

The evolution of personally disadvantageous punishment among cofoundresses
of the ant *Acromyrmex versicolor*

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Abstract

Cofoundresses of the desert fungus garden ant *Acromyrmex versicolor* exhibit a forager specialist who subsumes all foraging risk prior to first worker eclosion (Rissing et al. 1989). In an experiment designed to mimic a "cheater" who refuses foraging assignment when her lot, cofoundresses delayed/failed to replace their forager, often leading to demise of their garden (Rissing et al. 1996). The cheater on task assignment is harmed, but so too is the punisher, as all will die without a healthy garden. In this paper we study through simulation the cofoundress interaction with haploid, asexual genotypes which either replace a cheater or not (punishment), under both foundress viscosity (likely for *A. versicolor*) and random assortment. We find replacement superior to punishment only when there is no foraging risk and cheating is not costly to group survival. Generally, punishment is evolutionarily superior, especially as forager risk increases, under both forms of dispersal.

Key Words: Cheater, punishment, evolution.

JEL Classification: Z00, C70

Summary. Cofoundresses of the desert fungus garden ant *Acromyrmex versicolor* exhibit a forager specialist who subsumes all foraging risk prior to first worker eclosion (Rissing et al. 1989); laboratory observation suggests a "coordination" mechanism assigning task-specific risk without contention among (unrelated) cofoundresses (Rissing et al. 1996). In an experiment designed to mimic a "cheater" who refuses foraging assignment when her lot, cofoundresses delayed/failed to replace their forager, often leading to demise of their garden (Rissing et al. 1996). Such behavior is compatible with game-theoretic, personally disadvantageous punishment, where the cheater on task assignment is harmed, but so too is the punisher, as all will die without a healthy garden. Here we simulate cofoundress interaction with haploid, asexual genotypes which either replace a cheater or not (punishment), under both foundress viscosity (likely for *A. versicolor*) and random assortment. We find replacement superior to punishment only when there is no foraging risk and cheating is not costly to group survival. Generally, punishment is evolutionarily superior, especially as forager risk increases, under both forms of dispersal. In many cases coordination may be lost, but only probabilistically over 500,000 years; when so, coordination is usually more stable under viscosity than random assortment. Allowing backmutation from cheaters to coordinators, coordination may recover high frequency after loss.

Evolutionary stability appears as a cycle of population states: coordination is lost to one type of cheater, but this cheater is in turn invaded by another which, in turn, can be re-invaded by the punishing coordinator; mutation is governed by a "heuristic" which defines admissible mutants based on present types (Dawkins 1980). A more detailed summary of results is provided below. Overall, *A. versicolor* natural history suggests conditions supportive of coordination with personally disadvantageous punishment as revealed by simulation, but not uniquely so. Our model of *A. versicolor* enhances the persistence of punishment within cycles of population states of strategies,

but it is not necessary. If, however, stability is seen as a *probablistic measure*, our simulations predict coordination (and punishment) will be most observable under conditions suggested by *A. versicolor*.

Introduction

Cooperation among non-relatives rests on the credible threat to withdraw cooperation in response to similar withdrawal by others. If, by credible threat, one means a response which is personally advantageous under encountered non-cooperation, our thesis is that this transparent statement need not be true, and that it is natural history that tells us so. Rather, evolutionarily viable cooperation can rest on the strategic decision to refrain from a personally best response to the non-cooperation of others. By making the best of a bad lot one can enhance the frequency of such events (bad lots) among strategy clones (those genetically encoded with the same strategy, even if not direct descendants) in the future, leading to the elimination of all cooperative behavior within the population.

Our model is derived from field and laboratory observations of cofounding queens of the obligate fungus-garden ant *Acromyrmex versicolor* (Higgins 1988; Rissing et al., 1989, 1996). Unlike most independently founding ant species, *A. versicolor* queens (or "foundresses") must tend fungus (taken at dispersal from their parental colony) by foraging for leaf substrate prior to the emergence of workers. Foundresses of this species often establish nests together; surprisingly, a single female in such a group subsumes all foraging risk by uniquely performing this task (Rissing et al. 1989). By asking, through laboratory experiment (Rissing et al. 1996) and computer simulation (herein), what happens if this female refuses such unique risk, we reveal an evolutionary dynamic where cooperation is viable precisely because some personally best responses are avoided--viable cooperation requires groupmates that refuse the task of others, even though all would thereby do better.

We begin by reviewing field and laboratory observations of *Acromyrmex*

versicolor cofoundresses. Our computer simulations are closely tailored to these observations, save for restrictions motivated by computational simplicity which we detail. We then examine the game-theoretic structure suggested by natural history, focusing on three forms of cooperation and two forms of "defection" or "cheating on cooperation" (after Williams 1966; Maynard Smith 1964; Axelrod 1981; Dugatkin 1990) where a female refuses to forage (one form of cooperation and defection are actually different phenotypes of the same strategy). One cooperative form employs a personally best response when exposed to a "cheater" (replaces her); another accepts foraging risk when so assigned (detailed shortly), but refuses to replace a female shirking assigned risk. While the former is often thought game-theoretically preferable (after Selten 1975; Farrell and Maskin 1989), the latter is nonetheless "evolutionarily stable" whenever the former is, *but not conversely*. Rather, the morph avoiding some personally best responses is evolutionarily stable under a wider range of conditions, as foraging risk increases or when both cooperative morphs appear within the same population.

We also simulate deviations from *A. versicolor* natural history (random, population-wide foundress assortment; mild inter-colony competition) to explore the range of stable, personally disadvantageous punishment.

Natural history of *Acromyrmex versicolor*

Mating and dispersal

In the Sonoran valley surrounding Phoenix, Arizona, USA, *A. versicolor* sexuals ("alates"; Hölldobler and Wilson 1990) usually fly from their parental nest after heavy rains in late summer (Wheeler 1917; Rissing et al. 1986; Higgins 1988). Alates form small, local mating aggregations (Higgins 1988; Rissing et al. 1986), perhaps the product of 6 to 8 nearby adult colonies; local aggregations sometimes seem to form a "line", somewhat evenly spaced, fading in the distance (Rissing, pers. obs.). Such "mini-swarm" spacing seems a consequence of the relatively regular spacing of adult colonies contributing

sexuals. Adult colonies are territorial, generally located under mature dominant Sonoran trees (e.g., *Olneya tesota*; Gamboa 1974; Rissing et al. 1986), whose leaves they harvest (Gamboa 1975). Limited water forces some distance between large trees; hence adult colonies are similarly spaced and, under low, *viscous* (*sensu* Hamilton 1964) dispersal, so too are mating aggregations. This inference will be crucial for some simulation results.

Immediately after mating female alates (now foundresses) leave the local aggregation in search of a nesting site. They do not seem to go far, often removing their wings near the mating aggregation, surveying their environs by foot (Rissing, pers. obs.). Foundresses prefer to establish nests under the canopy of the same tree species associated with adult colonies; indeed, they prefer the canopy edge of these trees, where branches frequently droop to the ground, permitting easy and relatively safe access to leaves during future colony development. Consequently, starting nests are clumped (Rissing et al. 1986). Foundresses collected from such single-tree clumped natal nests exhibit little electrophoretic genetic variation (Hagen et al. 1988), consistent with field observation suggesting low dispersal.

Since adult colonies are territorial, starting colonies underneath an "occupied" tree are almost certainly eliminated within the first year (cf Hölldobler 1976, 1981; Mabelis 1979; Hölldobler and Carlin 1985; Pollock and Rissing 1989; Pfennig 1995 for examples of the elimination of nearby weaker colonies among territorial ants). Similarly, and crucially for our simulations, clumped starting nests can expect unavoidable inter-colony competition for sole possession of a currently "adult-unoccupied" tree. This expectation shapes subsequent foundress behavior.

Cofoundress interaction during nest foundation--nest excavation
Acromyrmex versicolor foundresses are facultatively "pleometrotic"

(Hölldobler and Wilson 1977, 1990; Rissing and Pollock 1988), establishing nests together cooperatively (Rissing et al. 1986; cf Higgins 1988). As foundresses dig they are often joined by others ("cofoundresses"). There is no evidence that foundresses select one another (contrast Nonacs 1992; Noë and Hammerstein 1994) in the field (Hagen et al. 1988; Higgins 1988; Rissing, pers. obs.) or in the laboratory (Rissing et al. 1986, 1989, 1996; Higgins 1988); nor is there any evidence that some are coerced into joining others (Higgins 1988; Rissing et al. 1986, 1996).

Yet, as nest excavation proceeds, a division of labor emerges which ultimately places one cofoundress under exclusive risk. Once sufficient underground space has been excavated one foundress tends to exclusively remove soil to the surface (Higgins 1988; Rissing et al. 1996), her cofoundresses digging underground. In another desert ant species with a similar population structure of pleometrosis, clumped natal nests, and adult territoriality (cf Pollock and Rissing 1989; Rissing and Pollock 1989), *Messor (Veromessor) pergandei*, cofoundresses in laboratory vertical "ant farm" nests sometimes produce a "fireman line" during soil excavation, with one female digging at nest bottom, depositing her soil in the middle of the nest, another taking this soil then just below the surface, and a last removing it to the surface (Rissing and Pollock 1986). When cofoundresses fail in this task coordination they can be quite inefficient, blocking each other from entry/exit during soil removal, sometimes removing one another as large pieces of dirt! Task coordination among ant workers is common (e.g., Franks et al. 1992; Deneubourg and Franks 1995; Sendova-Franks and Franks 1995), and there seems no reason to deny this simple variant to cofoundresses.

Cursory evidence suggests *A. versicolor* is more adept at producing such an "surface excavator specialist" than *M. pergandei* as, within the laboratory, the former almost always have one while the latter do not

(contrast Rissing and Pollock 1986 with Rissing et al. 1996). The reason may be in their divergent mating ecologies. *Messor pergandei* alates "trickle out" over 6+ weeks (Pollock and Rissing 1985) while *A. versicolor* nests coordinate their production of alates locally over a few days (Higgins 1988; Rissing et al. 1986). Focused predation should consequently be greater in the latter, especially among night rodents and lizards, who dig about the surface in search of foundresses (Rissing, pers. obs.). The *A. versicolor* surface excavator does not, then, subsume unique risk in her task, but simply plays her part in efficiently producing a haven beyond the (olfactory) inspection of predators, where all are likely to die in common. Yet, days after this danger, the surface excavator "voluntarily" assumes a most risky task, exposing herself uniquely to above-ground predation for weeks by foraging for her cofoundresses.

Cofoundress interaction during nest foundation--foraging specialization

In most obligate fungus gardening ant species, foundresses initially rear their fungus on their own body reserves, producing "trophic" eggs consumed by the fungus (e.g., Mintzer and Vinson 1985; Hölldobler and Wilson 1990; Diehl-Fleig and de Araújo 1996) until the first cohort of workers forage for leaves. *Acromyrmex versicolor* foundresses seem unable to avoid foraging for their fungus until prior to worker production. Remarkably, a single foundresses assumes all pre-worker foraging risk (Higgins 1988; Rissing et al. 1989); more remarkably, the task is not competitively allocated (*sensu* West Eberhard 1981; Heinze et al. 1994), but, rather, performed by the prior surface excavator specialist (Rissing et al. 1996).

In laboratory colonies several days elapse between nest excavation and foraging. Yet cofoundresses are never seen to either overtly or "ritually" (*sensu* West Eberhard 1981; Hölldobler and Carlin 1985; Heinze et al. 1994)

contest or avoid the forager role (Rissing et al. 1989, 1996). Nor, as noted, is the surface excavator role itself the subject of contention; there predation threat precludes "negotiation". Nor does kin selection seem operative, as cofoundresses collected from the field are not related as measured by available electrophoretic variance (Hagen et al. 1988) and, unlike, e.g., Polistine wasp cofoundresses, who are differentially hostile to non-relatives and/or non-parental nestmates (e.g., Ross and Gamboa 1981; Post and Jeanne 1982; Klahn and Gamboa 1983), *A. versicolor* foundresses associate "randomly" (Rissing et al. 1986; Hagen 1988; cf Bartz and Hölldobler 1982; Ross and Fletcher 1985; Rissing and Pollock 1986, 1988; Hölldobler and Wilson 1990; Sasaki et al. 1996 for similar tolerance among cofoundresses in other ant species). The correlation between surface excavator and later forager specialization does, however, conform to the game-theoretic definition of a "coordination mechanism" (Aumann 1974; Rosenthal 1974; Myerson 1986; Cripps 1991).

