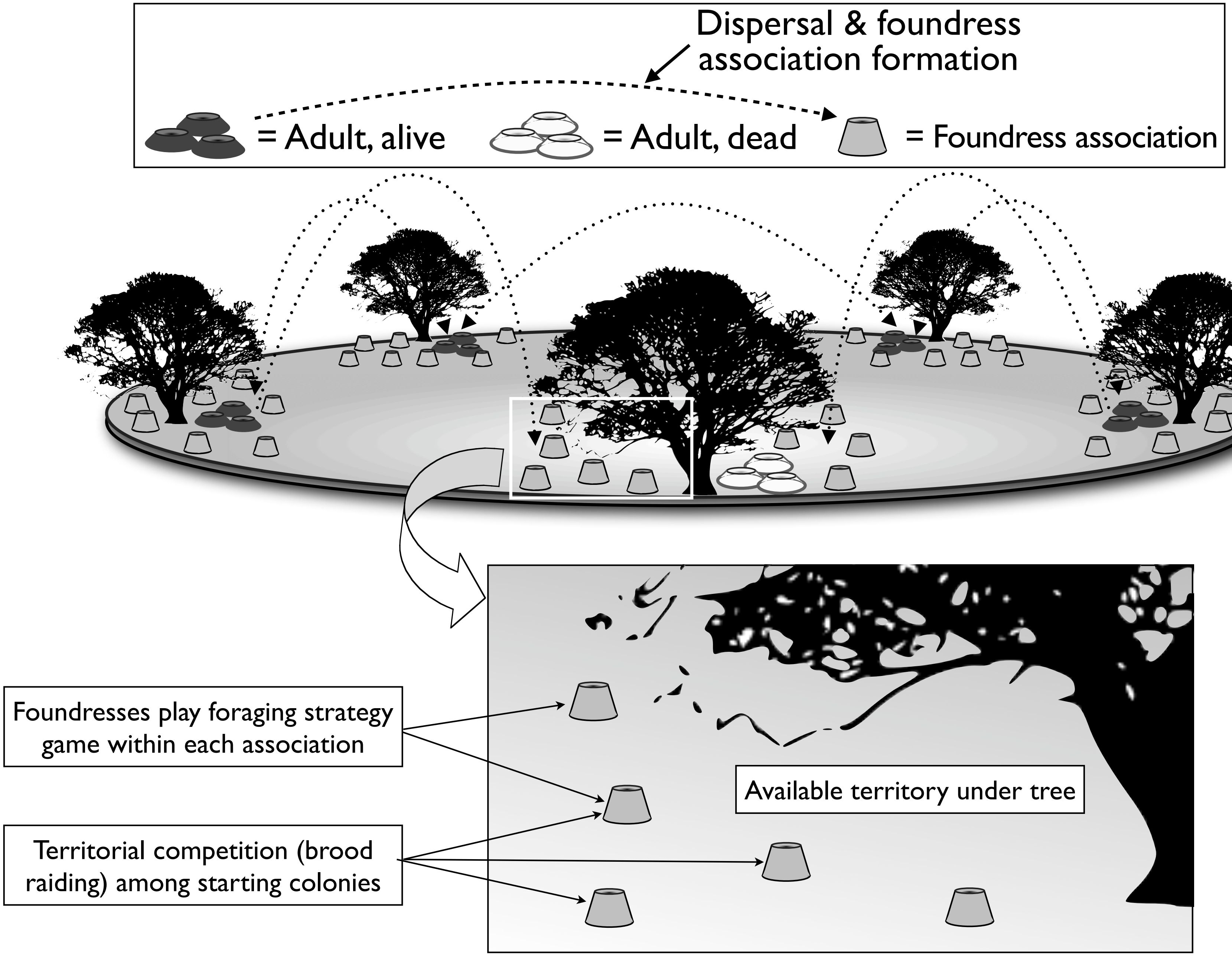


Figure 2. Simulation of viscous dispersal of foundresses in *Acromyrmex versicolor*. Foundresses (haploid asexual) exit their parental colony, alighting only under nearest neighboring trees on the idealized circle. When trees have a resident adult colony, starting nests are ultimately destroyed. When a tree has no living adult colony, starting colonies will ultimately compete via brood raiding for exclusive possession of the tree territory (Figure 3). Under random dispersal (also simulated) foundresses exiting a focal parental colony alight under all trees. In either *A. versicolor* viscosity or simulated random dispersal, foundresses alighting at a tree readily associate with one another irrespective of parental origin.

