
On suicidal punishment among *Acromyrmex versicolor* co-foundresses: the disadvantage in personal advantage

Gregory B. Pollock,^{1*} Antonio Cabrales² and Steven W. Rissing³

¹*KALX, LLC, USA,* ²*Department d'Economia Universitat Pompeu Fabra,
Ramon Trias Fargas 25–27, 08005 Barcelona, Spain and*

³*Department of Evolution, Ecology, and Organismal Biology,
College of Biological Sciences, The Ohio State University,
Columbus, OH 43210, USA*

ABSTRACT

Co-founding queens ('co-foundresses') of the obligate 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 observations suggest a 'coordination' mechanism (*sensu* Aumann, 1974; Rosenthal, 1974; cf. Pollock, 1994b, 1996) that assigns task-specific risk without contention among (unrelated) co-foundresses (Rissing *et al.*, 1989, 1996). In an experiment designed to mimic a 'cheater' who refuses a foraging assignment when it is her lot, co-foundresses delayed/failed to replace their forager, usually leading to demise of their garden (Rissing *et al.*, 1996). Such behaviour is 'suicidal', as the essential fungus garden cannot be replaced. Failing to replace a cheater is here an extreme punishment where the punisher harms herself to harm the cheater (after Radner, 1980). We simulate co-foundress allocation of foraging risk with haploid, asexual genotypes that either replace a cheater (at some point, the personally best response) or not (suicidal punishment), under both foundress viscosity (likely for *A. versicolor*) and random assortment. Simulation 'fair contests', with populations initially a 50 : 50 mix of *potential* replacers and punishers, exposed to mutant cheaters across evolutionary time, reveal (latent) suicidal punishment to be superior (under viscosity) to replacing a cheater. While replacing is a personally best response to cheating, viscosity correlates the descendants of replacers and cheaters, ultimately eliminating the former. Suicidal punishment, however, removes cheaters before they reproduce; under viscosity, patches of latent punishers can be quite robust, removing phenotypic cheaters as they appear, relative to patches of latent replacers, which rather incubate more cheaters by assuming the risky foraging task for them. In particular, simulations of *A. versicolor* population ecology reveal (latent) punishment to be superior, supporting laboratory evidence for suicidal punishment in this species (Rissing *et al.*, 1996).

Keywords: *Acromyrmex versicolor* co-foundresses, cheating, coordination mechanisms, group selection, personally best response, suicidal punishment, viscosity.

* Author to whom all correspondence should be directed. e-mail: g.pollock@worldnet.att.net
Consult the copyright statement on the inside front cover for non-commercial copying policies.

INTRODUCTION

If you want to learn life you must simultaneously learn death.
(Dainin Katagiri, 1988, p. 34)

Self-sacrifice is generally explained as either delayed personal return or advantage redirected to a relative. Usually, these are the only acceptable caveats to immediate personal gain. Self-sacrifice as an aid to a non-relative is suspect, plausible only if it is an investment in one's future. 'Suicidal' sacrifice in such a context is *a priori* impossible unless channelled ultimately back to a relative. Yet suicide to harm others, with no clear return to relatives, is known among humans. Our first response to such behaviour is to label it an unsustainable aberration, at best a transient ideological manipulation of an otherwise sound behavioural program (Atran, 2003). Here we suggest we pause before dismissing such events as unsustainable by considering what we believe is suicidal punishment among group-founding, unrelated queens (or *co-foundresses*) of the desert fungus garden ant *Acromyrmex versicolor* (Pollock and Rissing, 1995; Rissing *et al.*, 1996).

We advocate no direct analogy with humans, apart from what appears to be suicidal sacrifice to harm another; here, as punishment when a group-mate (co-foundress) appears to deviate from equilibrium play ('cheat') in an evolutionary game. Less than suicidal self-sacrificial punishment is well known in experimental negotiation games among humans (Güth *et al.*, 1982; Camerer and Thaler, 1995; Fehr and Rockenbach, 2003; cf. Gintis, 2000) and is perhaps possible in the capuchin monkey *Cebus apella* (Brosnan and de Waal, 2003). Such punishment follows another's failure to offer a 'fair' return, deviating (cheating) from expected equilibrium play. Structurally, the punishment exhibited by *A. versicolor* is similar to that revealed in primate experiments; an individual harms herself, thereby harming her game partner as well, upon the latter's refusal to respond 'appropriately'. Here we focus on how population structure can amplify such punishment to the point of suicide among ant co-foundresses.

We shall detail the natural history and laboratory design revealing the game environment of *A. versicolor* queens shortly. Briefly, the (ultimately) suicidal queen has a personally better option when exposed to a cheater which experiments have revealed she (usually) refuses to take. Her refusal probably leads to the death of her incipient colony as a whole, including herself and her cheating fellow queen. Here we focus, via computer simulation of *A. versicolor* population ecology and variants thereon, on what would happen if she *failed* to suicidally punish, instead taking the clearly identifiable, personally better option. We find that such personal survival rarely outperforms suicide in evolutionary time, often doing much worse, even though these group-founding queens are known to be non-relatives (e.g. Hagen *et al.*, 1988; Rissing *et al.*, 1989).

This conclusion seems bizarre if we imagine suicidal punishment as normal play, in every colony in every generation. In fact, however, punishment occurs only when another queen deviates (cheats) from normal game play; cheaters refuse the assigned risky yet essential task of foraging for the group (detailed below). Suicidal sacrifice amounts to refusing to forage in replacement of the cheater, leading ultimately to removal of the colony through later inferior competitive ability in inter-colony brood raids (again, detailed below). Non-punishment is simply replacing the cheater as forager, clearly a personally best response over what amounts otherwise to colony starvation. Perhaps surprisingly, our computer simulations show that, generally but not always, the descendants of a personally best

response replacer are ultimately removed from the population, a process that takes several generations.

The mechanism eliminating these descendants is remarkably simple. Failure to punish nurtures the cheater as well, as the cheater avoids the mortality risk associated with foraging. Descendants of the cheater, when they are co-foundresses in new colonies, repeat the cheating exploitation exhibited by their mother, depressing the fitness of descendants of those refusing to punish. While a frequency-dependent mixture of the two morphs may result, under parameters simulating the population ecology of *Acromyrmex versicolor* (low dispersal or 'population viscosity' *sensu* Hamilton, 1964; significant brood 'wars' among adjacent natal colonies; detailed below), the non-punishing morph often fails badly, risking stochastic elimination.

In contrast, a suicidal punisher, by removing the original, exploitative cheater from the population, can preserve *latent* punishment among *clones in other natal nests*, clones not presently exposed to deviating game play (i.e. they are not exposed to a cheater). A contingent strategy of punishment reveals itself, phenotypically, only when exposed to cheaters. Such unexposed clones are not relatives of the suicide in the normal sense, as measured by coefficients of relatedness; but they transmit the *potential* to punish through their offspring, offspring relatively unexposed to cheaters themselves because of the prior suicidal punishment (cf. Pollock, 1988, and below). In *Acromyrmex versicolor* structured populations consisting of both latent punishers and non-punishers (replacers), the continual introduction of game deviation (mutant cheaters) leads usually, but not always, to the elimination of both cheater and non-punisher. Simulating alternatives to *A. versicolor*'s population ecology while retaining the foraging game weakens this result, revealing some cases where non-punishment outlasts (latent) suicidal punishment in evolutionary time. Yet the parameter space inducing this reversal is surprisingly small. While the population ecology of *A. versicolor* leads to a robust result sustaining latent suicide, we find weaker, similar results over a wider range of parameters.

The phenomenon of suicidal punishment identified in *A. versicolor* is not so much aberrant as sporadic, removing mutant deviators, or cheaters, in an already established game; punishment is latent most of the time, and that is why suicidal punishment can endure evolutionarily. If our results have any bearing beyond *A. versicolor* (and possibly another ant species where co-foundresses appear embedded in a similar game; Trunzer *et al.*, 1998), it is, we suggest, that our sometimes unvoiced assumptions of the *sustainable* socially possible may need revision. In *A. versicolor*, the relative trajectories of suicidal punishment and its alternative become clear only after several generations. Sole focus on the immediate, individual advantage of behaviour *a priori* denies the evolutionary dynamic our simulations reveal can support *contingent* suicide. What fosters personal success in our own lives, or that of most creatures most of the time, cannot, by definition, describe the process we identify here. That need not deny this or similar processes operate somewhere. How so and how far, we submit, is a salient, open question.

We begin by detailing field and laboratory evidence identifying the population structure and foraging game of *Acromyrmex versicolor* co-foundresses. Our simulations, based on this evidence, are limited herein to a single question: Under what conditions can latent suicidal punishment outlast, in evolutionary time, an alternative personally best reply, beginning with an equal frequency of both types in the population? Our focus is not on whether the personally best reply *cannot* be evolutionarily viable (e.g. when punishers are excluded), but on the *relative superiority* of latent suicide over this alternative across generations. Nuanced

results on the evolutionary stability of both types, when either combined in a population or present without the other, will be presented elsewhere.

NATURAL HISTORY OF *ACROMYRMEX VERSICOLOR*

Mating and dispersal

Acromyrmex 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 (Rissing *et al.*, 1986; Higgins, 1988), perhaps the product of 6–8 nearby adult colonies; local aggregations sometimes appear somewhat evenly, linearly spaced, fading in the distance (S.W. Rissing, personal observation). Such 'mini-swarm' spacing may be a consequence of the 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.

Immediately after mating, female alates (now foundresses) leave the local aggregation in search of a nesting site. They seem not to go far, often removing their wings near the mating aggregation, surveying their environs by foot (S.W. Rissing, personal observation). 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 observations 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). Similarly, and crucially for our simulations, clumped starting nests can expect unavoidable inter-colony competition for sole possession of a currently 'adult-unoccupied' tree (Pollock and Rissing, 1989). This expectation shapes subsequent foundress behaviour.