Surface excavation as a coordination mechanism

A coordination mechanism uses some arbitrary, public event to assign tasks or roles differentially among game partners or groupmates (Aumann 1974; Rosenthal 1974; see Pollock 1994; 1995a; 1996 for an evolutionary exposition). The event is arbitrary in that task assignment is not a consequence of individual *ability* but rather of (correlated) circumstance, so that initial random task assignment to one individual shifts the expected assignment of others; the event is public in that the "outcome" of task assignments are "known" (in the game theoretic sense of inferable; e.g., Myerson 1991) to all partners. A surface excavator specialist meets these conditions. If no one deposited soil to the surface digging would be impossible--there would be no room to maneuver within the nest; the disappearance of soil indicates someone is a surface excavator. Those digging inside the nest "know" this, as does the surface excavator herself; assignment

is public. And, as noted earlier, surface assignment is not contested but rather the outcome of arbitrary position within the nest as all frantically dig while in common jeopardy, employing spatial task assignments common among social insect workers. Once such a mechanism exists it may be employed to assign tasks of similar structure (one surface excavator, one forager).

The existence of such a mechanism does not guarantee evolutionary viability. Consequent task assignment (forager specialist) must be an equilibrium, with "strategy morphs" refusing assignment eliminated in evolutionary time. An individual foraging when she need not seems trivially inviable, but what of an assigned forager refusing her task? In this case an individual replacing her would perform a personally best response. But, if so, an assigned forager may indeed be tempted to shirk her task. The simplest solution is to refuse the personally best response when exposed to a shirker, contrary to the heuristic of individual advantage common in behavioral ecology (e.g., Dawkins 1976, 1982; Pollock 1994a). Experimentally, this is the case (Pollock and Rissing 1995; Rissing et al. 1996).

Experimental evidence for punishment

While unable to force a cofoundress to refuse her task ("cheat" on coordination) we can alter the perceptions of her cofoundresses so that she appears to cheat (Pollock and Rissing 1995; Rissing et al. 1996; the individually specific *information sets* of economic game theory [Myerson 1991]). Consider a set of three-queen laboratory natal colonies which have developed a (uniquely marked) forager specialist. Divide the colonies into two treatments. In one the forager is removed while foraging (she "dies" while outside the nest)--the *controls*; in the other, the forager is blocked when trying to leave the nest, but her cofoundresses are not--the *experimentals*. Details may be found in Rissing et al. (1996). In the controls remaining cofoundresses experience an event which occurs in nature

(forager death) and must replace her. In the experimentals they perceive an assigned forager failing to leave the nest even though, upon personal inspection, exit is unblocked. The differential response time of non-foragers (ultimately, replacing the original forager) between treatments is a measure of game-theoretic reply to potential cheating (deviation from coordination). To the extent treatment non-foragers delay replacement of a "cheater" beyond the time it takes to replace a lost forager, they *punish* (*sensu* Axelrod 1980; Radner 1980; Boyd and Richerson 1992; and below) the cheater by suppressing potential colony fitness; but, as resources are held in common (see below), punishers hurt themselves as well.

Call an original non-forager a *replacement* when she appears near the nest entrance, whether or not she exits to the surface. We say a replacement *forages* when she actually leaves the nest to inspect a small attached foraging arena. Table 1 summarizes (original) nonforager response by treatment across 4 variables. While all control colonies exhibited a foraging replacement (on average after 10 days), some experimentals failed to do so for 29 days, when the experiment was terminated. The fungus garden died in a majority of the latter (7 of 10; Rissing et al. 1996); these colonies would have no chance of survival. Crucially, the experimentals suffer a seven-fold reduction in fungus mass and exhibit fewer pre-worker pupae and larvae. Other laboratory and comparative evidence suggest such a reduction in colony development would be disastrous in nature.

Intercolony competition as brood raiding

As noted earlier, adult territoriality in *A. versicolor* implies that natal nests clumped under a tree without a prior adult colony must ultimately engage in intense inter-colony competition for sole possession of the tree. Several ant species with such adult territoriality exhibit competition among natal nests in the form of "brood raiding" in both laboratory (Bartz and

Hölldobler 1982; Rissing and Pollock 1987, 1991; Tschinkel 1992a; Sommer and Hölldobler 1995) and field (Tschinkel 1992a,b), with supportive laboratory evidence for *A. versicolor* (Higgins 1988; Rissing et al. 1989; Pollock and Rissing 1995; see Pollock and Rissing 1989 for further cases). Once workers eclose (emerge from pupae), some begin to forage. When foragers encounter a "rival" natal nest they rush in, absconding with brood which they take to their own nest, returning for more (cf Rissing and Pollock 1987; Tschinkel 1992a). While workers from competing nests may fight upon encounter, the attacked nest begins reciprocal "brood raids" on the attacking nest, once located.

The size of the initial worker force is crucial to brood raiding success. In at least three species with brood raiding among clumped natal nests, those nests with more queens produce more workers (Rissing and Pollock 1987, 1991; Tschinkel 1992a; Sommer and Hölldobler 1995) and, where measured, are more likely to win the raiding contest (Rissing and Pollock 1987, 1991; Tschinkel 1992a). Intense intercolony competition among natal nests leading to adult territoriality seems, then, a likely selective force underlying pleometrosis (Rissing and Pollock 1987; Pollock and Rissing 1989; see Pfennig 1995 for another view). Relative worker number likely affects competitive success nonlinearly (Tschinkel 1992a; cf Wilson 1990).

Summary

Our simulations will "idealize" the following field and laboratory evidence. *Acromyrmex versicolor* foundresses disperse locally, with foundresses from just a few colonies congregating under preferred trees and forming nests pleometrotically. Their nests are thus clumped and destined to undergo intense rivalry upon production of the initial worker force. Cofoundresses use a prior "surface-excavator" coordination mechanism to allocate the risky task of foraging for the common fungus to a single

foundress. Game theoretically, a foundresses may accept risky task assignment when it is her lot, or not; her cofoundresses may replace her, or not. Colony fitness (brood raiding potential) is maximal under uncontested coordination and minimal under common refusal by all to forage (i.e., a queen refuses assignment and her cofoundresses refuse to replace her); replacing a shirker should produce some intermediary colony fitness. Experimentally, cofoundresses seem to punish shirkers (harming themselves) severely, undoubtedly handicapping the colony in future brood raids. We show this behavior is most stable under simulation when coupled with low foundress dispersal and strong, nonlinear, intercolony competition, both suggested by field and laboratory evidence.

Simulation design

We consider a population of 100 adult colonies, each under its own tree, connected as the circumference of a circle. Each year (*not* colony generation, as a colony may live many years) each living adult colony produces haploid asexual foundresses which disperse to the two neighboring trees. Foundresses are haploid asexual to avoid allele dominance or penetrance; the assumption is common in models of behavioral ecology (e.g., Wilson and Dugatkin 1991; Taylor 1992a,b). If the neighboring location has an active adult colony, all foundresses settling there are destroyed; only when the adult colony has died is successful colony foundation possible. Each year, each adult colony dies with a given probability, independently of its age and independently of its neighbors, with one proviso: to insure an unoccupied tree will always be "seeded" by a new natal colony, three contiguous colonies never die in the same year, for neighbor dispersal would then leave the middle tree unoccupied; this proviso is for programming ease and computational speed. We use an "independent" adult colony death rate of 5%, giving an expected adult lifetime of 20 years, a bit on the high side of *A. versicolor*, but not implausible (Rissing, per. obi.).

Each natal colony is established by three cofoundresses.⁴ Underneath a simulation tree-location foundresses sort randomly, without preference for parental nestmates; kin recognition does not occur. For computational speed 5 natal colonies are created under a vacant tree, all surviving until the brood raiding phase. Each natal colony produces a colony fitness derived from cofoundress behavior on task assignment; once fitnesses are assigned the brood raiding winner is a random draw of the five colonies, weighted by their fitnesses.

We idealize foraging as a single event. Once a forager, if any, is assigned, she makes one foraging trip, falling prey to above ground mortality with some uniform probability per simulation. If she dies, she nonetheless manages to return with food before death. *Thus forager death does not affect colony fitness; only the initial presence or absence of a forager does.*⁵ In at least two species of pleometrotic ants with brood raiding, cofoundresses engage in lethal combat with one another for sole possession of the nest after cooperative production of the initial "brood raiding force" (*Messor [Veromessor] pergandei*, Rissing and Pollock 1987 and *Lasius niger*, Sommer and Hölldobler 1995). *Acromyrmex versicolor* does not; rather, cofoundresses coexist peacefully for several years in the laboratory. Thus, in simulated colonies, only forager mortality and brood wars filter queen reproduction.

⁴82.5% of all foundresses collected at one site in one year had a cofoundress, with an average 7 cofoundresses per pleometrotic colony (Rissing et al. 1986). Nonetheless, the modal number of foundresses per colony was only 2 (16 of 36 pleometrotic colonies); because 2 foundress nests are likely to lose the brood wars relative to the 55% of pleometrotic nests with 3 or more queens (after Rissing and Pollock 1987, 1991; Tschinkel 1992a), we restrict attention to the simplest n-person environment, yet acknowledge our simulations do not in this respect duplicate field evidence.

⁵Actually, of course, a forager may die over many trips, her death truncating colony fitness until replaced. By ignoring the fine grain of multiple forager trips and, possibly, multiple replacements after forager deaths, we have a best-case scenario for cheaters on coordination; for instance, a cheater who is replaced is never subject to forager mortality, as she would if the only surviving foundress after 2 forager deaths. Apart from the advantage to cheaters we avoid finer detail in because of computation time and the added parameter of average number of foraging trips.

Adult colonies with multiple queens likely produce no more alates than those with single queens (Hölldobler and Wilson 1990); worker number plateaus to cover the foraging arena centered under their tree, and it is worker, not queen, number which limits alate production by food availability. Each adult colony thus produces the same (assumed large) number of alates, shared equitably by remaining queens.

Strategies

We restrict strategies to the minimal two stage game permitting a response to cheating on coordination. In the first stage only the "assigned forager" (chosen randomly among the three queens at natal colony foundation) makes a "strategic decision"--to accept her risky assignment or not. If she accepts, the game is over; if not, the game enters the second stage, where her cofoundresses decide whether or not to replace her. We consider four (haploid) strategies:

- P** "punisher", which accepts original foraging assignment but never replaces a shirker refusing foraging assignment; motivated by experimental data.
- Q** "quiter", which never accepts original assignment nor replaces another shirking assignment; motivated by the cheater critique (e.g., Williams 1966; Pollock and Rissing 1995).
- R** "replacer", which accepts original forager assignment and also replaces another shirking such assignment. **R** plays a personally best response (after, e.g., Selten 1975; West Eberhard 1981; Myles 1988; Farrell and Maskin 1989) against **Q** where **P** would not.

C a "sophisticated cheater", included to complete the "strategy space", which will *not* accept original forager assignment but *will* replace another shirking such assignment. **C** is a "cheating variant" on **R** in the same sense that **Q** is a cheating variant on **P**.

Table 2 categorizes the strategies by the two sequential properties of accepting assignment and replacing. Sometimes there will be two replacing morphs (**RR**, **RC**, or **CC**) in a group with a shirker on original coordination (**Q** or **C**); when so, we choose the replacer randomly.