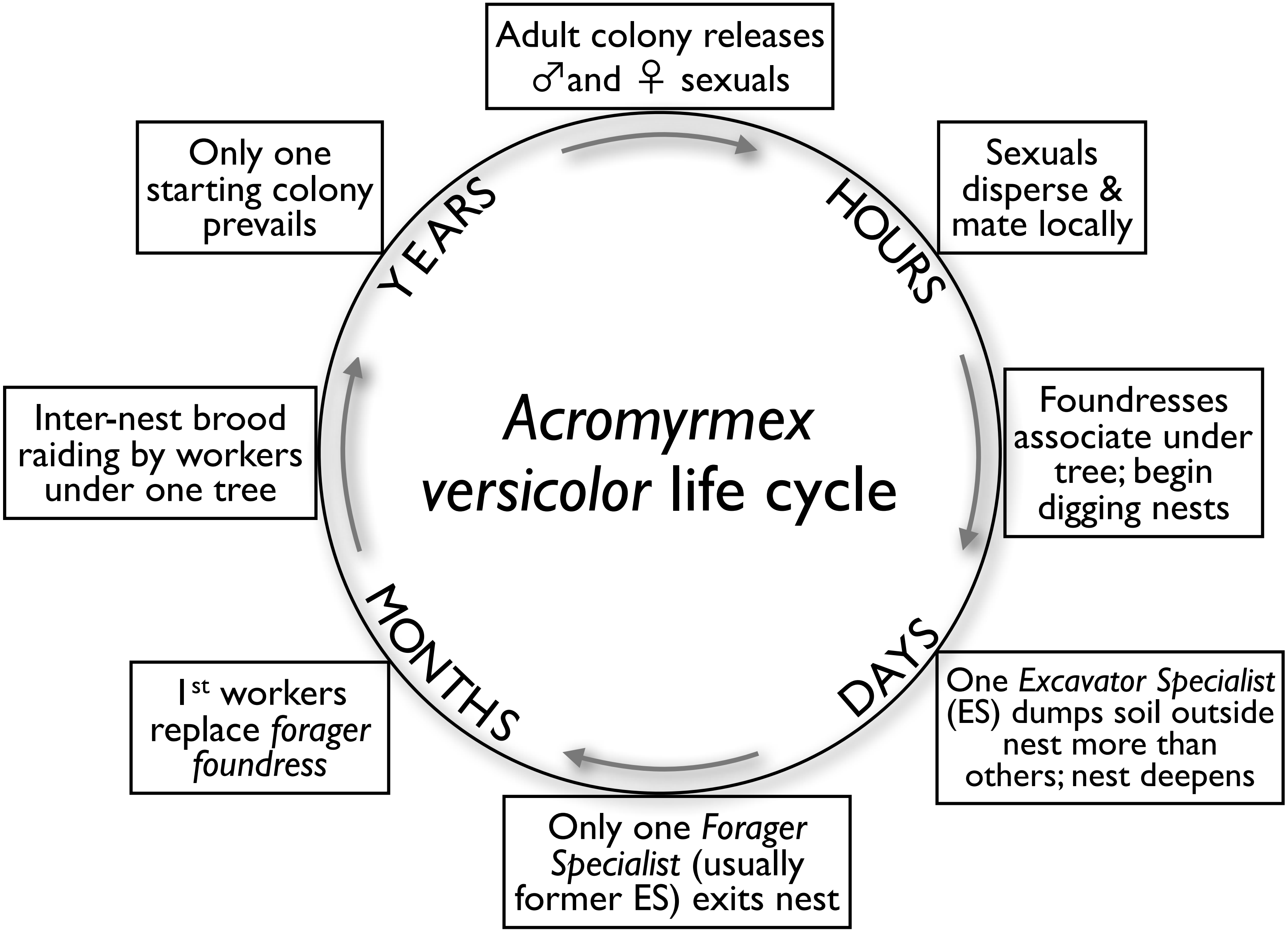
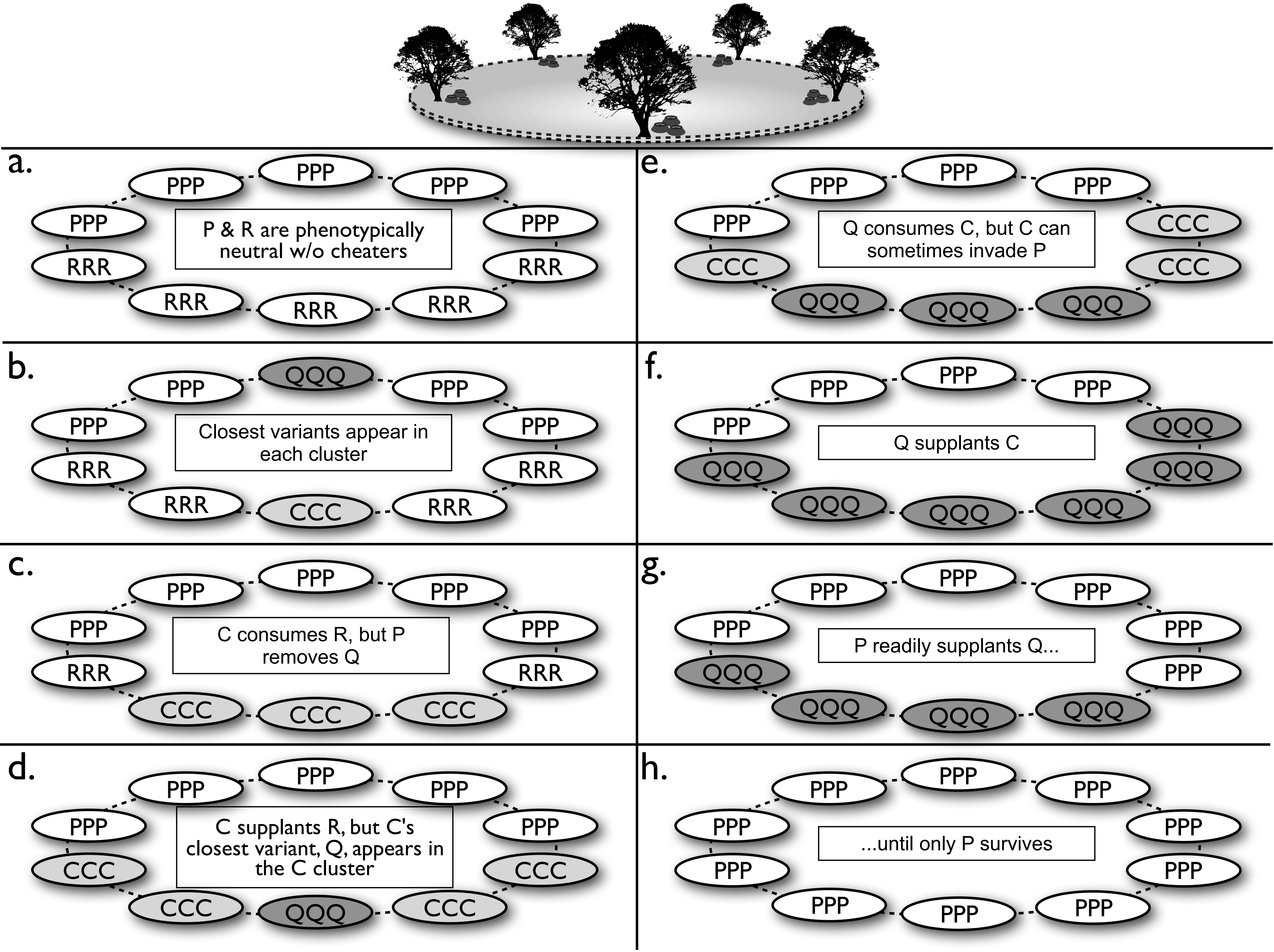