Co-foundress interaction during nest foundation: task partitioning during 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 ('co-foundresses'). 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; S.W. Rissing, personal observation) or in the laboratory (Rissing *et al.*, 1986, 1989, 1996; Higgins, 1988); nor is there any evidence that some are coerced into joining others (Rissing *et al.*, 1986, 1996; Higgins, 1988). As excavation proceeds, a division of labour emerges, which, ultimately, places one co-foundress under exclusive risk. Once sufficient under-

ground nest space exists, one foundress tends exclusively to remove soil to the surface (Higgins, 1988; Rissing *et al.*, 1996), her co-foundresses (more or less) excavating underground. Such task partitioning speeds construction of an underground haven beyond the (olfactory) inspection of above-ground predators such as night rodents and lizards, which dig about the surface in search of co-foundress burrows (S.W. Rissing, personal observation; cf. Rissing and Pollock, 1986; Anderson and Ratnieks, 2000). The surface excavator does not, then, subsume unique risk in her task, but simply plays her part in efficiently producing a haven where exposure otherwise would likely lead to common death. Yet, days after this communal danger has passed, the surface excavator 'voluntarily' assumes a most risky task, exposing herself uniquely to above-ground predation for weeks by foraging for her co-foundresses.

Co-foundress interaction during nest foundation: foraging specialization

In most obligate fungus gardening ants, 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 forages for leaves. *Acromyrmex versicolor* foundresses appear unable to avoid foraging for their fungus prior to worker eclosion (emergence from pupae). Remarkably, a single foundress assumes all pre-worker foraging risk (Higgins, 1988; Rissing *et al.*, 1989); more remarkably, the task is not competitively allocated (*sensu* West Eberhard, 1981; Hölldobler and Carlin, 1985; Heinze *et al.*, 1994; Kolmer and Heinze, 2000), but is rather assumed by the prior surface excavator specialist (Rissing *et al.*, 1996).

In laboratory colonies, several days elapse between nest excavation and foraging. Yet co-foundresses are never seen to either overtly or 'ritually' contest or avoid the forager role (Rissing *et al.*, 1989, 1996) (*Pachycondyla villosa* also exhibits uncontested forager assignment: Trunzer *et al.*, 1998). Nor, as noted, is the surface excavator role itself the subject of contention, as predation threat precludes 'negotiation'. Nor does kin selection appear to be operating, as co-foundresses collected from the field are not related as measured by available electrophoretic variance (Hagen *et al.*, 1988) and, unlike, for example, Polistine wasp co-foundresses, who are differentially hostile to non-relatives and/or non-parental nest-mates (e.g. Ross and Gamboa, 1981; Post and Jeanne, 1982; Klahn and Gamboa, 1983), *A. versicolor* foundresses associate freely (Rissing *et al.*, 1986; Hagen *et al.*, 1988; for similar tolerance among co-foundresses in other ant species, see Bartz and Hölldobler, 1982; Ross and Fletcher, 1985; Rissing and Pollock, 1986, 1988; Hölldobler and Wilson, 1990; Sasaki *et al.*, 1996; Carew *et al.*, 1997; Trunzer *et al.*, 1998; Heinze *et al.*, 2001 [with latent, contingent aggression, see Kolmer and Heinze, 2000]). The correlation between surface excavator and later forager specialization does, however, conform to the game-theoretic definition of a 'coordination mechanism' in economics (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 group-mates (Aumann, 1974; Rosenthal, 1974; cf. Pollock, 1994b, 1995a, 1996). The event is arbitrary in that task assignment is not a consequence of individual ability or propensity (contrast, for example, Nonacs, 1992; Reeve

and Nonacs, 1992), but rather of (correlated) circumstance, with initial random task assignment to one individual shifting the expected assignment of others; the event is public in that the ‘outcome’ of task assignments is ‘known’ (in the game-theoretic sense of inferred; 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 manoeuvre 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 (Hölldobler and Wilson, 1990; Schatz *et al.*, 1995; Ratnieks and Anderson, 1999; Robson and Traniello, 2002). 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 an assignment eliminated in evolutionary time. An individual that forages when she need not appears trivially unviable, but what of an assigned forager refusing her task? In this case, an individual replacing her would perform a personally best response, assuming no other group-mate is willing to forage. But, if this is the case, an assigned forager may be tempted to shirk her task and assigned risk. The simplest game-theoretic solution is to refuse the personally best response (replacement) when exposed to a shirker (cf. Aumann, 1974; Rosenthal, 1974; Radner, 1980), contrary to the heuristic of individual advantage common in behavioural ecology (e.g. Dawkins, 1976, 1982; Pollock, 1994b). Experimentally, this is the case (Pollock and Rissing, 1995; Rissing *et al.*, 1996).

Experimental evidence for punishment

While unable to force a co-foundress to refuse her task (‘cheat’ on coordination), we can alter the perceptions of her co-foundresses so that she *appears* to cheat; such perceptions constitute the individually specific ‘information sets’ of economic game theory (Myerson, 1991). Consider a set of three-queen laboratory natal colonies, each having developed a (uniquely marked) forager specialist. We 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 co-foundresses are not – the *experimentals* (details may be found in Rissing *et al.*, 1996). In the controls, remaining co-foundresses experience an event that occurs in nature (forager death) and should replace her. In the experimentals, they perceive an assigned forager failing to leave the nest even though, upon personal inspection, exit is unblocked. The between-treatment differential response time for non-foragers to replace the original forager is a measure of co-foundress response to cheating. To the extent experimental 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 see below) the cheater by suppressing potential colony fitness, measured as health of the fungus garden; we shall see shortly that fungus health probably has a non-linear effect on natal colony survival. As resources are held in common, 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

Table 1. The effect of experimentally induced ‘cheating’ on colony development (mean \pm standard deviation)

	Control	Experimental	<i>P</i> (two-sample, two-tailed <i>t</i> -test)
Days until replacement appears	5.4 \pm 4.7 (<i>n</i> = 9)	17.2 \pm 4.6 (<i>n</i> = 10)	0.001
Days until replacement forages ^a	9.9 \pm 6.6 (<i>n</i> = 9)	22.8 \pm 4.1 (<i>n</i> = 10)	0.001
Number of pupae and large larvae at termination	1.6 \pm 1.8 (<i>n</i> = 9)	0.2 \pm 0.6 (<i>n</i> = 10)	0.05
Fungus garden mass (mg) ^b	52.2 \pm 51.8 (<i>n</i> = 8)	2.0 \pm 3.7 (<i>n</i> = 8) ^c	0.02

^a The experiment was terminated on day 29, when the last control colony exhibited a replacement; as some experimentals had not, this measure truncates experimental replacement time.

^b The fungus mass from one control and two experimental colonies was lost during measurement.

^c While the fungus garden died in 7 of 10 experimentals, these were provided with more fungus thereafter to continue observations; in no case did the garden die among controls.

^d From Rissing *et al.* (1996).

leaves the nest to inspect a small attached foraging arena. Table 1 summarizes (originally coordinated) the non-forager response by treatment across four measures. While all control colonies exhibited a foraging replacement, thereby retaining a healthy fungus garden, 7 of 10 experimentals allowed their fungus to die (Rissing *et al.*, 1996); these latter colonies would have had no chance of survival, so the co-foundresses refusing to replace their perceived ‘cheater’ *suicidally punished*. Overall, experimentals took twice as long to produce a replacement forager, suffering an eight-fold reduction in pupae/larvae and a seven-fold reduction in fungus mass relative to controls. Other laboratory and comparative evidence suggest such a reduction in colony development would be disastrous in nature.

Inter-colony competition as brood raiding

As noted earlier, adult territoriality in *A. versicolor* implies that natal nests clumped under a tree 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 the laboratory (Bartz and Hölldobler, 1982; Rissing and Pollock, 1987, 1991; Tschinkel, 1992a; Sommer and Hölldobler, 1995) and field (Tschinkel, 1992a,b; S.W. Rissing, personal observation). Hahn and Tschinkel (1997, p. 335) suggest competition among clumped natal nests leads to exclusive, regularly spaced, adult territoriality in the arboreal ant *Crematogaster ashmeadi*; laboratory evidence suggests the same for *A. versicolor* (Higgins, 1988; Rissing *et al.*, 1989; Pollock and Rissing, 1995; see Pollock and Rissing, 1989, for further cases). When foragers from clumped natal nests encounter a ‘rival’ nest, they rush in and abscond with the 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 raiding, with relative worker number probably having a non-linear effect on competitive success (cf. Wilson, 1990; Pollock and Rissing, 1995). In at least three species with brood raiding among clumped natal nests, the nests with more queens produce more workers (Rissing and Pollock, 1987, 1991; Tschinkel,

1992a; Sommer and Hölldobler, 1995) and are more likely to win the raiding contest (Rissing and Pollock, 1987, 1991; Tschinkel, 1992a). Intense inter-colony competition among natal nests leading to adult territoriality seems, then, a likely selective force underlying group life among *A. versicolor* queens (Rissing and Pollock, 1987; Pollock and Rissing, 1989), with intra-colony punishment leading to the competitive demise of colonies with cheaters upon a brood war encounter of an internally (forager game) coordinated, rival colony.

SIMULATION DESIGN

Our simulation design allows us to duplicate *Acromyrmex versicolor*'s (inferred) population ecology as well as create significant deviations thereon, reducing the importance of brood raiding for colony survival and/or allowing foundresses to mix randomly throughout the population, rather than viscously. We begin with 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 that disperse to the two neighbouring trees. Foundresses are modelled haploid to avoid allele dominance or penetrance; this assumption is common in models of behavioural ecology (e.g. Wilson and Dugatkin, 1991; Taylor, 1992a,b). Sex is precluded in this first blush analysis to avoid the extra parameter of relative male/female dispersal. If a location on our circle 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 neighbours, with one proviso: to ensure an unoccupied tree will always be 'seeded' by a new natal colony, three contiguous colonies on our circle never die in the same year, since neighbour 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 for *A. versicolor*, but not implausible (S.W. Rissing, personal observation).

Each natal colony is established by three co-foundresses. Eighty-two and a half per cent of all foundresses collected at one site in one year were pleometrotic, with an average of 3.67 queens per colony (Rissing *et al.*, 1986). But the modal number of queens per natal colony was two (16 of 36 pleometrotic colonies); as two foundress nests are likely to lose brood wars relative to the 55% of pleometrotic nests with three or more queens (after Rissing and Pollock, 1987, 1991; Tschinkel, 1992a), we restrict attention to the simplest *n*-person environment, although our simulations do not in this respect duplicate field evidence.

Underneath a simulation tree location, foundresses sort randomly, without any preference for parental nest-mates; kin recognition does not occur. For computational speed, five natal colonies are created under a vacant tree, all of which survive until the brood-raiding phase. Each natal colony produces a colony fitness derived from co-foundress behaviour on foraging 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' is assigned, either through initial coordination or replacement of a cheater, 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.* Actually, of course, a forager faces mortality over many trips, her death truncating colony fitness until she is replaced. By ignoring the fine grain of multiple trips and, possibly, multiple replacements after forager deaths, we have a best-case scenario for cheaters on coordination: a cheater who is replaced is never subject to forager mortality, as she would if she were the only remaining foundress upon death of her co-foundresses. Apart from the advantage to cheaters, we avoid finer grain for computational speed.