Mutation

We begin with two mutation regimes, $\mathbf{P,R} \Rightarrow \mathbf{Q}$ and $\mathbf{P,R} \Rightarrow \mathbf{Q,C}$ ($\mathbf{Q} \Leftrightarrow \mathbf{C}$), then expand mutation to include $\mathbf{P} \Leftrightarrow \mathbf{R}$ and, thereafter, allow backmutation from cheating (**Q,C**) to coordination (**P,R**). The first two assume violating coordination ("noncooperation") dominates mutation events, which seems the prevalent heuristic in behavioral ecology (e.g., Williams 1966; Dawkins 1976, 1982; cf Pollock 1994b, Pollock and Rissing 1995); the latter two introduce a *mutation heuristic* where mutation probabilities depend on present types (from which mutational variation must arise; Dawkins 1980), motivated by strategy definitions (detailed below).

Note that, without **Q**, **C** can identify itself in game play. Suppose two **C**'s in a two-person group, with one designated the forager. By definition, this **C** will not fulfill her task. Her groupmate **C**, however, will replace her.

If strategy **C** is the only kind of shirker, this latter **C** "knows" her assumption of risk aids a strategy clone (the shirking **C**); no other (non-trivial) combination of the four strategies and original task assignment provides such guarantee. **C** without **Q**, then, can enjoy a "green beard effect" (Dawkins 1976). We prevent this by always allowing **Q** as a mutant on **C**;

replacing **C** does not know if it aids a clone or a **Q**.

Precluding **C** as a mutant has non-trivial consequences. We will see that allowing both types of cheater rather than just **Q** depresses the range of stable coordination, *not necessarily in favor of C, rather sometimes in favor of Q*; **C** can create intermediate population states, relative to either **P** or **R**, which are more readily invaded by **Q**.

Mutations occur immediately after natal colony creation, before coordinated forager assignment. Once a "colony genotype" is created by local random choice of three females from the tree-specific alate pool, each cofoundress undergoes a "mutation opportunity"⁶ from her present type as allowed by the simulation specific mutation regime. Allowed mutations are usually at the high rate of .001, except **P** \Rightarrow **R** which is at .0001 for reasons advocated below. High rates are employed for clear results; as the highest rates favor cheaters (not coordinators), we do not think this limiting.

Colony efficiency and failed coordination

Failed coordination entails a depression in colony fitness, the degree of which we vary. We standardize perfect coordination as a colony fitness of 1000; this value is obtained by any colony with either **R** or **P** the (randomly) designated forager, regardless of cofoundress strategy types. Ideally a **QQQ** colony (or, e.g., **PPQ** with **Q** the assigned forager; **QQC** with **C** the assigned forager) should have zero fitness, as the colony's fungus must die. It would then be possible for all natal colonies under an unoccupied tree to die,

⁶Each simulation employs numerous random number calls over as many as 500,000 years, for adult ths, creation of cofoundress genotypes, mutation events, forager deaths, and brood war victorie e random number generator must robustly mimic a uniform distribution in (0,1); we employ "ran2" ocated in Press et al. (1992:281-282), which should not cycle for at least 2×10^{18} calls. The hors boast (p.281): "We think that, within the limits of its floating-point precision, ran2 vides perfect random numbers; a practical definition of "perfect" is that we will pay \$1000 to t st reader who convinces us otherwise (by finding a statistical test that ran2 fails in a nontriv ...)". We have not tried.

leaving the tree empty. For computational simplicity we avoid this, assigning such a colony a fitness of 1, not zero; after some long delay even a **QQQ** colony manages some foraging to avoid pre-brood war death. Such a small colony fitness is usually unimportant unless all natal colonies under a tree have "no forager".

Our results hinge on the reduction in colony fitness born by colonies with realized replacers (a replacing **R** or **C**). There are two reasons for believing this reduction relatively great. First, brood wars likely amplify fitness as measured by fungus mass or worker number non-linearly; the reduction is not, e.g., reduced fungus mass, but rather the affect of relative fungus mass on brood raiding success. Second, the coordination mechanism, by employing the unique cofoundresses with most prior above ground exposure (the surface excavator), "picks" the cofoundress most likely to efficiently orient herself to the nest during initial foraging exploration. The effect should amplify with effort, as social insect workers learn with experience (e.g., Schmid-Hempel and Schmid-Hempel 1984; Hölldobler and Wilson 1990; O'Donnell and Jeanne 1992; Dukas and Visscher 1994; Schatz et al. 1995). The replacer of a shirker lacks this initial experience, which should depress her efficiency (see "mistakes and the evolution of coordination", below). We employ two values for reduced fitness, 200 vs 900, supplementing these with 400 and 600 on occasion.

Simulation sets

We address three questions by slight variants on simulation starting conditions. First, of **P** and **R**, which is relatively superior, regardless of ultimate evolutionary stability, and under what mutation regimes. We measure relative superiority by placing 50 contiguous **PPP** colonies on the circle, the rest contiguous **RRR**, running the simulation until either (a) one but not both

of **P,R** has vanished, with the survivor at least 95% of the population (relative to cheating morphs **Q** or **C,Q**) or (b) both **P,R** are lost and some cheating morph is at least 95% of the population. Each simulation can run for 100,000 years (usually < 10,000) and is duplicated 200 times. A run terminating at year 100,000 (with neither condition fulfilled) is a "tie" no matter what the relative frequencies of the strategies, with surviving strategies listed as "tied"; this happens rarely. The relative number of **P** vs **R** "wins" across 200 trials provides a measure of the morphs' relative superiority under "fair starting conditions" for **P** and **R**. We are sampling the various event pathways favoring one over another strategy; these paths are non-trivial under viscous dispersal. To permit clear victory, backmutation to **P,R** from **Q,C** is here precluded; similarly **P** \leftrightarrow **R** mutation.

A **P** win does not imply evolutionary stability, for **P** might succumb to **Q** or **Q,C** given sufficient time. On those occasions when there is a clear winner across the prior 200 trial sets, we test evolutionary stability by beginning a simulation with all 100 colonies of this type, running it for 500,000 years, likely longer than the present duration of the desert habitat in which pleometrotic *A. versicolor* is found (xxrefxx). A starting morph is "evolutionarily stable" under a given mutation regime if it does not vanish after 500,000 years. Although some "evolutionarily stable" morphs dip as low as 50% of the population, they are well over 90% overall. We find that, without **P** \leftrightarrow **R** mutation, both **P,R** may be stable; but, conforming to the relative superiority results, **P**'s range of stability subsumes **R**'s.

We next consider **P** \leftrightarrow **R** mutation. Under what we think a plausible mutation heuristic linking the four strategies, **R** does poorly, occasionally drifting to saturation but unable to resist re-invasion by **P**. The primary

affect of $P \leftrightarrow R$ mutation under the heuristic is to shift some populations to complete uncoordinated first stage game play (e.g., C and/or Q saturate, so surface excavators never accept task assignment; CCC groups exhibit coordination, but only in second stage game play, under reduced group fitness). Even so, under our 4-strategy mutation heuristic the stability of P expands, but only *probablistically*, while R persists solely through a combination of $P \leftrightarrow R$ mutation and drift. 100 replicates of 500,000 year run parameter sets under the heuristic often diverge in "stable morph" outcome; "evolutionary stability" becomes a probablistic measure of morph persistence for 500,000 years.

Lastly, we add backmutation from cheaters (Q,C) to first-stage coordinators (P,R). We find that, even when coordination is lost, P , never R , may re-invade and saturate, beginning the cycle anew (R reappearing through mutation on P). The emergence of coordination (P) becomes a secondary result of our stability simulations ("mistakes and the evolution of coordination" below also discusses emergence). Probablistic re-invasion is contingent on simulation parameters (forager death, replacement fitness); P 's evolutionary persistence can thus be probablistic in two senses (loss and re-emergence). There are, however, conditions where *first-stage* coordination cannot re-emerge: when the frequency of C is sufficiently high (relative to Q) after loss of P,R .

We duplicate many of the parameter sets under "random assortment", where all living adult colonies contribute alates to a global (free-mixing) pool, from which 5 natal colonies are produced for each vacant tree. As expected, P 's evolutionary persistence is significantly worse under random mixing, yet here too cycles of population-wide coordination loss, re-saturation of P are possible. We denote simulations employing, say, 200 replacement fitness, .5

forager death under viscosity by {200, .5, **v**}, under random assortment by {200, .5, **r**}.

Results

Relative superiority of P,R

1. Under viscosity, P often out performs R; otherwise they "win" equally.

Table 3 presents "fair contest" results with the relatively low replacement fitness (high cost for lost coordination) of 200, for mutation to **Q,C** and solely to **Q**; a foundress should, nonetheless, replace a cheater to maximize expected personal fitness. At no value of simulated forager death does **R** do better than **P**.⁷ Within the range [.5,.8] **P** outperforms **R** robustly (except for the "tie" at .5 forager death with **Q** only mutation, discussed shortly); with 90% forager death **Q** predominates.

While an **R** exposed to a cheating **Q** does personally better than a **P** so exposed, **R**'s personal superiority "incubates" **Q** offspring for the next generation; *if she survives, so does her cheating colonymate*. Neighboring-tree alate dispersal places these incubated **Q** offspring disproportionately among the offspring of this very **R**; by surviving, **R** enhances the frequency of group (brood war) inefficient cheating environments encountered by her immediate descendants (cf Pollock 1989a). As forager death increases, **Q**'s supplanting of **R** quickens, as there are fewer surviving replacement foragers to dilute the representation of **Q** in future local alate pools. A relatively long-lived *spatially specific* **Q** frequency, beyond the background mutation probability globally experienced by **R**'s "rival" **P**, is focused on future **R**'s.

⁷Over numerous simulations we have noticed reversals in relative **P,R** wins of, occasionally, up 0. Differentials of 30+ seem, however, robust. We will use the latter as a measure of significance.

P, in contrast, sacrifices itself to eliminate encountered cheating **Q**;⁸ under viscous dispersal her neighboring rival natal colonies often consist of **P** as well, as they are derived from the same pool of local alates. Sacrificing herself by punishing **Q**, she aids her strategy clones in nearby groups (Pollock 1988), eliminating the offspring of encountered **Q** from the social environment of the brood war victor's descendants. Inspecting the spatial trajectory of simulations, one sees **Q** grow in a patch of **R** until the latter are eliminated ([.5,.8] forager death, Table 3); then, encountering **P** along the boundary of a now **Q** patch, the patch is pushed back until eliminated (see J. B. Wilson 1987; Pollock 1989b for similar processes). Viscosity now works against **Q** for, as it disproportionately encounters itself, it is more likely to exist in abysmally inefficient social environments (uncoordinated) with a colony fitness of 1 (cf Pollock 1989a,b); as in kin selection, uncooperative **Q** is eliminated via self-clumping (Wade and Breden 1980).

But, for sufficiently high forager death, **P** fails against **Q**. Suppose forager death unavoidable; **P** can then persist only if foraging (apart from punishment) aids relatives (clones) in her group (kin selection). Viscous dispersal mediated by neighboring trees seems incapable of providing sufficient intra-group relatedness (probability of clonal encounter) to preserve **P** (Tables 3,4; cf Murray and Gerrard 1984; J. B. Wilson 1987; Wilson et al. 1992; Taylor 1992,a,b for similar limitations on viscosity). Spatial proximity is less exclusive to foreign genotypes than a rule *insuring* common ancestry by immediate descent. Kin grouping can actively preclude group association among different types; viscosity can not. The latter process permits, stochastically, more **PQQ** groups with **P** the designated forager than the former; under the extreme case of asexual haploid inheritance, such groups cannot occur under sibling assortment except by mutation. With

⁸Of course, a **Q** not assigned the forager role is phenotypically neutral with respect to similar this just delays the affect of **Q**, if it survives chance elimination when rare.

mandatory forager death these groups occur sufficiently in our model to insure **P**'s elimination. Continuity implies similar logic for sufficiently high yet uncertain forager death, with evolutionary advantage (partly through the removal of **Q**'s through punishment) shifting to **P** as forager death decreases.