Figure 3. Life cycle of *Acromyrmex versicolor* colonies producing the forager game (Figure 1) and its consequences.

Figure 4. Idealized sequence of adult colony population states under viscosity with closest variant mutation. **P** supplants **R**, mediated by their divergent reaction to cheaters. Adult colonies are shown as clonal in one strategy for clarity; actually, colonies such as **QPP, CRR, CPP, CCP**, etc would appear in a long temporal sequence of transitional population states. At [b, c] punishing **P** eliminates **Q** appearing in a predominately **P** locale; at [b, c] self preserving **R** incubates its closest mutant variant **C**. At [d] **C**, in self preservation, incubates its closest variant mutant **Q** until, at [f], **C** is eliminated. At [g, h] **P** punishes **Q** encountered at its boundary until only **P** remains.

(Figure 4 on next page)


a.
PPP
PPP
PPP
PPP
PPP
P & R are phenotypically neutral w/o cheaters
RRR
RRR
RRR
RRR
RRR
b.
QQQ
PPP
PPP
PPP
PPP
Closest variants appear in each cluster
RRR
RRR
RRR
RRR
CCC
c.
PPP
PPP
PPP
PPP
PPP
C consumes R, but P removes Q
RRR
RRR
CCC
CCC
CCC
d.
PPP
PPP
PPP
PPP
PPP
C supplants R, but C's closest variant, Q, appears in the C cluster
CCC
CCC
CCC
CCC
QQQ
e.
PPP
PPP
PPP
PPP
CCC
Q consumes C, but C can sometimes invade P
CCC
CCC
QQQ
QQQ
QQQ
f.
PPP
PPP
PPP
PPP
QQQ
Q supplants C
QQQ
QQQ
QQQ
QQQ
QQQ
g.
PPP
PPP
PPP
PPP
PPP
P readily supplants Q...
QQQ
PPP
QQQ
QQQ
QQQ
h.
PPP
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PPP
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...until only P survives
PPP
PPP
PPP
PPP
PPP