In at least two species of pleometrotic ants with brood raiding, co-foundresses 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; *Lasius niger*: Sommer and Hölldobler, 1995; perhaps, also, the monogynous form of *Solenopsis invicta*: Tschinkel, 1992a,b). *Acromyrmex versicolor* does not; rather, co-foundresses co-exist peacefully for several years in the laboratory (cf. Bekkevold *et al.*, 1999, for another apparently polygynous *Acromyrmex*). Thus, in simulated colonies, only forager mortality and brood wars filter queen reproduction. Adult colonies with multiple queens probably produce no more alates than those with single queens (Hölldobler and Wilson, 1990); worker number plateaus to cover the foraging arena centred under their tree, and it is worker, not queen, number which limits alate (sexuals) production through food availability. Each adult colony thus produces the same (assumed large) number of alates, shared equitably among remaining queens.

Strategies

We restrict strategies to the minimal two-stage game permitting a response to cheating on coordination. In the first stage, 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, with her mortality and colony fitness calculated; if she does not accept, the game enters the second stage, where her co-foundresses decide whether or not to replace her. We consider four (haploid, single-locus) strategies that define response in both stages:

- *Punisher (P)*, who accepts the original foraging assignment, but never replaces a shirker who refuses the assignment; motivated by experimental data.
- *Quitter (Q)*, who neither accepts the original assignment nor replaces another who shirks the assignment; motivated by the cheater critique of 'group optimal' behaviour (e.g. Pollock and Rissing, 1995; Williams, 1966). **Q** unilaterally refuses to forage, ignoring initial coordination or its loss, and thus 'quits' the game.
- *Replacer (R)*, who accepts the original foraging assignment and also replaces another who shirks such an assignment. **R** plays a personally best response (after Selten, 1975; West Eberhard, 1981; Myles, 1988; Farrell and Maskin, 1989) when exposed to a cheater who refuses the foraging assignment.
- *Sophisticated cheater (C)*, included to complete the 'strategy space', who will *not* accept the original foraging assignment but *will* replace another who shirks such an assignment. **C** shirks the original assignment but acknowledges, when exposed to a shirker, that replacement is personally best. Thus **C** is a 'cheating variant' on **R** in the same sense that **Q** is a cheating variant on **P** (Table 2).

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	-	+

Note: '+' indicates presence, '-' absence.

Table 2 categorizes the strategies by the two sequential decision properties of accepting assignment and replacing. Both **P** and **R** accept coordination, whereas **Q** and **C** do not. Neither **P** nor **Q** will replace a shirker, whereas **R** and **C** will, the latter two employing a personally best response to failed coordination by another. Whether a punishing **P** or **Q** is suicidal depends on whether a replacer is (not) also present in the colony. Suicide is not an immediate consequence of punishment, but becomes so when colonies contain only punishers; even so, commitment to endure suicide as a potential consequence is absolute. Sometimes there will be two replacing morphs in a group (**RR**, **RC** or **CC**), with a (randomly assigned) shirker on original coordination (**Q** or **C**). When this is the case, we choose the replacer randomly and ignore contests among multiple replacers, such as a potential war of attrition (e.g. Bishop and Cannings, 1978; Maynard Smith, 1982).

Mutation

Here we are only interested in how robust coordination strategies **P** and **R** are to cheating. Denote 'X mutates to Y' by ' $X \rightarrow Y$,' with ' \leftrightarrow ' indicating mutation in both directions. We consider two mutation regimes: (1) $P, R \rightarrow Q$, where first-stage (surface excavator) coordinators mutate to quitting the game, refusing to forage at all; and (2) $P, R \rightarrow Q, C$, where initial coordination is lost while replacement may (with **C**) or may not (with **Q**) exist, with $Q \leftrightarrow C$. $Q \leftrightarrow C$ is allowed in the latter case to enhance the potential diversity of cheaters, as our focus is on the relative resistance of **P** and **R** to generic cheating. Precluding the sophisticated shirker/replacer, **C** as a mutant has non-trivial consequence. We will see that allowing both types of cheater rather than just **Q** depresses the range of coordination, *not necessarily in favour of C, but sometimes in favour of Q*. **C** can create intermediate population states that are more readily invaded by quitter **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 co-foundress undergoes a 'mutation opportunity' from her present type as allowed by the simulation-specific mutation rule. A high mutation rate of 0.001 is employed for clear results; as a high rate favours cheaters (not coordinators), we do not consider this limiting. Of course, real queens do not mutate in natal colonies. Since queens assort neither positively nor negatively by strategy type, it matters not when we mutate types, so long as it is before the foraging game. 'Mutation' after colony foundation is a simulation convenience, reducing random number calls.

Each simulation employs numerous random number calls over as many as 100,000 years: calls for adult colony death, creation of co-foundress genotypes, mutation events, forager deaths and brood war victories. The random number generator must robustly mimic a uniform distribution in (0,1); we employ 'ran2' advocated in Press *et al.* (1992, p. 281–282), which should not cycle for at least 2×10^{18} calls. Our simulation is in C++[®].

Colony efficiency and failed coordination

Failed coordination entails a depression in colony competitive ability (fitness) via brood raiding, 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** as the (randomly) designated forager (as both accept foraging assignment), regardless of co-foundress strategy types. Ideally, a **QQQ** colony (or, for example, **PPQ** with **Q** as the assigned forager; **QQC** with **C** as the assigned forager) should have zero fitness, as neither **P** nor **Q** replacements forage, so the colony's fungus must die. It would then be possible for all natal colonies under an unoccupied tree to die, leaving the tree empty. For computational simplicity we avoid this, assigning such a colony a fitness of one, not zero; after some long delay, even a **QQQ** colony manages some foraging to avoid fungus death. This is somewhat compatible with our experimental colonies, which exhibited replacement before fungus death in 3 of 10 trials, albeit after significant delay and considerable reduction in fungus mass (Rissing *et al.*, 1996; Table 1). Such small colony fitness will be two or three orders of magnitude less than any competing colony with a forager (see below); we think this differential sufficiently close to suicide while avoiding the computational cost of vacant trees over potentially several generations. Thus a non-foraging colony's fitness is important only when all natal colonies under a tree have no forager.

Many results hinge on the reduction in colony fitness borne by colonies with realized replacers (a replacing **R** or **C**). There are two reasons for believing this reduction to be relatively great. First, brood wars likely amplify colony fitness differentials (measured by fungus mass or worker number) non-linearly, the essential reduction being in (zero sum) brood-raiding success. Second, recall that the coordination mechanism employs the co-foundress with unique prior above-ground exposure (the surface excavator). This prior surface activity makes her most efficient at orienting to the nest during initial foraging exploration (cf. Bisch-Knaden and Wehner, 2003). The effect should amplify with effort (repeated surface excavation trips), 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; Ratnieks and Anderson, 1999). A co-foundress replacing a prior surface excavator as forager lacks this initial experience, which should both depress her relative foraging efficiency and amplify her relative predation risk; recall that worker number increases with queen number, so enhanced predation risk in itself will depress later colony brood-raiding ability. Since brood wars are zero sum in outcome, replacement colony fitnesses represent the non-linear effect of (potentially) small changes in both foraging efficiency and predation risk on brood raiding, rather than absolute reduction in fungus mass alone. We employ two values for reduced colony fitness upon replacement of the assigned forager, 200 and 900, relative to a perfect colony coordination of 1000, simulating either an 80% or 10% reduction in absolute colony competitive ability upon loss of the surface excavator's prior orientation (*strong* versus *weak* brood raiding).

Simulation initial conditions and ‘fair contest wins’

Suicidal punishment in *Acromyrmex versicolor* aids neither self nor colony relative, as the suicide’s group is destroyed *en masse*. We cannot, then, measure a direct gain for suicide as, say, for a sterile social insect worker aiding her mother or sisters. But strategy **P** is only contingently suicidal, so we can measure changes in its relative frequency after suicidal acts; abstractly, this is similar to measuring the fitness of an allele coding for worker sterility by examining the fitness of her mother. Since we do not have a focal recipient to monitor, we examine *long-term* relative frequencies of both **P** and best response alternative **R**. Intuition focuses on the dilemma of suicide by considering an individual deciding whether or not to replace. Our simulations cannot do this directly, as the strategies are deterministic. We capture this choice by beginning each simulation trial as a *fair contest* with 50 contiguous adult **PPP** colonies on the tree circle, and 50 contiguous **RRR** colonies. Each simulation trial runs until either: (a) one but not both of **P** and **R** has vanished, with the survivor at least 95% of the population (relative to present cheating morphs, either **Q** or both **C**, **Q**); or (b) both **P** and **R** are lost and some cheating morph is at least 95% of the population. Each simulation parameter set can run for 100,000 years (usually <10,000 years) 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 surviving strategies; this happens rarely (but crucially, in one case; see Table 6). The relative number of **P** versus **R** ‘wins’ across 200 trials provides a measure of each strategy’s standing against the other under ‘fair starting conditions’. To permit clear victory, back-mutation to **P**, **R** from **Q**, **C** is precluded; similarly **P** ↔ **R** mutation. Our results do not examine evolutionary stability in the usual sense, but rather the relative viability of suicide over replacement. We find that, under most simulation parameters, punishment outperforms replacement: **P** wins against **R**, or coordination is lost to cheaters. Simulations directly addressing evolutionary stability (allowing back-mutation from cheaters and **P** ↔ **R** mutation) confirm the superiority of suicidal punishment over personally best replacement under the same conditions yielding relative superiority in fair contest wins herein; but the stability results are sufficiently nuanced to merit separate, deferred analysis.

We duplicate the parameter sets (various forager mortalities ranging from 0 to 1; colony fitness upon forager replacement of 200 or 900) under both viscosity and ‘random assortment’; in the latter, living adult colonies contribute alates to a global (free-mixing) pool, from which five natal colonies are produced for each vacant tree. While suicidal **P** does (sometimes significantly) worse under random assortment, wins generally shift to some combination of cheaters rather than to **R**. That is, generally, *first-stage coordination (surface excavator becoming forager) is lost when suicidal punisher **P** does poorly*. We denote simulations employing, say, 200 replacement fitness, 0.5 forager death under viscosity by {200, 0.5, **v**} and under random assortment by {200, 0.5, **r**}.