C facilitation of Q

While **C** is itself inviable at 200 replacement fitness, **P** fairs significantly better against **Q** when **C** is precluded (Table 3). When present, **C** wins on only one occasion (with certain forager death); yet **P**'s relative success over **Q** is enhanced dramatically at 90% forager death when **C** is excluded. Clumped **C**'s colony fitness is 200 times that of clumped **Q**, as **C** replaces its own phenotypically refusing type while **Q** does not. Clumped **C** will thus be harder for **P** to defeat (push back) than clumped **Q**. For the same reason, **R** patches are even more vulnerable to **C** than **Q**. But, similarly, **C** is even more vulnerable to **Q** than **R** is to **Q** (maximally fitness differential across colonies is 200:1, not 1000:1); inspecting the spatial trajectory of simulations, **R** patches become **C** patches which become **Q** patches. **P** then "eats" the **Q** patch, as before. The cycle repeats, as **R** persists for some time by drifting into **P** patches when phenotypically neutral.

Two factors work against **P**, often terminating the cycle in a **Q** win. First, **C** causes the size of **Q** patches encountered by **P** to be greater. Stochastically, it takes longer, so is more difficult, to eliminate **Q**. Second, **C** can, again stochastically, create a self-cluster without **R** by mutating from **P**; these clusters can expand by drift which, when themselves invaded by a mutant **Q**, continue the cycle without **R**. Repeated dips in **P**'s frequency can ultimately lead to its stochastic elimination in the finite 100 colony population. As we shall see, in an evolutionary stability run of **P** with only **C, Q** mutants, **P** persists at overall high frequency for over 450,000

years, with the (spatially local) cycle **P** --> **C** --> **Q** --> **P** repeating until **P**'s stochastic loss (cf Pollock 1989b for a similar, albeit deterministic process); without mutation to **C**, **P** is robustly high for 500,000 years against **Q** under the same parameters ($f_P \geq .5$; $f_P > .9$ 92.1%; Table 8, below).

Clumped **C** as a transition to **Q** is similar to an intermediate stage of a game-theoretic "renegotiated equilibrium" (Farrell and Maskin 1989; van Damme 1989; motivated by Selten 1975). Once deviation from coordination occurs, game partners (here, cofoundresses) have no interest in retaining their previous roles; replacement is personally advantageous (the first phase of renegotiation). Yet self-interest leads immediately to a new commons dilemma (*sensu* Hardin 1982; Boyd and Richerson 1988; Dugatkin 1990): if a colonymate will replace the shirker, let her (the second phase). **C** solves this problem with a new (implicit) coordination mechanism (we allow only one forager) but is thereby vulnerable to **Q**. In our simulation of intergroup competition, clustered **C**'s "stochastic viability" among **P** (e.g., 1000:200 colony fitness ratio) is related directly to **C**'s resistance to **Q** (e.g, 200:1 colony fitness ratio); as **C** improves against **P,R** it also improves against **Q**.

Table 4 duplicates Table 3 with a replacement colony fitness of 900. With **C,Q** mutation, shirking is ubiquitous, with **Q** replacing **C** for sufficiently high forager mortality ($\geq .8$). We have truncated the game to two stages, so only **Q** can shirk replacing a shirker. But, once **C** is prevalent, we could apply the same logic to further reduce colony efficiency (cf Selten 1978; Selten and Stoecker 1986; Schuessler 1989; Pollock 1991, 1995; Cressman 1996 for similar processes); **C**'s success at low foraging mortality is more an artifact of our 2-stage game than a biological prediction. We will argue later that "stable" **C** would likely unravel into more **Q**-like shirkers, leading, incrementally, to an all **Q** population ("Stable **C**?" below). Ironically, this

later population may be re-invaded by **P** even when the intermediate **C** population can not (cf Pollock 1995 and below).

Under 900 replacement fitness and forager deaths in [.5, .9], **P** wins robustly when **C** is precluded, surpassing its performance with the same range of forager death under 200 replacement fitness (Tables 3,4). High replacement fitness causes **R** to successfully incubate more **Q**, accelerating the former's demise. **P**, however, continues to eliminate **Q** clusters at the same rate as under 200 replacement fitness, as neither **P,Q** replace. **P**'s success thus hinges less on the (in)efficiency of forager replacement than on the combined effects of viscosity (clumping types) and the sequential loss of colony fitness throughout the population via intermediary strategies (**C**; cf Pollock 1995).

R predominates ("wins") over **P** with no forager death and both **C,Q** mutation (Table 4); this is the only instance of **R** predominance under viscosity. With positive forager death replacement is *weakly altruistic* (*sensu* Wilson 1979, 1990); a replacer enhances her personal fitness, but her groupmates gain more. Viscosity enhances the cost of weak altruism by assorting the descendants of replacers with the descendants of cheaters. Without forager death this cost vanishes even under viscosity; **R** should always be superior to **P**.

But **R**'s advantage must be translated into evolutionary competition. Without forager death **Q** is never a best response; mutant **Q**'s appearing in either **P** or **R** patches are eliminated, so **Q** can affect **P,R** success only when all three strategies appear within the same arena (empty tree). Under viscosity such **PQR** foundress pools are relatively infrequent; noise appears to mask any advantage for replacement under **Q** only mutation, with **P,R** winning

equally (Table 4, {900, 0, \mathbf{v} }). \mathbf{C} mutants, however, consume \mathbf{P} clusters by forcing replacement opportunities at the \mathbf{C},\mathbf{P} cluster boundary via \mathbf{CCP} vs \mathbf{CPP} groups; \mathbf{R},\mathbf{C} boundaries are neutral (\mathbf{CCR} , \mathbf{CRR} are phenotypically identical when cheating occurs). At {900, 0, \mathbf{v} } the cost of cheating (in \mathbf{CCP} groups with both cheater and replacer \mathbf{C}) to induce non-replacement (depressing the fitness of \mathbf{P} in \mathbf{CPP} groups) seems sufficiently small to shift population "wins" to \mathbf{R} (Table 4). With low replacement fitness (200; Table 3) the effect seems lost in noise, as replacement leads infrequently to placement (brood war victory) as an adult colony; \mathbf{P},\mathbf{R} win "equally". Once there is a true cost to replacement (possible forager death), \mathbf{C} outperforms \mathbf{R} as well at their cluster boundary (as \mathbf{R} replaces more often than \mathbf{C}), yielding \mathbf{C} wins under moderate forager death ([.2,.5], 900 replacement fitness; Table 4).

2. Under random assortment \mathbf{R} improves its relative performance to \mathbf{P} .

Removing the spatial correlation between the descendants of personally advantageous replacers and successful cheaters, random offspring dispersal should enhance (relative) \mathbf{R} wins, as is mildly apparent under 200 replacement fitness at [.8,.9] forager deaths (\mathbf{Q} only mutation; Table 5 vs Table 3). Some \mathbf{P} wins under viscosity are now distributed to \mathbf{R} and \mathbf{Q} , reflecting how these latter strategies harm themselves under viscosity (e.g., \mathbf{P} clusters no longer destroy neighboring \mathbf{Q} clusters, as neither exist). Note that both \mathbf{P},\mathbf{R} sometimes "win" under certain forager death, which is evolutionarily impossible. Recall, however, that "fair contest" simulations are designed to reveal the relative standing of \mathbf{P},\mathbf{R} , not predict stability (addressed shortly). Our initial population is 50% \mathbf{PPP} , \mathbf{RRR} groups; random assortment expands stochastic pathways of selection which can induce "victory" not necessarily reflecting long term resistance to recurrent cheating.

3. Random assortment yields unique superiority for \mathbf{R} under high

replacement fitness, with a stable polymorphism of R,Q (or C,Q when C is allowed) under moderate forager death.

Table 6 duplicates Table 5 with 900 replacement fitness. The high viability of colonies with replacers (900 vs 200) enhances the success of cheating, which in turn, enhances the success of replacement since the fitness of phenotypic replacers and cheaters is not correlated spatially. Without **C** mutants **R** outperforms **P** within the range [0,.5]; at greater forager death predominance shifts to **Q**. The value of cheating increases with forager death; at {900, .5, **r**} a clear polymorphism is reached, where neither **R** nor **Q** achieves a 95% frequency for 100,000 years.

C couples the benefits of both **R** and **Q** (Table 2); when present, **R**'s relative performance against **P** declines (in the range [.1,.2], Table 6), with **C** replacing **R** in polymorphism with **Q** {900, .5, **r**} (Table 6). Random assortment here conforms to the logic of personally best, situationally specific, responses (cheat when you can get away with it, but limit costs when exposed to cheaters; e.g., Selten 1975; West Eberhard 1981; Myles 1988), but only under low group cost to cheating (Table 5 vs 6). This is not surprising since, under high group cost, colony success is so unlikely as to be undetectable in our *finite* population.

Evolutionary stability of P,R

4. Without $P \leftrightarrow R$ mutation, P is always stable when R is, but not conversely.

Predominate strategy "wins" in the fair contest trials predict evolutionary stability (survival at mostly +90% of the population for 500,000 years) under the same mutation regime as the contest. Thus, under combinations of .2,.8 forager death and 200,900 replacement fitness, viscous dispersal, **P** is stable whenever **R** is, *but not conversely* (Tables 7,8).

Without $P \leftrightarrow R$ mutation, R is stable against both C and Q at .2 forager death for both replacement values, but not for .8 (Table 7); P is similarly stable at .2 forager death, but also at .8 against Q under both replacement fitnesses (Table 8). With both Q, C mutation, P mostly retains high frequency under $\{200, .8, \mathbf{v}\}$, with occasional peaks of C , then Q , back to P for some 455,000 years, ultimately undergoing stochastic elimination when low (discussed previously; Table 8). Envisioning forager mortality as "periodically high", P is more stable than R , irrespective of high/low replacement fitness. Yet this difference is most pronounced when cheaters are restricted to Q . To clarify the role of C in P, R relative stability we next introduce a heuristic structuring mutation by "baseline" pre-mutant type.

A mutation heuristic on strategy properties

Mutation is a physical process, creating new variants from pre-existing types (Darwin 1859; Dawkins 1980). Present types restrict the space of novel forms and, within this space, mutation probabilities need not be identical; some errors are more likely than others. Our "fair contests" assumed that prior types P, R do not shape their mutational variants; yet, examining these strategies, this seems unlikely. Table 2 defines each strategy within a two-locus "property space": accepting initial assignment and replacing a shirker refusing assignment. We see no reason to link these properties at mutation. Single event "double mutation" on properties is then most unlikely, giving prevalent mutational paths $P \leftrightarrow R$; $P \leftrightarrow Q$; $C \leftrightarrow Q$; $R \leftrightarrow C$ (Table 2). Note that R 's most damaging invader, C , is then more likely to come from itself than from P . *Under viscosity herein, a clumped prior type shapes its own mutational adversaries, as these mutants are derived from itself, and generally interact disproportionately with the prior type (cf Pollock 1989b, 1995).*

The four prevalent mutation pairs are not symmetric in probability. Consider, for example, $P \Rightarrow Q$. P recognizes task assignment and acts upon it; Q does nothing, so need recognize nothing. On the assumption that errors inducing behavioral loss are more likely than errors shaping "constructive" behavior (e.g., pathways for loss are shorter in code length), $P \Rightarrow Q$ seems more likely than $Q \Rightarrow P$. At present, we preclude the latter mutation, as we are concerned with the stability of coordination against eroding cheaters; we will add mutation to coordination later. Similarly, $C \Rightarrow R$ is excluded for the moment. The remaining two mutational pairs ($P \Leftrightarrow R$; $C \Leftrightarrow Q$) lose/gain propensity to replace while fixing initial task acceptance. We assign the loss pathway probability .001, the gain pathway .0001. We think the gain assignment generous but, at present, this is a matter of taste.

Stability under the heuristic

5. With viscosity and $P \Leftrightarrow R$ mutation under the heuristic, P 's resistance to R increases with forager death.

Although our mutation heuristic focuses C invaders on R patches under viscosity, $P \Leftrightarrow R$ drift also occurs, so P is ultimately exposed to C via R . While P should be *relatively* more robust than in our previous stability simulations, there is no *a priori* reason to exclude its demise by C ; nor can we preclude $P \Leftrightarrow R$ drift eliminating P in the absence of realized cheater mutations. Table 9 presents one sample 500,000 year run under the heuristic for each of the parameter combinations .2,.8 forager death, 200, 900 replacement fitness, viscous dispersal, for both initial all P and all R populations. P is stable with 200 replacement fitness; R not (Table 9); R was stable with cheater-only mutation (Table 7). Predominately P locales are less vulnerable to self-derived mutants than R locales, shifting the population to P . But this is true only so long as C has a foothold in R clusters. Over

long sequences this may not occur, leading to high f_R by drift, then decay once **C** invades. While **P** is 500,000-year stable at $\{200, .2, \mathbf{v}\}$, with $f_P \geq .9$ about 80% of the time, it dips as low as 10% of the population (Table 9); **P**'s relative stability against **R** is probabilistic, with pathways of elimination clearly possible.

Table 10 measures probable **P** loss for 200 replacement fitness under various forager deaths by repeating runs of .2, .5., .8 forager death 100 times each. As forager death increases **P** becomes more resistant to loss through **R** drift. **R** "incubates" more cheaters, focused on its own type through viscosity, with increasing forager death, curtailing **P** elimination by drift; so average maximal f_R decreases with increasing forager death. When lost, **P** is readily regained through $\mathbf{R} \Rightarrow \mathbf{P}$ mutation, drift, and resistance (via punishment) to cheaters, ultimately preponderant in frequency again. For sufficiently high forager death, however, **P**'s loss leads to $f_Q = 1$ (.8; Table 10). Without backmutation from cheating to coordination, **P**'s loss is here irrecoverable. At high forager death **R** is quickly eliminated by "its" mutant **C**, so **P**'s loss through **R** drift is curtailed; but the frequency of **P** encounter of large **C** clusters is also enhanced, leading to occasional stochastic elimination of **P**. Paradoxically, **P**'s *continuous presence* is related inversely to probable population-wide loss of coordination; **P**'s occasional loss to drifting **R** enhances **P**'s long term persistence.

We would expect, then, **Q** saturation more likely under **R** stability runs, as the population is initially all **R**. Under the mutation heuristic an all **R** starting population shifts to all **Q** about 3.6 times as often as an initial all **P** population (43 vs 12, with .8 forager death; Tables 10,11). **R** is always lost over simulated forager deaths ([.2,.8]), with **P** predominant over all (Table 11). While the mutation heuristic favors **P** over **R** ($\mathbf{P} \Rightarrow \mathbf{R} @ .0001$; **R**

$\Rightarrow P @ .001$), shifting mutation in favor of **R** would simply enhance the probability of **Q** saturation at high forager death under viscosity.

6. Random assortment shifts the population between R and P at "moderate" forager death, although P remains mildly resistance to complete loss; at high forager death, population-wide loss of coordination is very likely.

Table 12 duplicates Table 10 (**P** stability) with random assortment. Populations shift between prevalent **P,R** under forager deaths in $[.2,.5]$, but **P** remains mildly resistant to complete loss (in 14 of 100 500,000 year runs); when lost **P** often re-emerges through $R \Rightarrow P$ mutation, readily recovering population dominance (Table 12). When **P** is preponderant, rare mutant **C,Q** are likely eliminated when phenotypically expressed (at 200 replacement fitness), leaving little room for **R** increase beyond drift; preponderant **R** is kinder to **Q**, as well as to **P** in **PR[Q/C]** groups (themselves more frequent under random assortment). High frequency **P** is thus less inclined to downward drift than high frequency **R**, so **P** remains slightly resistant to loss even under random assortment (Table 10 vs 12); the bias is, of course, amplified under viscosity, where **R** clusters encounter cheaters at a higher rate than **P** clusters.

The low replacement fitness (200) used for Table 12 makes *group success* (brood raiding success) unlikely when *combined R,P* predominate; the personal advantage of realized replacement is difficult to detect in our 100 adult colony population, even under random assortment (cf the parallel "fair contest" results in Table 5). **P**'s loss at $[.2,.5]$ forager death does not jeopardize the persistence of *coordination* (**P** or **R**) in the population; at the $R \Rightarrow P$ mutation level .001 used herein, **P** is regained before **R** too is lost stochastically. Recall that the adult population is not replaced yearly; on

average, (about) 5 adult colonies die per year, leaving little yearly opportunity for successful replacement. In simulations (deferred here) with high adult colony death (over 50% per year), coordination is indeed lost under random assortment where retained here.

Yet, without the protection against cheaters provided by viscosity (interaction restricted to "cluster boundaries" and "self-damaging" clustered cheater interaction), **P** (so too **R**) is unable to resist elimination by cheaters at high forager death (.8): $f_Q = 1$ in 93 of 100 trials (in 6 of the remaining 7 cases, **P** is never lost during the 500,000 years; Table 12); under viscosity $f_Q = 1$ in 12 of 100 trials under otherwise identical conditions (Table 10). Clearly an all **R** starting population would induce, if anything, greater loss of population-wide coordination (cf Tables 10, 11). Cheaters, incubated population-wide at a high rate (due to high forager death) by **R**'s, cannot be "driven back" through punishing **P**'s. As we shall see, **P** may invade and eliminate **Q** under {200, .8, **r**} (Table 14, below); but, without constant backmutation from cheating to coordination ($Q \Rightarrow P$), the stochastic elimination of **P** through recurrent high frequency **Q** is quite likely.

7. Under the heuristic with $P \leftrightarrow R$ mutation, random assortment induces the population-wide loss of coordination more than viscosity ; when not, P predominates.

Table 13 expands the space of simulated replacement fitnesses (200, 400, 600, 900), testing only for the population-wide loss of coordination (populations of all first-stage cheaters) under viscosity and random assortment (100 trials per parameter set of 500,000 years each). For low (.2) forager death, coordination is retained under both forms of dispersal from 200 to 600 replacement fitnesses; **P** predominates, albeit with less variability under viscosity (cf, e.g., Tables 11, 12 for 200 replacement fitness).

Viscosity is *not* necessary for evolutionarily persistent (in contrast to continuously present) **P** as measured herein (cf Table 12). A greater opportunity for realized replacement can be tolerated for sufficiently low forager death for replacing **R**, as simultaneously surviving **R** dilutes the cheater's impact on population frequencies.

With greater forager death viscosity provides unique stability for coordination ($\{200, .8, \mathbf{v}\}$, $\{400, [.5, .8], \mathbf{v}\}$; Table 13). Stability appears not as uniformly high **P** vs **R** (or vice versa) but as *usually* high *combined* **P,R**, biased toward **P** overall; as we shall see, this bias will become greater when we allow backmutation from cheating to coordination (Table 14). Note that, without **P**, coordination as **R** would be lost under high forager death, even with low replacement fitness (Tables 7, 13 and above). We stress that replacement is personally advantageous under all simulated parameter sets; yet it is clearly inferior to **P** as a *first stage game coordination strategy* (we focus on replacing **C** shortly). Nor does **R** require a "kin fitness component" (via viscosity) to be evolutionarily successful (after, e.g., Maynard Smith 1964).

In the "fair contests", **R** does *worse* under viscosity (Tables 3-6). Rather, *under the heuristic, R persists through mutation from P and drift when P,R are phenotypically identical where it would otherwise be eliminated.*

8. Under the heuristic, replacement is stable solely through the cheater morph C.

Coordination loss overall follows the same trajectory under both viscosity and random assortment. **P** is fairly resistant to its "self-induced" mutant **Q** under the heuristic, much less to **C** (Tables 3-6, 8). High frequencies of **R**, due to drift, allow greater mutation to **C**, causing significant dips in the frequency of **R**. As **C** increases in frequency it encounters **Q** through mutation on **C** or **P**. Whether **P** survives depends on its

resistance to **C** and **C**'s resistance to **Q**, as **P** can usually push back high frequencies of **Q** under many parameter sets. Under random mixing **P,R** decrease together against **C** (**R** more rapidly than **P** partly because of **PRC** groups). Under viscosity **P**'s frequency remains relatively unchanged until the **C** invaded **R** patch is eliminated; **P** then struggles against **C** until the latter is eliminated, if possible, from within by **Q**; **P** then pushes back **Q**. This **P** → **R** → **C** → **Q** → **P** cycle repeats until, with parameter dependent probability, both **P,R** are eliminated; cycles are brief under random assortment, more prolonged under viscosity.

At high forager death coordination loss invariably yields predominately **Q** populations, irrespective of viscosity (e.g., Tables 10-12; cf Tables 3-6 "fair contest" results). Since **C** replaces a cheating groupmate (**C,Q** assigned but refusing the foraging role), evolutionarily persistent **C** should imply some **Q** in polymorphism. This is true of random assortment, but not necessarily of viscosity; viscosity depresses **Q**'s frequency by augmenting self-play, limiting its frequency dependent fitness (cf Grafen 1979; Pollock 1989a, 1996). Under random assortment **C,Q** are polymorphic at 900 replacement fitness, .5 forager death; under viscosity the population is essentially all **C**, save sporadic **Q** via mutation (cf Tables 4,6).

P's reliance on **Q** to eliminate **C** accounts for the only anomaly in Table 13. At {600, .5, **v**} coordination is lost in all 100 trials, but in only 68 of 100 trials at {600, .8, **v**}. At .5 forager death the population stabilizes as essentially all **C**. At .8 forager death **Q**'s performance against **C** increases, leading to the latter's elimination *sometimes before the elimination of P*; when so, **P** may recover predominance. Note that coordination is lost essentially identically at {600, .5, **r**} and {600, .8, **r**}, as **Q**'s success is not suppressed by local self-assortment (Table 13). Paradoxically, *under*

viscosity, high forager death can **augment P's persistence by eliminating C in favor of Q**, while moderate forager death eliminates P by favoring C over Q.

Table 13 suggests P's recovery in predominately Q populations is contingent on viscosity. While sensible, in that punishment aids P's in other local groups while Q self-assorts detrimentally under viscosity, we conclude by showing this only weakly true. By allowing backmutation from cheaters (Q,C) to coordination (P,R), we find coordination often replaces cheating under both forms of dispersal.

9. Adding backmutation from cheating to coordination to the heuristic, population-wide coordination is usually recovered when its loss leads to a predominately Q population under either viscosity or random assortment; viscosity simply reduces the frequency of loss and speeds recovery. Recovery from predominately C populations is possible, but usually only under low replacement fitness.

Table 14 duplicates Table 13 with $Q \Rightarrow P$ and $C \Rightarrow R$ mutation @ .0001; conforming to the heuristic (above), we preclude the other two backmutation paths as orders of magnitude less likely. As in Table 13, the proportion of 100 trials per parameter set in which coordination is lost throughout the population is given, now followed by the probability of recovered coordination through backmutation. Recovery is defined as at least 15% P,R combined morphs at year 500,000 after complete loss; almost always recovery entails 100% P some point after recovery. With two exceptions backmutation does not alter the probability of coordination loss (Tables 13, 14). At {600, .8, v} probability of loss declines from .68 without to .55 with backmutation. As P backmutates only from Q, this likely reflects an "early start" in P's elimination of Q patches by appearing within these patches; Q pushes C back while P attacks Q from within (cf point 8 above). The other exception is

{400, .5, **v**} where loss decreases from .14 to .07. Its significance is unclear. It may reflect the precariousness of **C** victories under low replacement fitness, with backmutation opening other "fronts" against **C**; or **C** may be prone to higher variance in victory precisely because it is weak, with backmutation playing no real role.