RESULTS

‘Fair contest’ wins under *Acromyrmex versicolor*’s population ecology

Acromyrmex versicolor foundresses disperse locally, with natal colonies later enduring significant brood raiding for sole possession of a tree. Table 3 presents ‘fair contest’ results for this ecology by employing a low colony forager replacement fitness (high cost for lost

Table 3. Proportion of ‘fair contest’ wins by forager death^a (colony fitness under replacement 200; strong brood raiding, viscous dispersal)

Forager death	P wins	R wins	C wins	Q wins	P, R tie	P, Q tie
1.0	0, 0.005	0, 0	0.005, NA ^b	0.995, 0.995	–, –	–, –
0.9	0.04, 0.73	0, 0	0, NA	0.96, 0.265	–, –	–, 0.005
0.8	0.81, 0.95	0, 0.005	0, NA	0.185, 0.045	–, –	0.005, –
0.5	0.635, 0.54	0.36, 0.45	0, NA	0, 0	0.005, 0.01	–, –
0.2	0.495, 0.49	0.5, 0.49	0, NA	0, 0	0.005, 0.02	–, –
0	0.455, 0.485	0.545, 0.505	0, NA	0, 0	0, 0.01	–, –

^a Fair contests begin with populations 50% (latent) suicidal punisher **P**, 50% replacer **R**; proportions are based on 200 trials per parameter set. Inter-group competition (relative inter-colony brood-raiding ability) and dispersal are defined in the text. *Forager death* is the probability that a forager dies in the idealized single event foraging game (see text). **P** (**R**) wins upon obtaining 95% of the population with rival **R** (**P**) eliminated; cheater morphs **C** or **Q** win upon reaching 95% of the population with both **P** and **R** eliminated. A tie among surviving strategies results when neither condition has been met by generation 100,000. Thus **P** (**R**) outperforms **R** (**P**) as their ratio of wins increases beyond 1; relative performance does not imply absolute superiority in the strategy space, as a ‘cheater’ morph may win overall. *First cell entry* is the proportion of wins for column strategy under mutation paths **P**, **R**, **C**, **Q** → **C**, **Q** with uniform mutation probability 0.001 (see text for discussion). *Second cell entry* provides the same proportion under mutation paths **P**, **R** → **Q**, again with probability 0.001, where strategy **C** has been excluded (see text). Comparing entries within a cell measures the presence (absence) of shirker/replacer **C** on the focal strategy’s performance; comparing first (second) entries across columns measures the relative performance of strategies under identical mutation paths. The table simulates the population ecology of *Acromyrmex versicolor*. Personally best response **R** (marginally) outperforms suicidal punisher **P** only under zero forager death, where the foraging game has been removed, while (latent) suicidal **P** outperforms all admissible rivals under significant (0.5, 0.8) forager mortality.

^b NA = ‘not applicable’, as here strategy **C** is precluded.

coordination, so strong brood raiding) of 200. Even with a replacement colony fitness of 200 and a simulated forager mortality as high as 0.8, a foundress should replace a cheater to maximize expected personal gain:

$$[\text{forager survival}] \times [\text{replacement fitness}] / [3 \text{ foundresses}] = .2(200/3) \\ > [\text{minimal fitness}] / [3 \text{ foundresses}] = 1/3$$

At no value of simulated (positive) forager death does personally best replacement **R** fair better than suicidal punishment **P** (Table 3). **P** outperforms **R** robustly at a forager mortality of 0.8; with 90% forager death, quitter **Q** predominates whether or not the more sophisticated shirker/replacer **C** is allowed.

While personal best response **R** exposed to a quitting (cheating) **Q** trivially does personally better than a suicidal **P** so exposed, **R**’s personal superiority ‘incubates’ **Q** offspring for the next generation; *if she survives, so does her cheating co-foundress*. Neighbouring-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, 1988, 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.

Suicidal **P**, in contrast, sacrifices itself to eliminate encountered cheating (coordination denying) **Q**. Of course, a **Q** not assigned the forager role is phenotypically neutral with respect to similar **P**, but this just delays the effect until **Q** descendants are so assigned. Under viscous dispersal, a suicidal **P**'s neighbouring *rival* natal colonies often consist solely of **P**, as they are derived from the same pool of local alates. *Sacrificing herself to eliminate Q, the cheater exposed P aids her strategy clones in nearby groups* (Pollock, 1988), *eliminating the (potential) offspring of encountered Q from the social environment of the brood war victor's descendants*. Paradoxically, what would be an evolutionary rival of our focal, suicidal **P** under perfect coordination (another nearby natal colony engaged in brood raiding) becomes, under expressed punishment, the indirect recipient of her (punishing) aid. Under viscosity, suicide is effective when the frequency of **P** is high among rival tree arena natal colonies. Suicide, eliminating a cheater *and her descendants* from the locale, helps retain this high frequency in future tree arenas. A personally best response of replacement has the opposite effect.

Inspecting the spatial trajectory of simulations with forager mortalities 0.5 and 0.8, one sees quitter **Q** grow in a patch of replacer **R** until the latter are eliminated; then, encountering punishing **P** along the boundary of a now **Q** patch, **P** pushes the patch back until **Q** is locally eliminated (for similar processes, see Wilson, 1987; Pollock, 1989b). Viscosity now works against **Q** for, as it disproportionately encounters itself, it is more likely to exist in abysmally inefficient social (forager uncoordinated) environments with a colony fitness of 1 (see above; cf. Pollock, 1989a,b); as in kin selection, uncooperative **Q** is eliminated via self-clumping (cf. Wilson, 1983; Pollock, 1996; Wilson and Dugatkin, 1997).

Even so, for sufficiently high forager death, **P** fails against **Q**. Suppose forager death is unavoidable (forager death of 1 in Table 3); **P** can then persist only if foraging (apart from punishment) aids relatives (clones) in *her* group (kin selection). Viscous dispersal mediated by neighbouring trees seems incapable of providing sufficient intra-group relatedness (probability of clonal encounter) to preserve **P** (Tables 3 and 4; cf. Murray and Gerrard, 1984; 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 kin rule *ensuring* common ancestry by immediate descent. Kin grouping can actively preclude group association among different types; viscosity cannot. Viscosity forms more **QQP** groups with

Table 4. Proportion of 'fair contest' wins by forager death^a (colony fitness under replacement 900; weak brood raiding, viscous dispersal)

Forager death	P wins	R wins	C wins	Q wins	R, C tie	P, R tie
1.0	0, 0	0, 0	0.005, NA	0.995, 1.0	–, –	–, –
0.9	0, 0.705	0, 0	0, NA	1.0, 0.295	–, –	–, –
0.8	0.01, 0.995	0, 0	0.01, NA	0.98, 0.005	–, –	–, –
0.5	0.005, 0.98	0, 0	0.995, NA	0, 0.02	–, –	–, –
0.2	0.005, 0.49	0, 0.505	0.995, NA	0, 0	–, –	–, 0.005
0	0.09, 0.48	0.66, 0.495	0.245, NA	0, 0	0.005, –	–, 0.025

^a See Table 3 for explanation of entries. Weak inter-group competition (high replacement fitness after a cheating event; see text) shifts wins away from punisher **P** to cheaters **C** and **Q**, rather than to personal best response **R** (Table 4 vs Table 3), with **R** significantly outperforming **P** only under no forager death, where the forager game is absent.

P the designated forager than will kin assortment; indeed, under the extreme case of asexual haploid inheritance employed herein, such kin groups cannot occur under sibling assortment except by mutation. With mandatory forager death, these groups occur sufficiently frequently under viscosity to ensure **P**'s elimination. Thus while a suicidally punishing **P** in a **PQQ** group eliminates cheaters, **P** foraging under certain death incubates these **Q**, much as a replacing **R** does. Continuity implies similar logic for sufficiently high yet uncertain forager death, with evolutionary advantage (through the removal of **Q**'s through punishment) shifting to **P** as forager death decreases. Stability simulations (deferred) show **P** robustly stable (for 500,000 years) under {200, 0.8, v } with **Q**-only mutation, slightly less so when the shirker/replacer **C** is allowed.

C facilitation of Q

While the shirker/replacer **C** is itself unviable at a replacement fitness of 200, suicidal **P** fares significantly better against quitter **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 (i.e. **CCC** groups have a forager, while **QQQ** groups do not; cf. Table 2). Clumped **C** will thus be harder for **P** to defeat (push back) than clumped **Q**. For the same reason, replacer **R** patches are even more vulnerable to **C** than **Q**, as **C** limits the harm it does to itself when clumped. But **C** is even more vulnerable to **Q** than **R** is to **Q** (maximal fitness differential across colonies is 200 : 1, **CCC** vs **QQQ**, not 1000 : 1, **RRR** vs **QQQ**). Inspecting the spatial trajectory of simulations, when **C** is allowed, **R** patches become **C** patches which become **Q** patches. **P** then 'eats' or 'pushes back' the **Q** patch, as before. The cycle repeats, as **R** persists for some time by drifting into **P** patches when phenotypically neutral (i.e. absent cheaters).

Even so, with recurrent shirker/replacer **C** mutants, two factors work against **P**, potentially terminating the cycle in a **Q** win. First, **C** invading an **R** patch causes the ultimate size of **Q** patches encountered by **P** to be greater. Stochastically, it takes **P** longer, and so is more difficult, to eliminate **Q**. Second, **C** can, under our mutation rule, create a self-cluster without **R** by mutating from **P**. Stochastically created **CCC** groups, although inferior to forager coordinated **PPP** groups, are eliminated (stochastically) at a slower rate than are similarly placed **QQQ** groups, the latter refusing to forage at all. These **C** clusters can expand by drifting against selection, which, when themselves invaded by a mutant **Q**, continue the cycle without prior **R** incubation of **C**, **Q**. Repeated dips in **P**'s frequency result, which can ultimately lead to its stochastic elimination in the finite 100 adult colony population. Put simply, as **P** pushes back **Q** clusters only stochastically, each (partly) stochastic dip in **P**'s frequency increases the chances of its population-wide elimination.