Once coordination is lost, the best predictor of recovery is whether **Q** predominates in the uncoordinated state. **P** usually recovers (e.g., 534 of 576 runs [92.7%] at .8 forager death, combined across replacement fitnesses and dispersal; Table 14) via backmutation in mostly **Q** populations. Under random assortment the population jumps from all **P** to all **Q** and back, with brief high frequencies of **C** during **P**'s (re-)demise. Most backmutant **P**'s are eliminated through drift when phenotypically identical with **Q** (as neither replaces); foraging **P**, when rare, tends to eliminate itself through high forager mortality. Occasionally, however, **P** drifts to higher frequency through repeated placement in non-foraging roles. **P** begins to encounter itself within groups; when foraging aids a clone the 1000:1 group fitness differential boosts **P**'s representation in the next population of adult colonies. Repeated "boost opportunities" ultimately increase **P**'s frequency sufficiently to eliminate **Q** in a more deterministic fashion. Viscosity slows **P**'s loss and speeds its recovery, clumping both **P** and **Q** irrespective of population frequencies (above).

Cheating is resistant to backmutation only within preponderantly **C** populations. In all cases where coordination fails to re-emerge, **C** predominates in the all cheater population (all parameter sets with .06 or less recovery in Table 14). Here **R** has already been destroyed by its "self-derived" mutant **C**; that only **R** backmutates from **C** gives coordination little scope for recovery.

Preponderantly **C** populations permit coordination recovery in two cases, both under viscosity ($\{400, .5, \mathbf{v}\}$; $\{600, .2, \mathbf{v}\}$; Table 14). In both, coordination is lost only 7% of the time, suggesting **C**'s success is mostly stochastic. Inspection of these simulations shows that, although **C** predominates under coordination loss, up to 30% of the population may become one or more **Q** patch(es). Such patches husband backmutated **P** which, once sufficiently frequent, seem able to resist **C** under viscosity and low/moderate replacement fitness/forager death (cf Table 8 for similar resistance by **P**). Random assortment confirms this logic in one case: coordination loss is an order of magnitude higher, with recovery less frequent in $\{400, .5, \mathbf{r}\}$ relative to $\{400, .5, \mathbf{v}\}$ (Table 14), suggesting backmutating **P** benefits from **Q** clumps in the latter. $\{600, .2, \mathbf{v}\}$ and $\{600, .2, \mathbf{r}\}$ are, however, nearly identical in loss/recovery, with coordination rarely lost in either case.

Table 14 provides the only clear instance where viscosity *harms* coordination. Under both $\{900, .5, \mathbf{v}\}$, $\{900, .5, \mathbf{r}\}$ coordination is almost always lost. Under random assortment coordination (as **P**) is always regained; under viscosity almost never (3 of 100 opportunities). Under random assortment **C, Q** co-exist in about equal proportions, providing ample opportunity for **P** recovery through backmutation as outlined above. Under viscosity **C** predominates, as **Q** harms itself through self-clumping; 900 replacement fitness seems to preclude the (stochastic) **Q** clumps which permit **P** recovery under $\{400, .5, \mathbf{v}\}$, where replacer **C** is less group efficient.

Conclusion

Mistakes and efficient coordination

There is remarkably little evidence supporting the intuition that personally advantageous replacement is evolutionarily viable among non-

cheating morphs. Only when the cheating variant of **R**, **C**, is precluded do simulations support the intuition of personal advantage, and then only under high replacement fitness, low/moderate forager death, and random assortment ($\{900, (0, .5], \mathbf{r}\}$; "fair contests" of Table 4). But to preclude **C** is capricious. **C** is a mutant of **R** in the same way **Q** is a mutant of **P**. There is, moreover, no reason why cheating and replacement cannot be properties of the same strategy; indeed, an evolutionary "war of attrition" on waiting times for replacement (after Parker 1970; Bishop and Cannings 1978; Parker and Thompson 1980; Maynard Smith 1982; discussed further below) essentially combines cheating and replacement (positive but finite waiting time) in the same individual.

Strategies always perform correctly in the simulations, responding to their social environment without error. Successful replacement (a group with a phenotypic replacer surviving to adulthood) thus necessarily augments the fitness of the cheater (**C** or **Q**) forcing replacement, depressing **R**'s *relative* advantage. Deviation from coordination need not, however, be strategic. A **P,R** assigned the forager role might mistakenly "believe" otherwise (after Sugden 1985; Boyd 1989); such a purely phenotypic effect would provide an advantage to replacing **R** without affecting the future frequency of encountered genotypic cheaters.

We have excluded this possibility for two reasons. A coordination mechanism must, by definition, be unambiguous, for ambiguity is open to exploitation (Aumann 1974; Myerson 1986; 1991:244-258; Fudenberg and Triole 1991:53-59). *Acromyrmex versicolor* seems to exhibit such a mechanism; there is usually only one surface excavator and, when there are two (in laboratory 3 foundress colonies) only one (the future forager) goes to the surface once

excavation is well underway.⁹ A "coordination mistake" is then tantamount to cheating, as it requires a female to "not know" she goes to the surface.

There is, furthermore, another kind of mistake, detrimental to **R**, which seems much more plausible. A replacer must "decide" coordination failure (mistake or genotypic cheating) has occurred. The only clear indicator of failure is a torpid fungus garden in the presence of an ostensive assigned forager. A garden, however, may be torpid not because of coordination failure, but because the assigned forager has had a run of bad luck. That these desert ant foundresses place their nests directly under the canopy of the tree whose leaves they harvest suggests sensitivity to resource variability (Rissing et al. 1986); they prefer this location even though there is a high probability that an adult colony "owner" will eliminate them. In a temporally variable desert habitat *temporary* foraging failure must be common.

Why, then, have a specialized forager at all? We have already noted how experience improves individual foraging efficiency. But colony *foraging* efficiency would similarly improve with the number of foragers. Recall, however, that we believe foundresses form associations to enhance their colony's later success at brood raiding by augmenting initial worker (raider) number (Rissing and Pollock 1987, 1991; Pollock and Rissing 1989, 1995; Rissing et al. 1989). A relatively inexperienced foundress is more vulnerable to surface predation. Distributing foraging effort over cofoundresses with variable experience can then be *less* efficient for colony survival if worker production is curtailed through death of the inexperienced.

Similarly, hymenopteran workers must often accept coordination tasks which

⁹The empirical correlation between surface excavator and forager is imperfect partly because foundresses sometime surface excavate (Rissing et al. 1996). It increases if one looks only at the sequence of excavation. Assignment failure happens mostly when the predominate surface excavator at the end of surface excavation is not the predominate surface excavator overall (which we define the "true" excavator). In those cases with two excavators, the third foundress never assumed the foraging task.

are inefficient *at the moment* because coordination is efficient for the colony *over the distribution of coordinated tasks* (xx include Rissing book chapter).

A short-run decision to replace (or aid) an unsuccessful foundress may be costly for long term survival. While our simulations assume coordination is never mis-identified, they also assume replacers never incorrectly infer the presence of a cheater. Variable short term foraging failure in a desert habitat suggests that mistaken replacement should be much more common than "mis-read" task assignment. Indeed, the evolution of task coordination may be little more than the progressive elimination of mistaken replacement.

The emergence of foraging specialization

Briefly, we envision the following scenario for the evolution of *A. versicolor* foraging specialization. Tropical fungus garden ant foundresses are often solitary and claustral (Hölldobler and Wilson 1990), feeding their fungus pellet from their own biotic reserves (eggs) and environmentally plentiful moisture. Even when group living, fungus garden cofoundresses are usually claustral (e.g., Mintzer and Vinson 1985) or facultatively so (Diehl-Fleig and de Araújo 1996). *Acromyrmex versicolor* lives at the xeric extreme of known fungus garden ants. We suggest lack of near surface moisture forces foundresses to forage, initially more for moisture (within fresh leaves) for the fungus than anything else; the fungus may later become dependent on early leaf nutrients once foundress foraging is established.

Once foraging foundresses begin to form associations to enhance victory in inter-colony brood wars, the efficiency trade-offs we have sketched shape task assignment (cf, e.g., Page and Kim Fondrk 1995 for an empirical analysis of inter-colony selection and foraging efficiency, involving indirect [passive] intergroup competition [Pollock and Rissing 1995], in the honeybee *Apis mellifera*). As noted earlier, a surface excavator can arise solely

through selection for excavation efficiency to limit near surface predation at nest foundation (Rissing and Pollock 1986; Pollock and Rissing 1995). This slight asymmetry in surface experience can then be amplified through a *progressively greater reluctance for non-surface excavators to abandon the fungus even when it appears torpid, so long as the surface excavator lives with them* (see, e.g., Wilson 1985 for similar coordination, over brood care, in the ant *Pheidole pubiventris*; Rissing 1984 for task replacement upon removal of current practitioners in the ant *Myrmecocystus mexicanus*). *Acromyrmex versicolor* workers are capable of task coordination for long term efficiency; cofoundresses simply activate the coordination potential prevalent among their workers. *Punishment* (greater reluctance to refuse task assignment among coordinated non-foragers) becomes a *by-product of usually successful* long term coordination.

Rather than biasing simulations in favor of **P**, our exclusion of mistakes more likely harms **P**. Population-wide loss of coordination occurs because **R** drifts to high frequency, with mutant **C** then eliminating both **R,P** either "deterministically" (e.g., {900,.2, **r**}; Tables 13,14) or stochastically (e.g., {200, .8, **v**}; Tables 13, 14). A "mistaken replacement" cost to **R** should depress such outcomes, especially under viscosity, as **R** drift is now subject to a constant downward pressure; **C**, as a possible replacer, should also be subject to this cost, albeit perhaps not as severely, as true cheating occurs among clumped, viscous **C** much of the time. Both processes eliminating **P** are thus weaker under the most likely mistakes.

Stable C?

Under the heuristic with backmutation **P** is evolutionarily persistent even when lost, continually re-invading the population to at least temporary fixation, except when the all cheater population is predominately **C** (Table

14). This may be an artifact of our analysis. We have truncated foundress social ecology to a two stage game; at the second stage selection of a replacer when two are present (**RR**, **CC**, **RC**) is random, without contention. Consider, however, a "hesitant **C**, (**H**) who waits a little longer than **C** to replace, hoping that her non-foraging partner is **C** rather than **P,Q**. Group fitness of a replacing **H** will be less than that of a replacing **C** but, with sufficient encounter of first replacing **C**, small delay times should insure **H** some share of the population; this is just an evolutionarily war of attrition in waiting times *sensu* Maynard Smith (1982).

Under viscosity an **H** invading a **C** cluster may do quite well, eliminating **C** just as **C** eliminates **R** where, under random assortment, both (**R,C**; **C,H**) should persist in polymorphism. But **Q** could not invade **C** because of the latter's relative high replacement fitness (Tables 3, 4, 13, 14); **H** has a lower replacement fitness, so *might* be invadable by **Q**. If not, an **H**^{*} having a slightly longer waiting time may invade **H** just as the latter invaded **C**. Repetition of such invading, incrementally longer waiting times will ultimately permit **Q** invasion; **P** can then re-invade as discussed earlier. *Under viscosity, a simple extension of our game suggests coordination and punishment will always be **persistent** as defined herein even though coordination may be periodically lost* (cf Pollock 1989b, 1995b for further discussion of the cyclic loss, re-invasion of cooperative [group efficient] strategies). Random assortment, in contrast, will yield a stable variation in replacement times (Maynard Smith 1982). While simulations indicate only a mild persistence advantage for **P** under viscosity (**P** not lost as frequently), viscosity's ability to eliminate frequency dependent fitness states (e.g., Table 4 vs 6) may shape a unique, synchronous, *uniform* potential for punishment over much of a population's evolutionary history (cf Wilson 1990).

We did not model first stage game assignment of forager as a war of attrition in continuous waiting times because of the empirical correlation between surface excavator and forager (Rissing et al. 1996). One could treat the first-stage game as an asymmetric war of attrition, with waiting times biased by excavation role (Hammerstein 1981; Maynard Smith 1982); indeed, for any imperfect empirical correlation, sufficient weight to surface excavation will conform to data. But this is just another coordination mechanism, still based on prior surface role (Aumann 1974; Rosenthal 1974; Myerson 1986). It is less group efficient, so less plausible under empirically likely viscosity (see above) and, at present, superfluous. Our simulations herein focus on cheating after assignment, requiring only that some female be uniquely assigned as forager in a public manner, as is always, empirically, the case (Rissing et al. 1989, 1996).