This effect is confirmed by extended simulations of **P**'s evolutionary viability against repeated invasion by either **C** and **Q** combined or **Q** alone (absent replacer **R** in both cases). While we defer detailed discussion, in an evolutionary stability run of **P** with continual **C**, **Q** mutation under {200, 0.8, v } (beginning with an all-**P** population), suicidal **P** persisted at overall high frequency for over 450,000 years, with the (spatially local) cycle **P** → **C** → **Q** → **P** repeating until **P**'s fairly rapid stochastic loss to quitter **Q** around year 455,000 (cf. Pollock, 1989b, for a similar, albeit deterministic process). When allowing only

Q mutation, however, **P** was robustly high for 500,000 years (**P**'s relative frequency, $f_P > 0.5$; $f_P > 0.9 = 92.1\%$). Personally best response **R** was eliminated by year 4500 under otherwise identical stability trials (absent **P**) whether mutation was either **Q** or **C**, **Q**.

Reducing inter-group competition

Table 4 duplicates Table 3 with a colony fitness of 900 under replacement foraging (weak brood raiding). Here brood-raiding ability is rather unaffected by a cheating/replacement event, being reduced by just 10%. We should then expect higher (stochastic) local frequency 'bursts' of coordination shirkers **Q** or **C**, once introduced as mutants. Such is the case, but the effect need not be inevitably detrimental to **P**, as we shall shortly see.

C, Q mutation

With **C**, **Q** mutation, shirking original forager assignment is ubiquitous in $\{900, [0.2, 1], \nu\}$, with quitter **Q** replacing **C** for sufficiently high forager mortality (≥ 0.8 ; Table 4). Recall that clustered **C**'s 'stochastic viability' among **P** (e.g. 1000 : 200 colony fitness ratio; Table 3) is related directly to **C**'s resistance to clustered **Q** (e.g. 200 : 1 colony fitness ratio). As shirker/replacer **C** improves against coordinated groups (with a 1000 : 900 colony fitness ratio), it also improves against **Q** (with a 900 : 1 colony fitness ratio). But a replacing **C** nonetheless potentially incubates quitting **Q**, more so as forager mortality increases. For sufficiently great mortality ($\{900, 0.8, \nu\}$; Table 4), such incubation so depresses the creation of **CCC** groups that **Q** is victorious.

We have truncated the game to two stages, so (absent **P**) only **Q** can shirk replacing a shirker (in **CQQ** groups, with one of the **Q** the assigned forager). But, once **C** is prevalent, we could apply the same logic to further reduce colony efficiency, introducing a shirker who waits just a little longer than an average **C** to replace the originally assigned forager (for similar processes, see Selten, 1975, 1978; Selten and Stoecker, 1986; Schuessler, 1989; Pollock, 1991, 1995b; Cressman, 1996); **C**'s success at high colony replacement fitness and low forager mortality (Table 4) may be more an artifact of our two-stage game than a biological prediction. We defer further analysis to concentrate on the relative advantage of (first stage game) surface excavator/forager coordinators **P**, **R** herein.

Q-only mutation

Under 900 replacement fitness and forager deaths in $[0.5, 0.9]$, **P** wins robustly when **C** is precluded (Table 4), much as under 200 replacement fitness (Table 3). Interestingly, **P** *surpasses* its performance at forager death 0.5, relative to 200 replacement fitness (Tables 3, 4). High replacement fitness causes replacing **R** to successfully incubate more **Q** quitters, as failed first-stage coordination groups with a replacement forager are more likely to survive (colony fitness ratio is 1000 : 900 rather than 1000 : 200). In consequence, replacer **R** patches are more easily invaded, accelerating **R**'s demise; while **R** won 45% of all fair contest trials at $\{200, 0.5, \nu\}$ with **Q**-only mutation (Table 3), **R** never wins a parallel $\{900, 0.5, \nu\}$ trial (Table 4). Punisher **P**, however, continues to eliminate **Q** clusters at the same rate as under 200 replacement fitness, as neither **P** nor **Q** replaces. Consequently, **P** here fairs better under weak rather than strong brood raiding with **Q**-only mutation, winning 98% of the former while just 54% in the latter ($\{900, 0.5, \nu\}$ vs $\{200, 0.5, \nu\}$). When shirker/replacer **C** is allowed, **P** fairs better under strong brood raiding, which limits the

invasion potential of this strategy. However, absent **C**, **P** fairs best under weak brood raiding, as replacer **R** there more rapidly destroys itself by incubating its own future exploiter, **Q**.

Inter-group competition-absent forager risk: replacement outperforms suicidal punishment

With 900 replacement fitness, personally best response **R** predominates ('wins') over suicidal punisher **P** with no forager death and **C**, **Q** mutation ($\{900, 0, v\}$; Table 4); *this is the only instance of personally best R predominance under viscosity*. Zero forager mortality removes the foraging game and so the utility of coordination assignment, but focusing on this value allows us to disentangle the (somewhat stochastic) effects of reduced colony replacement fitness and forager mortality. With positive forager death, foraging is *weakly altruistic* (*sensu* Wilson, 1979, 1990); a forager enhances her personal fitness, but her group-mates gain more. Without forager death, this cost vanishes; replacing **R** should always be superior to suicidal **P**. But **R**'s advantage must be translated into evolutionary competition. Viscosity effectively precludes such competition under **Q**-only mutation, as we next show.

Q-only mutation

Without forager death, **Q**, unilaterally refusing to forage, is never a best response; mutant **Qs** appearing in either a **P** or **R** vacant tree patch are eliminated, as their sole consequence is to reduce colony fitness by forcing replacement (when **Q** is the assigned forager). So quitter **Q** can affect **P**, **R** relative success only when all three strategies appear within the same arena (empty tree). Under viscosity, such **PQR** (pre-nest) foundress pools are relatively infrequent; here noise appears to mask any advantage for replacement **R**, with **P** and **R** winning equally (48 vs 49.5%; Table 4, $\{900, 0, v\}$).

C, Q mutation

Shirker/replacer **C** consumes **P** clusters by forcing replacement opportunities at the **C**, **P** cluster boundary via **CCP** versus **CPP** groups; groups with two or more **Cs**, on average, fair better than groups with just one. **R**, **C** boundaries, however, are neutral, as **CCR** and **CRR** are phenotypically identical when cheating occurs, both exhibiting replacement foragers. At $\{900, 0, v\}$, the cost of cheating in **CCP** groups with both cheater and replacer **C** is offset by the fitness depression endured by **P** in **CPP** groups where **C** is the assigned (refusing) forager. Clustered **R**, free of this effect, does quite well, winning 66% of trials relative to **P**'s 9% ($\{900, 0, v\}$, **C**, **Q** mutation; Table 4). With low replacement fitness (200; Table 3), the effect is reduced if not lost in noise, as replacement leads infrequently to brood war victory and placement as an adult colony; here **P** and **R** win nearly equally in fair contests (45.5 vs 54.5%; Table 3, $\{200, 0, v\}$, **C**, **Q** mutation).

If **P**'s vulnerability at $\{900, 0, v\}$ is due to self-clustering, **P** should fair better without clustering. Such is the case: holding replacement fitness at 900, **P** wins 37% of fair trials when co-foundresses group randomly throughout the population ($\{900, 0, r\}$, **C**, **Q** mutation; Table 6), relative to its parallel 9% under viscosity ($\{900, 0, v\}$, **C**, **Q** mutation; Table 4). As expected, **P**'s enhanced victory at $\{900, 0, r\}$ is at the expense of **C**. While **R** wins almost identically here under either viscosity or population-wide dispersal, **C** *never* wins a trial at $\{900, 0, r\}$, but does capture 24.5% of all trials under viscosity ($\{900, 0, v\}$; Table 4).

Weak altruism benefits suicidal punishment

Once there is true personal cost to replacement (possible forager death), shirker/replacer **C**'s performance against **R** at their cluster boundary improves, as a shirking **C** forces **R** to assume true risk, yielding 99.5% **C** wins under low to medium forager death and weak brood raiding ($\{900, [0.2, 0.5], v\}$; Table 4); **R** shifts from predominance without forager mortality (winning 66% of all trials) to complete failure. The effect is duplicated under strong brood raiding, where now either **P** or quitter **Q** predominates, but requires greater forager risk for complete failure of **R** (at $\{200, 0.8, v\}$ with **C**, **Q** mutation; Table 3). Groups with replacing **R** are then more readily eliminated via brood raiding, requiring greater mortality (weak altruism) per instanced replacement to generate the same effect. Similarly, when the sophisticated shirker/replacer **C** is precluded, suicidal punishment's elimination of rare (phenotypic) quitter **Q** creates predominately **P** wins at $\{200, 0.8, v\}$ and $\{900, 0.5, v\}$ (Tables 3, 4).

Random assortment with strong brood raiding

Q-only mutation

By removing the spatial correlation between the descendants of personally best response replacers and successful cheaters, population-wide offspring dispersal should enhance (relative) **R** wins, as is *mildly* apparent under 200 replacement fitness at $[0.5, 0.9]$ forager deaths with quitter **Q**-only mutation (Table 5 vs Table 3). Some **P** wins under viscosity are now distributed to **R** and **Q**, reflecting how these latter strategies harm themselves under viscosity (e.g. **P** clusters no longer destroy neighbouring **Q** clusters). Strong brood raiding still tends to remove first instanced phenotypic cheaters; combined with the removal of cheater incubation, **R** achieves more wins through drift, but never does significantly better than **P**, usually still performing worse.

C, Q mutation

Allowing mutation to **C** shifts even more wins to quitter **Q** at the expense of both suicidal **P** and replacing **R** (Table 5). **R** does improve its performance at $\{200, 0.5, r\}$ relative to viscous dispersal $\{200, 0.5, v\}$, winning 51% of all trials rather than just 36% (Tables 3, 5). The effect, however, is due not to **R** employing a (superior) personally best response, but to suicidal **P**'s failure to indirectly aid **P** clones within other arena colonies under random mixing: **P** wins decline from 63.5% under $\{200, 0.5, v\}$ (with **C** mutation) to 49% under $\{200, 0.5, r\}$. *Here, without viscosity, R does no better than winning randomly (51% for R vs 49% for P) given the 50 : 50 P, R starting conditions per trial.* Random victory is the best **R** can muster throughout Table 5.

Cheater/replacer polymorphism under random assortment

Table 6 employs random assortment with weak brood raiding, parameters most distant from the population ecology of *Acromyrmex versicolor*. Here the high viability of colonies with replacers (900 vs 200) enhances the success of cheating, which also enhances the success of replacement, since the fitness of phenotypic replacers and cheaters is not correlated spatially. Nor can suicidal **P** expect other arena colonies to contain mostly **P** clones. As expected, replacing **R** does its personally best.