Personally best response vs evolutionary predominance

Analyses of evolutionary stability are often handicapped by the existence of distinct strategies which are usually phenotypically identical (e.g., Maynard Smith 1982; Boyd and Lorberbaum 1987; Brown and Vincent 1987; Boyd 1989; Farrell and Ware 1989; Pollock 1989b; Swinkels 1992a,b; Samuelson 1997). Even when third strategies appear via mutation or phenotypic variance ("mistakes") which differentiate otherwise identical strategies, drift among the latter may ultimately shift population states (cf Kandori et al. 1993, Binmore et al. 1995 for shifts even when strategies are usually *not* phenotypically identical). Our mutation heuristic generates the population cycle

(all) **P** → (some to all) **R** → (mostly) **C** → (mostly or all) **Q** → (all) **P**
under both viscosity and random dispersal. In our simulations the locus of evolutionary stability is not a single population state of strategies, but a cycle of population states where mutants invading any given state are defined

by the prior strategies of that state (Darwin 1859; Brockmann and Dawkins 1979; Dawkins 1980; Pollock 1989b, 1995b). A strategy is *evolutionarily predominate* if its temporal duration at high frequency, averaged across all states of the cycle, is greater than that of any other strategy within the cycle (after Kandori et al. 1993; Binmore et al. 1995). It may well be that such predominance requires the strategy to be lost in one cycle state.

Strategies which are personally best responses to deviations by others (as **R** is relative to **P** when encountering rare **C,Q**; after Selten 1975; Boyd and Lorberbaum 1987; Farrell and Ware 1989) may be poor candidates for evolutionary predominance when the personally best response aids the deviator *more than self*, as a replacer aids her cheater. When so, the population can shift to a frequency dependent mixture of these strategies (e.g., **R**, **Q** or **C**, **Q**) which then shifts the population elsewhere upon introduction of a then admissible mutant. E.g., **C** is a personally best response to itself (a phenotypic cheating, **C**) relative to **P**; but, as we have seen, victorious **C** may be invaded by **Q**, which is then re-invaded by **P**.

Inter-group competition, mutation rates, and viscosity

The temporal duration of a strategy within an cycle depends on the frequency as well as kind of mutation. Our simulations employ high mutation rates for clear results (.001, .0001). The last phase of the cycle,

(mostly or all) **Q** → (all) **P**,

relies on **Q,P** drift under non-foraging task assignment, especially at .8 forager death under random assortment (see discussion in results). Such drift will often fail (as rare forager **P** is usually killed at .8 forager death), requiring recurrent **Q** ⇒ **P** backmutation to renew the cycle; our backmutation rate of .0001 may here over-estimate coordination recovery.

Results under viscosity should be less sensitive to mutation rate. Once a **P** survives the brood raiding transition into an adult colony (either by drift and/or surviving forager predation) her foundress descendants are clumped among neighboring trees. While success is still partly stochastic, requiring the death of a neighboring adult colony and survival of **P**'s own, expectations are now in her favor (one of two neighboring colonies is more likely to die before her own); clumping then provides a "deterministic" advantage for her descendants, relative to random assortment, a local "founder effect" *sensu* Cohen and Eshel 1976. Similarly, size of the adult colony population need have no effect on viscous clumping (e.g., enlarging the circle in our model) but reduces chance encounter of **P**'s under random assortment. Biologically more realistic mutation rates will likely cause greater temporal duration in the non-coordinated population state under random assortment relative to viscosity, with viscosity and observed coordination thereby correlated in nature.

Our model of viscosity is more extreme than that of *Acromyrmex versicolor*, where around 6 colonies likely contribute sexuals to a local mating aggregation (Rissing, estimate from field observation). Moreover, some foundresses undoubtedly disperse sufficiently from their mating aggregation to encounter those mated in other aggregations. Our conclusions must be qualitative. While viscosity seems a plausible process affecting the duration of coordination, the cost of cheating, expressed as relative brood raiding ability (inter-group competition), is also important. As replacement fitness (brood raiding ability) decreases, **C** (via drifting **R**) is less a threat to **P**, irrespective of dispersal (200-400 replacement fitness, .2-.5 forager death; Table 13); mutant **C**'s probable survival to colony maturity decreases, leaving **P** less exposed to future **C**'s (via output from an adult colony) per **C** mutation. Inter-group competition has no affect on the **Q** → **P** phase of the cycle, as no

replacement occurs; but low replacement fitness (non-linear effect of foraging delay on brood raiding success) increases waiting time for **P** → **C** transition, increasing observable coordination.

Both coordination loss and gain are contingent on mutation opportunities which, of course, vary with simulation length. As noted previously, our use of 500,000 years exceeds the total age of *A. versicolor*'s desert habitat. We do not find this limiting in a first analysis, as reducing simulation time will reduce net first loss of coordination, favoring our bias that coordination with personally disadvantageous punishment exists in *A. versicolor*. Our qualitative results without backmutation (Table 13) would survive time spans conforming with ecological history, but the ubiquitous retrieval of all **P** populations (over many parameter values; Table 14) would be less evident. This highlights, we think, a general quandary in the application of infinite time frame analyses to behavioral ecology (cf Samuelsen 1997). Not only may a population fail to be at "evolutionarily equilibrium" due to youth (e.g., the North American population of the imported fire ant, *Solenopsis invicta*; e.g., Ross 19xx); a population may be cycling across states in a predictable manner, but beyond the purview of the field ecologist.

Finally, we note one limitation of our simulations suggested by empirically likely viscosity. Simulations do not permit "empty" locations in any year; under viscosity, three contiguous adult colonies cannot die simultaneously. Such gaps are, however, a predictable outcome of viscous dispersal in some circumstances (e.g., Harada et al. 1995). It is not true, for example, that adult colony death is independent of colony age. Under viscosity patches of colonies of about the same age may appear, dying as a cohort; viscous re-invasion from the margins would again produce a patch of

colonies of about the same age. There is cursory evidence for this in the desert seed-harvester ant *Messor (Veromessor) pergandei*, which exhibits the same viscous dispersal, clumped starting colonies, adult territoriality complex as *A. versicolor* (*M. pergandei* is claustral; refs above). At one locale (near Boulder City, Colorado, USA), xx adult colonies, present for 4+ years, died with in 8 years of one another (Rissing, pers. obs.); as with *A. versicolor*, an expected *M. pergandei* colony life span of 15-20 years is not unreasonable. Such fine tuning of models to species life history may be important: in our current model, a colony longevity of about 2 (not 20) years causes coordination loss under (200, .8, \mathbf{v}) in all 100 trials within 100,000 years (contrast 12 of 100 trials of 500,000 years in Table 13); analysis of such results are deferred for elsewhere. One empirically plausible solution to possible local population extinction is a meta-population of intersecting circumferences, with each circumference a viscous dispersal path; colonies at intersections may travel either path. Local extinction and re-invasion would be endogenous, permitting locally correlated adult colony death beyond the scope of our present effort.

Summary of simulation results

Strategies are defined in Table 2. **P** ("punisher") and **R** ("replacer") are first stage game coordinators, accepting the foraging task when so assigned. **C,Q** are first stage game "cheaters", refusing initial foraging assignment. **R,C** will replace a first stage game cheater; **P,Q** will not (so **Q** never forages). While **C** will replace a cheater, a cheating **C** will not replace herself. There are four mutation regimes: two "cheater only" regimes, **P,R** \Rightarrow **Q** and **P,R** \Rightarrow **C,Q** (**C** \Leftrightarrow **Q**); a "mutation heuristic" with strategy properties defining mutation paths, **P** \Rightarrow **Q**; **R** \Rightarrow **C**; **P** \Leftrightarrow **R**; **C** \Leftrightarrow **Q**; and the mutation heuristic expanded to include the backmutation

pathways $Q \Rightarrow P$;

$C \Rightarrow R$. Cheating depresses group competitive ability (among clumped natal colonies), but less so when the cheater is replaced; a group with a phenotypic replacer has a *replacement fitness*, variable by simulation. Group fitnesses are ordered as Coordination > Replaced Cheater > No Forager. Foragers are subject to variable (by simulation) predation risk. Dispersal is either *viscous*, with foundresses aggregating at nearest neighboring trees (from their parental colony/tree location); or *random*, with foundresses forming a population wide pool. In the case of viscosity, trees are ordered on a circle. Further simulation details in text.

A *fair contest* begins with a population 1/2 all **P**, 1/2 all **R** groups, with same type groups contiguous under viscosity; mutation regimes here yield only cheaters; "wins", entailing the elimination of the rival coordinator, are defined in the text. Stability results usually begin with an all **P** population, except under cheater only mutation, where both all **P** or all **R**.

Fair contest results:

1. Under viscosity, **P** often out performs **R**; otherwise they "win" equally (Tables 3,4).
2. Under random assortment **R** improves its relative performance to **P**, but *coordination* (combined **P,R** wins) usually does worse (relative to viscosity); exceptions are detailed as points 3, 4 below (Tables 5,6).
3. Random assortment yields unique superiority for **R** (relative to **P**) under high replacement fitness, with a stable polymorphism of **R,Q** (or **C,Q** when **C** is allowed) under moderate forager death (Table 6).
4. **R** wins uniquely (without polymorphic **Q**) only with no forager risk and high replacement fitness (under either form of dispersal) (Tables 4,6).
5. Under viscosity, allowing **C** mutation shifts wins from **P** to **Q** at high

forager risk (**C** almost never wins itself; Tables 3,4).

6. Under random assortment, **C** wins at moderate/low forager risk with high replacement fitness, but never at low replacement fitness (Tables 5,6).

Stability result under cheater only mutation(s):

7. Under viscosity, **P** is stable when **R** is, but not conversely (Tables 7,8).

Stability under the heuristic without backmutation:

8. **P** usually predominates over **R**, irrespective of dispersal. **R** may supplant **P** via drift, but

P \leftrightarrow **R** mutation insures **P**'s recovery. Viscosity depresses the frequency of predominate

R as forager risk increases (Tables 9-12).

9. Under low replacement fitness, the population-wide loss of coordination (simultaneous loss of both **P,R**) occurs only at high forager risk, under both viscosity or random assortment; such loss is, however, much more likely under random assortment than viscosity (93% vs 12%; Table 13).
10. Overall, viscous populations are never more likely to exhibit total coordination loss and, for some combination of forager risk and replacement fitness, much less likely (Table 13).
11. Under the heuristic, *replacement* is stable (able to resist **P** recovery) solely through the cheater morph **C**; *replacement is stable only when first stage game coordination is not* (Table 13).

Stability under the heuristic with backmutation:

12. Allowing backmutation does not generally alter probable population-wide coordination loss (Table 13 vs 14).
13. Probable coordination loss is generally *not* correlated with the *population-wide* recovery of coordination beginning through

backmutation. Populations may lose and regain coordination repeatedly under both forms of dispersal (Tables 13, 14).

13. When coordination loss yields a predominately **Q** population, **P** readily re-invades and supplants all other strategies under both form of dispersal. Evolutionary stability lies not in a single population state, but in the cycle of population states (all) **P** → (some to all) **R** → (mostly) **C** → (mostly or all) **Q** → (all) **P**, a cycle with phases of drift [e.g., (all) **P** → (some to all) **R**] and "deterministic" selection [e.g., (some to all) **R** → (mostly) **C**]. When this cycle exists under both forms of dispersal for given replacement fitness and forager risk, time in the (all) **P** state is greater under viscosity, and [(some to all) **R** → (mostly) **C** → (mostly or all) **Q** → (all) **P**] transitions are quicker; *viscosity can enhance P's temporal share of the cycle* (see text).
14. Population-wide recovery of coordination is precluded only when its loss yields a predominately **C** population; such a population is more likely under viscosity because spatial clumping of **Q** can depress its frequency where, under random assortment, **Q** would be (more) polymorphic with **C**. *Thus viscosity can harm coordination (for some combinations of replacement fitness, forager risk) by preventing the [(mostly) **C** → (mostly or all) **Q**] phase of the cycle* (Table 14).
15. **C**'s success in eliminating **P,R** suggests a strategy which may in turn eliminate **C** even when **Q** cannot. This strategy will, however, be more vulnerable to **Q** than was **C**. *Expanding our strategy space through a new mutation on **C** may recover the cycle in extended form, ultimately yielding a mostly **Q** population which again permits re-invasion of **P*** (see text).