Table 5. Proportion of 'fair contest' wins by forager death^a (colony fitness under replacement 200; strong brood raiding, random assortment)

Forager death	P wins	R wins	C wins	Q wins
1.0	0.145, 0.23	0.025, 0.10	0.04, NA	0.79, 0.67
0.9	0.24, 0.41	0.025, 0.165	0.045, NA	0.69, 0.425
0.8	0.43, 0.515	0.14, 0.265	0.015, NA	0.415, 0.22
0.5	0.49, 0.51	0.51, 0.49	0, NA	0, 0
0.2	0.45, 0.535	0.55, 0.465	0, NA	0, 0
0	0.44, 0.51	0.56, 0.49	0, NA	0, 0

^a See Table 3 for explanation of entries. Personally best response **R** mildly outperforms suicidal punishment (**P**) under real but low forager mortality (0.2) (when strategy **C** is allowed; compare Table 5 and Table 3, which both hold colony replacement fitness constant at 200), although **R** still trails **P** at higher rates of mortality.

Table 6. Proportion of 'fair contest' wins by forager death^a (group fitness under replacement 900; weak brood raiding, random assortment)

Forager death	P wins	R wins	C wins	Q wins	C, Q tie	R, Q tie
1.0	0.015, 0.055	0, 0.005	0.065, NA	0.92, 0.94	–, –	–, –
0.9	0.045, 0.175	0, 0.01	0.065, NA	0.89, 0.815	–, –	–, –
0.8	0.065, 0.295	0, 0	0.06, NA	0.875, 0.705	–, –	–, –
0.5	0.115, 0.25	0, 0.015	0.145, NA	0, 0	0.74, –	–, 0.735
0.2	0.225, 0.305	0.11, 0.695	0.665, NA	0, 0	–, –	–, –
0	0.37, 0.385	0.63, 0.615	0, NA	0, 0	–, –	–, –

^a See Table 3 for explanation of entries. Table 6 represents conditions most at variance with those identified for *Acromyrmex versicolor*: population-wide, random assortment of queens, with weak inter-group competition (high brood colony fitness after forager replacement). Here personally best response **R** exhibits its best performance against suicidal punisher **P**, but only at low forager mortality (0.2; cf. Tables 4 and 5); elsewhere, **P** remains marginally better. *The C, Q and R, Q ties at 0.5 forager mortality are the only parameters where the theoretically expected frequency dependence between cheating (as Q) and replacement (as R or C) is confirmed by fair contest simulations (see text).*

Q-only mutation

Without **C** mutants, replacing **R** outperforms suicidal **P** within the forager mortality range [0, 0.5]; at greater forager death, predominance shifts to quitter **Q** (Table 6). The value of cheating increases with forager death; at {900, 0.5, **r**}, a robust polymorphism is reached, with neither **R** nor **Q** achieving a 95% frequency for 100,000 years.

C, Q mutation

Shirker/replacer **C** couples the benefits of both **R** and **Q** (Table 2). When **C** is present, **R**'s relative performance against **P** declines (in the range [0.1, 0.2], Table 6), with **C** rather than **R** in polymorphism with **Q** at {900, 0.5, **r**} (Table 6). {900, 0.5, **r**}, with or without **C** mutation, are the only fair contest runs that clearly conform to the logic of *sub-game perfection* (*sensu* Selten, 1975; cf. West Eberhard, 1981; Myles, 1988), with individuals

exhibiting a personally best, situationally specific, response (cheat when you can get away with it, but limit cost [replace] when exposed to a cheater), revealed as a ‘stable’ cheater/replacer polymorphism through 100,000 years. Cheating, of course, cannot be personally advantageous without replacement; so, under our strategy set, the two properties are frequency dependent. While replacement should be personally advantageous irrespective of weak/strong brood raiding, *sub-game perfect ‘ties’ (polymorphism in cheater/replacement) appear only under weak brood raiding; i.e. only under low group cost to cheating.* Under high group cost (strong brood raiding), colony success under replacement is so unlikely (relative to coordinated groups) as to be undetectable in our *finite* population. So, while {900, 0.5, **r**} reveals polymorphism and the clear elimination of suicidal **P**, {200, 0.5, **r**} trials reveal **P** and **R** equally likely to win fair contests (Tables 5, 6).

Wins against selection

Population-wide random assortment reveals nonsensical **P**, **R** wins under certain forager death irrespective of brood raiding and admissible mutation ({200, 1, **r**}, {900, 1, **r**}; Tables 5, 6). Recall that simulations begin each generation by ‘killing’, on average, five adult colonies (actually, a little less, given the restriction detailed earlier for computational ease). Under population-wide dispersal, frequencies defining co-foundress encounter are derived by aggregating the remaining queen genotypes in living adult colonies. Adult queen frequencies are then changed, after selection among natal colonies under vacated trees, by about five colonies. This feature of natural history is consistent across all brood raiding and forager death, and tends to shift adult colony genotype frequencies slowly across generations. Such incremental shifts allow for random walks which can drift against selection (cf. Binmore *et al.*, 1995, for a similar process). These walks may yield high disequilibrium frequencies of **P**, **R**, which, given our 95% stop criterion, can create a trial win. The walks are also biased in favour of suicidal **P**. As **P** achieves high frequency by chance, suicide against a phenotypic cheater will tend to preserve this frequency, relative to high frequency **R**, which will nurture a cheater. The long-term trajectories of both **P** and **R** are downward, but the opportunity to walk against selection is greater in **P** at increasingly higher **P** frequencies. Wins under certain death should then be more common for **P**, and so they are ({200, 1, **r**}, {900, 1, **r**}; Tables 5, 6); by contrast, viscosity exhibits only one win for **P** under certain forager death and none for **R** (Tables 3, 4).

More generally, we suspect such random walks are responsible for the paucity of cheater/replacer polymorphism in Table 6. While such polymorphism is expected theoretically, each trial must run for 100,000 years to declare a tie win. If the equilibrium frequency is sufficiently skewed to either cheater or replacer, walk away from that frequency over a prolonged simulation time is not surprising; our 95% frequency win condition may then incorrectly assign victory to a pure strategy. That {900, 0.5, **r**} polymorphism survives for 100,000 years only about 75% of the time (Table 6) suggests that the process is operating even there.

Limited polymorphism need not be interpreted as a simulation artifact; it may just as well be a consequence of the natural history simulated. While nature will not stop after a declared win, significant variance in expected frequencies may be common in *finite* populations of perennial colonies through an extended random walk, including saturation of a morph against equilibrium. Extended simulations of evolutionary stability support this. While **P** is always lost under the parameter sets of Table 6, in some of these sets it

almost always recovers to saturate given back-mutation from cheating to coordination (**P**). The effect is stochastic, requiring repeated long-term trials, but predictable, allowing us to infer when **P** may recover after loss and when it cannot. These results will be considered in a subsequent paper.

CONCLUSION

Suicidal punishment as altruism

Our fair contest trials support earlier evidence for suicidal punishment revealed experimentally among *Acromyrmex versicolor* co-foundresses (Rissing *et al.*, 1996). Such evidence is especially disconcerting because, in the isolated world of a single colony, there is no beneficiary for suicide. We have detailed by simulation that beneficiaries do exist – latent punishers (and their offspring, consequently, less exposed to cheating) within otherwise rival colonies (cf. Pollock, 1988). The effect is most sustainable under parameters inferred from *A. versicolor* natural history, but possible under a wider range of conditions; our simulations also reveal that sufficient divergence from *A. versicolor* natural history eliminates sustainable suicide.

Having identified a (same strategy type) beneficiary, we can claim suicidal punishers are altruistic. They are, moreover, maximally altruistic, removing themselves from the (potential) reproductive pool *without a standard kin structure* (cf. Wilson, 1987; Pollock, 1988, 1994a; Taylor, 1992a,b; Wilson *et al.*, 1992). Their altruism is not, however, *strong* (*sensu* Wilson, 1979), since the recipient of altruism lies *outside* of the group affected by their behaviour. Standard definitions of altruism fail to capture this long-distance beneficiary effect, biasing intuition against the *Acromyrmex versicolor* cheater experiment.

Without a prior understanding of *A. versicolor*'s population ecology, we would be unable to account for our earlier experiment. Here behaviour (suicidal failure to replace) is not just a strategic response; it is a strategic response embedded in population structure. Behavioural experiments are difficult enough when just considering 'game-playing' subjects. Overlaying population structure within the same experiment (e.g. forcing 'normal', single forager natal colonies to brood raid those with experimentally induced 'cheaters') would be herculean. Simulation, as employed here, allows us to link separate experiments as a single evolutionary process. Doing so, we find that what may be personally advantageous in one generation may so alter future genotype frequencies as to be catastrophic several generations later. Replacing a cheater does indeed aid self; but it aids the cheater more. Correlating the descendants of replacers and cheaters across generations through viscosity ultimately removes the personally best response replacer from the population, *even though replacement always remains the personally best response to cheating*. Suicidal punishment, by removing cheaters in their first instance, preserves cooperative environments for (latent) punishers in future generations through the same viscous process so lethal to replacers. An intuition of contingent personal advantage (Selten, 1975, 1978; West Eberhard, 1981; Myles, 1988) is simply unable to frame the dynamic we have articulated herein. Situationally specific, personally best response places a strategy in a single, focal environment; our results show that a strategy that cares not so much for itself in *all* possible social environments may radically outperform one that does (Pollock, 1988, 1994a).

Plausible mutant and stability

One might respond to the *Acromyrmex versicolor* cheating experiment by viewing it so artificial as to reveal nothing about true co-foundress strategies. Differential closing of the exit to make the prior surface excavator into a ‘cheater’ (detailed above) will certainly have no analogue in nature. One might argue that the other queens fail to replace this false cheater precisely because there is no natural analogue to this social environment. In the parlance of economics, the queens are *boundedly rational* (*sensu* Selten, 1978), unable to respond to what never occurs or is otherwise outside of their (evolved) perception. There is great force to this observation generally. Mutations are restricted to variation on prior types (Darwin, 1859; Dawkins, 1980; Maynard Smith, 1984), and there is no reason to expect experimentation will always conform in perception to mechanistically admissible mutants.