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Table 1
 The effect of experimentally induced "cheating" on colony development
 (from Rising et al. 1996)

	Control mean \pm SD (N)	Experimental mean \pm SD (N)	P (two-sample, two-tailed t-test)
Days until replacement appears	5.4 \pm 4.7 (9)	17.2 \pm 4.6 (10)	.001
Days until replacement forages	9.9 \pm 6.6 (9)	22.8 \pm 4.1 (10)	.001
Number of pupae and large larvae and termination	1.6 \pm 1.8 (9)	0.2 \pm 0.6 (10)	.05
Fungus garden mass, mg*	52.2 \pm 51.8 (8)	2.0 \pm 3.7 (8)	.02

*The fungus mass from one control and two experimental colonies were lost during measurement.

Table 2
Admissible strategies by two-stage game properties

Strategy	Accepts original foraging assignment	Replaces a shirker of original foraging assignment
P	+	-
Q	-	-
R	+	+
C	-	+

Table 3
Wins by forager death, colony fitness under replacement 200
viscous dispersal

forager death	P wins	R wins	C wins	Q wins	P,R tie	P,Q tie
1	0 <i>1</i>	0 <i>0</i>	1 <i>na*</i>	199 <i>199</i>	-- --	-- --
.9	8 <i>146</i>	0 <i>0</i>	0 <i>na</i>	192 <i>53</i>	-- --	-- <i>1</i>
.8	162 <i>190</i>	0 <i>1</i>	0 <i>na</i>	37 <i>9</i>	-- --	1 --
.5	127 <i>108</i>	72 <i>90</i>	0 <i>na</i>	0 <i>0</i>	1 <i>2</i>	-- --
.2	99 <i>98</i>	100 <i>98</i>	0 <i>na</i>	0 <i>0</i>	1 <i>4</i>	-- --
0	91 <i>97</i>	108 <i>101</i>	0 <i>na</i>	0 <i>0</i>	0 <i>2</i>	-- --

Mutation regimes: **P,R,C,Q** --> **C, Q** @ .001 in normal type; **P,R** --> **Q** @ .001
in italics

na* = "not applicable", as here mutation to **C is precluded.

Table 4.
Wins by forager death, group fitness under replacement 900
viscous dispersal

forager death	P wins	R wins	C wins	Q wins	R,C tie	P,R tie
1	0 <i>0</i>	0 <i>0</i>	1 <i>na*</i>	199 <i>200</i>	-- --	-- --
.9	0 <i>141</i>	0 <i>0</i>	0 <i>na</i>	200 <i>59</i>	-- --	-- --
.8	2 <i>199</i>	0 <i>0</i>	2 <i>na</i>	196 <i>1</i>	-- --	-- --
.5	1 <i>196</i>	0 <i>0</i>	199 <i>na</i>	0 <i>4</i>	-- --	-- --
.2	1 <i>98</i>	0 <i>101</i>	199 <i>na</i>	0 <i>0</i>	-- --	-- <i>1</i>
0	18 <i>96</i>	132 <i>99</i>	49 <i>na</i>	0 <i>0</i>	1 --	-- <i>5</i>

Mutation regimes: **P,R,C,Q** --> **C, Q** @ .001 in normal type; **P,R** --> **Q** @ .001
in italics

na* = "not applicable", as here mutation to **C is precluded.

Table 5
Wins by forager death, colony fitness under replacement 200
random assortment

forager death	P wins	R wins	C wins	Q wins
1	29 46	5 20	8 <i>na</i>	158 134
.9	48 82	5 33	9 <i>na</i>	138 85
.8	86 103	28 53	3 <i>na</i>	83 44
.5	98 102	102 98	0 <i>na</i>	0 0
.2	90 107	110 93	0 <i>na</i>	0 0
0	88 102	112 98	0 <i>na</i>	0 0

Mutation regimes: **P,R,C,Q** --> **C, Q** @ .001 in normal type; **P,R** --> **Q** @ .001
in italics
na* = "not applicable", as here mutation to **C is precluded.

Table 6.
Wins by forager death, group fitness under replacement 900
random assortment

forage r death	P wins	R wins	C wins	Q wins	C,Q tie	R,Q tie
1	3 <i>11</i>	0 <i>1</i>	13 <i>na</i>	184 <i>188</i>	-- --	-- --
.9	9 <i>35</i>	0 <i>2</i>	13 <i>na</i>	178 <i>163</i>	-- --	-- --
.8	13 <i>59</i>	0 <i>0</i>	12 <i>na</i>	175 <i>141</i>	-- --	-- --
.5	23 <i>50</i>	0 <i>3</i>	29 <i>na</i>	0 <i>0</i>	148 --	-- <i>147</i>
.2	45 <i>61</i>	22 <i>139</i>	133 <i>na</i>	0 <i>0</i>	-- --	-- --
.1	65 <i>79</i>	71 <i>121</i>	64 <i>na</i>	0 <i>0</i>	-- --	-- --
0	74 <i>77</i>	126 <i>123</i>	0 <i>na</i>	0 <i>0</i>	-- --	-- --

Mutation regimes: **P,R,C,Q** --> **C, Q** @ .001 in normal type; **P,R** --> **Q** @ .001
in italics

*na = "not applicable", as here mutation to **C** is precluded.

Table 7
R Stability runs, cheater mutants only
One run of 500,000 years per parameter set
viscous dispersal

Parameters	Replacement group fitness 200	Replacement group fitness 900
R,C -- > Q,C .001 .2 forager death	$f_R \geq .8; f_R \geq .9$ 99.9% $f_C < .2; f_Q < .1$	$f_C = 1$ around year 7,500 $f_Q < .2; f_Q \geq .1$.036%
R --> Q .001 .2 forager death	not necessary*	$f_R \geq .7; f_R \geq .9$ 99.14%
R,C --> Q,C .001 .8 forager death	$f_Q = 1$ around year 4,500	not necessary
R --> Q .001 .8 forager death	$f_Q = 1$ around year 4,200	not necessary

*not necessary---i.e., other cell implies current cell is (not) stable.

Table 8
P Stability runs, cheater mutants only
One run of 500,000 years per parameter set
viscous dispersal

Parameters	Replacement group fitness 200	Replacement group fitness 900
P,C -- > Q,C .001 .2 forager death	$f_p \geq .8$; $f_p \geq .9$ 99.92% $f_Q < .1$ $f_C \geq .1$.087%	$f_C = 1$ around year 8,000
P --> Q .001 .2 forager death	not necessary*	$f_p \geq .9$
P,C --> Q,C .001 .8 forager death	$f_Q = 1$ around year 455,000 before this population cycles locally: P → C → Q → P	not necessary
P --> Q .001 .8 forager death	$f_p \geq .5$; $f_p = 1$ @ year 500,000 $f_Q \geq .4$.0726% $f_p > .9$ 92.1%	$f_p \geq .5$; $f_p = .9967$ @ year 500,000 $f_Q \geq .4$.013%

*not necessary---i.e., other cell implies current cell is (not) stable.

Table 9
 Sample stability runs for P,R under the mutation heuristic*
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	$f_P > .5; f_P \geq .9$ 84.7% $f_P = .997$ @ 500,000 $f_R < .5; f_R \geq .3$ 0.46% $f_Q < .6, f_C < .7$ 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

*P → R, Q → C @.0001; P → Q, R → P, R → C, C → Q @.001; justification in text.

Table 10
P stability runs with mutation heuristic
 100 runs of 500,000 years each
 200 replacement fitness, viscous dispersal

forager death	probability P lost over 500,000 years	f_p @ year 500,000 when P lost mid-sequence	average maximal f_R	average minimal f_p	average maximal f_Q, f_C
.2	.28	$f_p > .9$ 20/28 (71.4%) $f_p < .5$ 3/28 (10.7%)	.827; $f_R > .9$ 0.593%	.169; $f_p < .5$ 5.22%	$f_Q, f_C < .100$
.5	.14	$f_p > .9$ 8/14 (57.1%) $f_p < .5$ 2/14 (14.3%)	.746; $f_R > .9$ 0.239%	.195; $f_p < .5$ 3.80%	$f_Q = .116$ $f_C = .159$
.8	.12 ($f_Q = 1$ in all cases)	no Q, C \Rightarrow P, R mutation so f_p remains 0	.493; $f_R > .9$ 2.2×10^{-5} %	.208; $f_p < .5$ 1.68% (when P not lost)*	$f_Q = .627$ $f_C = .403$

*Since the mutation heuristic precludes mutation from cheaters to coordinators, counts of $f_p = 0$ are meaningless once $f_Q = 1$; the 12 such runs are excluded in calculating percent years in which $f_p < .5$, but included in calculating average minimal f_p .

Table 11
R stability runs with mutation heuristic
 100 runs of 500,000 years each
 200 replacement fitness, viscous dispersal

forager death	probability R lost over 500,000 years	f_R @ year 500,000	$f_R \geq .9$
.2	1.00	$f_R > .9$ 0/100 $f_R > .5$ 6/100 (6%) [$f_P > .9$ 70/100 (70%)]	1.63%
.5	1.00	$f_R > .9$ 0/100 $f_R > .5$ 3/100 (3%) [$f_P > .9$ 80/100 (80%)]	1.57%
.8	1.00 ($f_Q = 1$ in 43/100 cases)*	$f_R < .2433$ $f_R < .1$ 96/100 (96%) [$f_P > .9$ 39/57 cases where $f_Q < 1$, $f_P \geq .68$ in other 18/57]	.275%

* without backmutation to coordination (P,R) from cheating (Q,C),

Table 12
P stability runs with mutation heuristic
 100 runs of 500,000 years each
 200 replacement fitness, random dispersal

forager death	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, $f_p = .987$; 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, $f_p \geq .6, .7$.

**The mutation heuristic precludes mutation from cheaters to coordinators; here averages include only those cases where some coordinators exist at year 500,000.

Table 13
Probability of population-wide coordination loss after 500,000 years
100 runs
Mutation heuristic, no backmutation, with all P groups initially

replacement fitness	neighbor dispersal forager deaths (.2,.5..8)	random assortment forager deaths (.2,.5..8)
200	0, 0, .12	0, 0, .93
400	0 , .14, .21	0, .80, .99
600	.02, 1, .68	0, .95, .99
900	.98, 1, .91	.96, .99, 1

Table 14
 Probability of population-wide coordination loss after 500,000 years
 (probability coordination regained¹⁰ after loss in parentheses)
 100 runs
 Mutation heuristic, with backmutation and all P groups initially

replacement fitness	neighbor dispersal forager deaths (.2,.5..8)	random assortment forager deaths (.2,.5..8)
200	*, *, .11 (1.0)	*, *, .96 (.98)
400	* , .07 (.86), .22 (1.0)	*, .77 (.30), .98 (.86)
600	.07 (1.0), 1.0 (.06), .55 (1.0)	.02 (1.0), .95 (0.0), .99 (.79)
900	1.0 (.01), 1.0 (.03), .95 (.99)	.97 (0.0), .99 (1.0), 1.0 (.96)

With Q P P and C P R backmutation of .0001

* = not done as coordination always present without backmutation

¹⁰Measured as 15% or more P,R combined morphs at year 500,000; coordination recovery at year ,000 usually has $f_p > .90$.

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