The present issue is not, however, the differentially blocked exit, but whether prior non-foraging queens can plausibly be expected to replace upon perceived demise of their fungus garden. We think whatever force bounded rationality has is removed herein by the simple fact that queens produce, in their workers, a genotype that regularly coordinates foraging and fungus tending; this genotype must be able to assess the garden’s health and the need for foraging replacement, and this genotype will exist among even unrelated co-founding queens. Once workers eclose, the forager queen continues to forage for a while, entraining her first workers; she removes herself only when the workers are able to proceed alone (Higgins, 1988). Indeed, the surface excavator specialist coordination event is itself simply an instance of coordinated excavation among workers (e.g. Anderson and Ratnieks, 2000). Our co-foundresses have these coordination mechanisms already built into them; (uninseminated) *A. versicolor* alates sometimes fail to disperse from their parental nest, instead removing their wings to become (foraging) workers (S.W. Rissing, unpublished data). *It is, then, a deviation on their prior worker genotype to refuse to forage even though their fungus is dying, a catastrophic event by any measure of colony viability.* Selection has acted on co-foundresses to suppress a prior response contingently, as revealed by controls, where co-foundresses do replace the assigned forager upon her demise (Pollock and Rissing, 1995; Rissing *et al.*, 1996). We suggest, then, that without a strategy designed to monitor potential cheating, our co-foundresses, employing their worker program, should forage rather than let their fungus die.

The issue of plausible mutation is perhaps more relevant to our constructed shirker/replacer strategy C. We think C implausible to a behavioural ecologist; but otherwise to a game theorist, who would demand the strategy space be flushed out before analysis. Because shirking and replacing are distinct behaviours in different phases of the (potential) two-stage game, we feel compelled to consider their combination as strategy C, especially in a haploid model where shirking/replacing are really no more than separate behaviours defined by two distinct loci (Table 2). Here game theory compels consideration of a Darwinian variant, which, while undetected in either ‘natural’ or ‘cheater induced’ colonies, significantly tilts results *against* both naturally revealed coordination (leading to saturation of either quitter Q or some mixture of C, Q) and experimentally induced punishment (in populations predominantly C).

Most importantly, C may facilitate the loss of coordination and then disappear itself, leaving an all-Q remnant. While behavioural ecology clues behavioural properties, game theory, by flushing these properties into a closed strategy space, may identify real, crucial evolutionary states that otherwise go unnoticed because they are ephemeral. If the *result* of

these ephemeral transitions is absent in the field (as is the case for *Acromyrmex versicolor* where collected), behavioural ecologists may have an important clue as to how the population is structured, so precluding the game theoretically possible transition state. Simulations reveal C acts as a transition more under strong brood raiding with random dispersal than with viscous dispersal (Tables 3 and 5, and above), the latter being the population structure inferred for *A. versicolor*. We argued earlier that shirker/replacer C, even where a dominant simulation outcome, may actually be little more than transitory upon introduction of plausible, replacement delaying, mutants. Under viscosity, C sometimes predominates (a likely transition state) under weak but never under strong brood raiding (Tables 3 and 4, and above). Laboratory evidence suggests brood raiding is strong (Rissing and Pollock, 1987, 1991; Tschinkel, 1992a). This confluence of viscosity and strong brood raiding is exactly where simulation predicts strategy C, urged by game theory, should fail as a transition, compatible with the laboratory assay of ubiquitous surface excavator/forager coordination.

A conjecture for human experiments

In this study, we employed simulation to link various experiments into a single evolutionary process. Such simulation may also facilitate experimental parallels across biology and social science. In economics, the *ultimatum game* is similar to the coordination game detailed herein. Briefly, a subject is given a divisible resource (often money) and told to divide it any way she likes with her game partner. The latter may either accept the offer or not; if he refuses, neither subject receives anything. Thus the recipient can veto the offered division at cost to both parties. A game-theoretically 'rational' recipient should accept any positive amount, for otherwise he gets nothing; his partner should provide the smallest divisible amount, keeping the rest for herself. Experiments reveal, however, that substantial offers – of as much as 20–30% – are rejected, with small amounts almost always so (Camerer and Thaler, 1995). Divisions approaching 50 : 50 equity are readily accepted. Our analysis of inter-group competition and sustainable personally harmful punishment suggests a mechanism for this revealed human irrationality. If subjects are sampled from (multiple) group environments where equity is expected, rejecting recipients may be punishing much as *Acromyrmex versicolor* queens do. We all know, from stories or experience, of groups in contention doing poorly relative to groups in harmony. It seems that both human and ant may produce more contention than is individually rational. Perhaps inter-group competition is a hidden selection agent in the ultimatum game; humans, subject generally to competitive group structures, may tend to retain responses moulded by such structure even isolated in the laboratory. But humans, unlike ants, can perceive something of their 'external' population structure; indeed, the human ability to rapidly entrain into groups may facilitate designs employing inter-group competition, relative to other species. We suggest that placing subjects in a perceived competitive group structure will augment the 'irrational' behaviour the ultimatum experiment reveals. If so, the parallel with *A. versicolor* will be even more striking.

ACKNOWLEDGEMENTS

G.B.P. and A.C. are indebted to Professor Ken Binmore, past Academic Director of the Centre for Economic Learning and Social Evolution, Economics Department, University College London,

where both were located for a year. G.B.P. was supported as a Research Fellow at the Centre, a Senior Fulbright Fellowship, Wirtschaftstheorie III (under Professor Dr Avner Shaked), Economics Department, University of Bonn (where simulation support was also provided), and KALX, LLC. A.C. was supported by the Human Capital and Mobility Program of the European Union (contract #ERB CHBGCT 930443), Spanish Ministry of Education grants #PB96-0302 (under the DGICYT program) and #BEC2000-1029, the Generalitat of Catalonia grant #1997SGR-00138, the visitor program of Wirtschaftstheorie III (under Professor Dr Avner Shaked), Economics Department, University of Bonn, and the Research Distinction Program of the Generalitat de Catalunya.

REFERENCES

- Anderson, C. and Ratnieks, F.L.W. 2000. Task partitioning in insect societies: novel situations. *Insectes Sociaux*, **47**: 198–199.
- Atran, S. 2003. Genesis of suicide terrorism. *Science*, **299**: 1534–1539.
- Axelrod, R. 1980. Effective choice in the iterated Prisoner's Dilemma. *J. Conflict Resolution*, **24**: 3–25.
- Aumann, R.J. 1974. Subjectivity and correlation in randomized strategies. *J. Math. Econ.*, **1**: 67–96.
- Bartz, S.H. and Hölldobler, B. 1982. Colony founding in *Myrmecocystus mimicus* Wheeler (Hymenoptera: Formicidae) and the evolution of foundress associations. *Behav. Ecol. Sociobiol.*, **10**: 137–147.
- Bekkevold, D., Frydenberg, J. and Boomsma, J.J. 1999. Multiple mating and facultative polygyny in the Panamanian leaf cutter ant *Acromyrmex echinator*. *Behav. Ecol. Sociobiol.*, **46**: 103–109.
- Binmore, K.G., Samuelson, L. and Vaughan, R. 1995. Musical chairs: modeling noisy evolution. *Games Econ. Behav.*, **11**: 1–35.
- Bisch-Knaden, S. and Wehner, R. 2003. Landmark memories are more robust when acquired at the nest site than en route: experiments in desert ants. *Naturwissenschaften*, **90**: 127–130.
- Bishop, D.T. and Cannings, C. 1978. A generalized war of attrition. *J. Theor. Biol.*, **70**: 85–124.
- Boyd, R. and Richerson, P. 1992. Punishment allows the evolution of cooperation (or anything else) in sizable groups. *Ethol. Sociobiol.*, **13**: 171–195.
- Brosnan, S.F. and de Waal, F.B.M. 2003. Monkeys reject unequal pay. *Nature*, **425**: 297–299.
- Camerer, C. and Thaler, R.H. 1995. Anomalies: ultimatums, dictators, and manners. *J. Econ. Perspect.*, **9**: 209–219.
- Carew, M.E., Tay, W.T. and Crozier, R.H. 1997. Polygyny via unrelated queens indicated by mitochondrial DNA variation in the Australian meat ant *Iridomyrmex purpureus*. *Insectes Sociaux*, **44**: 7–14.
- Cressman, R. 1996. Evolutionary stability in the finitely repeated Prisoner's Dilemma game. *J. Econ. Theory*, **68**: 234–238.
- Cripps, M. 1991. Correlated equilibria and evolutionary stability. *J. Econ. Theory*, **55**: 428–434.
- Darwin, C. 1859. *On the Origin of Species*. London: John Murray.
- Dawkins, R. 1976. *The Selfish Gene*. Oxford: Oxford University Press.
- Dawkins, R. 1980. Good strategy or evolutionarily stable strategy? In *Sociobiology: Beyond Nature/Nurture?* (G.W. Barlow and J. Silverberg, eds.), pp. 331–367. Boulder, CO: Westview Press.
- Dawkins, R. 1982. *The Extended Phenotype: The Gene as the Unit of Selection*. San Francisco, CA: W.H. Freeman.
- Diehl-Fleig, E. and de Araújo, A.M. 1996. Haplometrosis and pleometrosis in the ant *Acromyrmex striatus* (Hymenoptera: Formicidae). *Insectes Sociaux*, **43**: 47–51.
- Dukas, R. and Visscher, P.K. 1994. Lifetime learning by foraging honey bees. *Animal Behav.*, **48**: 1007–1012.
- Farrell, J. and Maskin, E. 1989. Renegotiation in repeated games. *Games Econ. Behav.*, **1**: 327–360.
- Fehr, E. and Rockenbach, B. 2003. Detrimental effects of sanctions on human altruism. *Nature*, **422**: 137–140.

- Gamboa, G.J. 1974. Surface behaviour of the leaf-cutter ant *Acromyrmex versicolor* Pergande (Hymenoptera: Formicidae). Masters thesis; Arizona State University, Tempe, AZ, USA.
- Gamboa, G.J. 1975. Foraging and leaf-cutting of the desert gardening ant *Acromyrmex versicolor* (Pergande) (Hymenoptera: Formicidae). *Oecologia*, **20**: 103–110.
- Gintis, H. 2000. Strong reciprocity in humans. *J. Theor. Biol.*, **206**: 167–179.
- Güth, W., Schmittberger, R. and Schwarze, B. 1982. An experimental analysis of ultimatum bargaining. *J. Econ. Behav. Organiz.*, **3**: 367–388.
- Hagen, R.H., Smith, D.R. and Rissing, S.W. 1988. Genetic relatedness among co-foundresses of two desert ants, *Veromessor pergandei* and *Acromyrmex versicolor* (Hymenoptera: Formicidae). *Psyche*, **95**: 191–201.
- Hahn, D.A. and Tschinkel, W.R. 1997. Settlement and distribution of colony-founding queens of the arboreal ant, *Crematogaster ashmeadi*, in a longleaf pine forest. *Insectes Sociaux*, **44**: 323–336.
- Hamilton, W.D. 1964. The genetical evolution of social behaviour II. *J. Theor. Biol.*, **7**: 17–52.
- Heinze, J., Hölldobler, B. and Peeters, C. 1994. Conflict and cooperation in ant societies. *Naturwissenschaften*, **81**: 489–497.
- Heinze, J., Trunzer, B., Hölldobler, B. and Delabie, J.H.C. 2001. Reproductive skew and queen relatedness in an ant with primary polygyny. *Insectes Sociaux*, **48**: 149–153.
- Higgins, M.R. 1988. Cooperation among unrelated individuals: group colony foundation in *Acromyrmex versicolor* (Hymenoptera: Formicidae). Masters thesis, Arizona State University, Tempe, AZ, USA.
- Hölldobler, B. 1976. Tournaments and slavery in a desert ant. *Science*, **192**: 912–914.
- Hölldobler, B. 1981. Foraging and spatiotemporal territories in the honey ant *Myrmecocystus mimicus* Wheeler (Hymenoptera: Formicidae). *Behav. Ecol. Sociobiol.*, **9**: 301–314.
- Hölldobler, B. and Carlin, N.F. 1985. Colony founding, queen dominance and oligogyny in the Australian meat ant *Iridomyrmex purpureus*. *Behav. Ecol. Sociobiol.*, **18**: 45–58.
- Hölldobler, B. and Wilson, E.O. 1977. The number of queens: an important trait in ant evolution. *Naturwissenschaften*, **64**: 8–15.
- Hölldobler, B. and Wilson, E.O. 1990. *The Ants*. Cambridge, MA: Harvard University Press.
- Katagiri, D. 1988. *Returning to Silence*. Boston, MA: Shambhala.
- Klahn, J.E. and Gamboa, G.J. 1983. Social wasps: discrimination between kin and non-kin. *Science*, **221**: 482–484.
- Kolmer, K. and Heinze, J. 2000. Rank orders and division of labour among unrelated co-founding queens. *Proc. R. Soc. Lond. B*, **267**: 1729–1734.
- Mabelis, A.A. 1979. Wood ant wars: the relationship between aggression and predation in the red wood ant (*Formica polyctena* Först). *Neth. J. Zool.*, **29**: 451–620.
- Maynard Smith, J. 1982. *Evolution and the Theory of Games*. Cambridge: Cambridge University Press.
- Maynard Smith, J. 1984. Evolution and the theory of games. *Behav. Brain Sci.*, **7**: 95–125.
- Mintzer, A. and Vinson, S.B. 1985. Cooperative colony foundation by females of the leaf-cutting ant, *Atta texana*, in the laboratory. *J. N. Y. Entomol. Soc.*, **93**: 1047–1051.
- Murray, M.G. and Gerrard, R. 1984. Conflict in the neighbourhood: models where close relatives are in direct competition. *J. Theor. Biol.*, **111**: 237–246.
- Myerson, R.B. 1986. Acceptable and predominant correlated equilibria. *Int. J. Game Theory*, **15**: 133–154.
- Myerson, R.B. 1991. *Game Theory: Analysis of Conflict*. Cambridge, MA: Harvard University Press.
- Myles, T.G. 1988. Resource inheritance in social evolution from termites to man. In *The Ecology of Social Behavior* (N. Slobodchikoff, ed.), pp. 379–423. San Diego, CA: Academic Press.
- Noë, R. and Hammerstein, P. 1994. Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism, and mating. *Behav. Ecol. Sociobiol.*, **35**: 1–11.

- Nonacs, P. 1992. Queen condition and alate density affect pleometrosis in the ant *Lasius pallitarsis*. *Insectes Sociaux*, **39**: 3–13.
- O'Donnell, S. and Jeanne, R.L. 1992. Forager success increases with experience in *Polybia occidentalis* (Hymenoptera: Vespidae). *Insectes Sociaux*, **39**: 451–454.
- Pfennig, D.W. 1995. Absence of joint nesting advantage in desert seed harvester ants: evidence from a field experiment. *Animal Behav.*, **49**: 567–575.
- Pollock, G.B. 1988. Population structure, spite, and the iterated Prisoner's Dilemma. *Am. J. Phys. Anthropol.*, **77**: 459–469.
- Pollock, G.B. 1989a. Suspending disbelief – of Wynne-Edwards and his reception. *J. Evol. Biol.*, **2**: 205–221.
- Pollock, G.B. 1989b. Evolutionary stability of reciprocity in a viscous lattice. *Social Networks*, **11**: 175–212.
- Pollock, G.B. 1991. Crossing Malthusian boundaries: evolutionary stability in the finitely repeated Prisoner's Dilemma. *J. Quant. Anthropol.*, **3**: 159–180.
- Pollock, G.B. 1994a. Personal fitness, altruism, and the ontology of game theory. *J. Quant. Anthropol.*, **4**: 193–209.
- Pollock, G.B. 1994b. Social competition or correlated strategy? *Evol. Ecol.*, **8**: 221–229.
- Pollock, G.B. 1995a. Simple game inevitable correlated equilibria. *J. Quant. Anthropol.*, **5**: 15–45.
- Pollock, G.B. 1995b. Pareto efficiency, simple game stability, and social structure in finitely repeated games. *J. Math. Sociol.*, **20**: 55–72.
- Pollock, G.B. 1996. Kin selection, kin avoidance, and correlated strategies. *Evol. Ecol.*, **10**: 29–43.
- Pollock, G.B. and Rissing, S.W. 1989. Intraspecific brood raiding, territoriality, and slavery in ants. *Am. Nat.*, **133**: 61–70.
- Pollock, G.B. and Rissing, S.W. 1995. Experimental evidence for punishment: of Evans-Pritchard, Wynne-Edwards, and ants. *J. Quant. Anthropol.*, **5**: 47–72.
- Post, D.C. and Jeanne, R.L. 1982. Recognition of former nestmates during colony founding by the social wasp *Polistes fuscatus* (Hymenoptera: Vespidae). *Behav. Ecol. Sociobiol.*, **11**: 283–286.
- Press, W.H., Teukolsky, S.A., Vetterling, W.T. and Flannery, B.P. 1992. *Numerical Recipes in C: The Art of Scientific Computing*, 2nd edn. Cambridge: Cambridge University Press.
- Radner, R. 1980. Collusive behaviour in noncooperative epsilon-equilibria of oligopolies with long but finite lives. *J. Econ. Theory*, **22**: 136–154.
- Ratnieks, F.L.W. and Anderson, C. 1999. Task partitioning in insect societies. *Insectes Sociaux*, **46**: 95–108.
- Reeve, H.K. and Nonacs, P. 1992. Social contracts in wasp societies. *Nature*, **359**: 823–825.
- Rissing, S.W. and Pollock, G.B. 1986. Social interaction among pleometrotic queens of *Veromessor pergandei* (Hymenoptera: Formicidae) during colony foundation. *Anim. Behav.*, **34**: 226–233.
- Rissing, S.W. and Pollock, G.B. 1987. Queen aggression, pleometrotic advantage, and brood raiding in the ant *Veromessor pergandei* (Hymenoptera: Formicidae). *Anim. Behav.*, **35**: 975–981.
- Rissing, S.W. and Pollock, G.B. 1988. Pleometrosis and polygyny in ants. In *Interindividual Behavioral Variability in Social Insects* (L. Jeanne, ed.), pp. 179–222. Boulder, CO: Westview Press.
- Rissing, S.W. and Pollock, G.B. 1991. An experimental analysis of pleometrotic advantage in the desert seed-harvester ant *Messor pergandei* (Hymenoptera; Formicidae). *Insectes Sociaux*, **38**: 205–211.
- Rissing, S.W., Johnson, R.A. and Pollock, G.B. 1986. Natal nest distribution and pleometrosis in the desert leaf-cutter ant *Acromyrmex versicolor* (Pergande) (Hymenoptera: Formicidae). *Psyche*, **93**: 177–186.
- Rissing, S.W., Pollock, G.B., Higgins, M.R., Hagen, R.H. and Smith, D.R. 1989. Foraging specialization without relatedness or dominance among co-founding ant queens. *Nature*, **338**: 420–422.
- Rissing, S.W., Pollock, G.B. and Higgins, M.R. 1996. Fate of ant co-foundresses containing a 'cheater'. *Naturwissenschaften*, **83**: 182–185.

- Robson, S.K.A. and Traniello, J.F.A. 2002. Transient division of labor and behavioural specialization in the ant, *Formica schaufussi*. *Naturwissenschaften*, **89**: 128–131.
- Rosenthal, R.W. 1974. Correlated equilibria in some classes of two-person games. *Int. J. Game Theory*, **3**: 119–128.
- Ross, N.M. and Fletcher, D.J.C. 1985. Comparative study of genetic and social structure in two forms of the fire ant *Solenopsis invicta* (Hymenoptera: Formicidae). *Behav. Ecol. Sociobiol.*, **17**: 349–356.
- Ross, N.M. and Gamboa, G.J. 1981. Nestmate discrimination in the social wasp *Polistes metricus* (Hymenoptera: Vespidae). *Behav. Ecol. Sociobiol.*, **9**: 163–165.
- Sasaki, K., Satoh, T. and Obara, Y. 1996. Cooperative foundation of colonies by unrelated foundresses in the ant *Polyrhachis moesta*. *Insectes Sociaux*, **43**: 217–226.
- Schatz, B., Lachaud, J.-P. and Beugnon, G. 1995. Spatial fidelity and individual foraging specializations in the neotropical Ponerine ant, *Ectatomma ruidum* Roger (Hymenoptera, Formicidae). *Sociobiology*, **26**: 269–282.
- Schmid-Hempel, P. and Schmid-Hempel, R. 1984. Life duration and turnover of foragers in the ant *Cataglyphis bicolor* (Hymenoptera, Formicidae). *Insectes Sociaux*, **31**: 345–360.
- Schuessler, R. 1989. The gradual decline of cooperation: endgame effects in evolutionary game theory. *Theory and Decision*, **26**: 133–155.
- Selten, R. 1975. Reexamination of the perfectness concept for equilibrium points in extensive games. *Int. J. Game Theory*, **4**: 25–55.
- Selten, R. 1978. The chain store paradox. *Theory and Decision*, **9**: 127–159.
- Selten, R. and Stoecker, R. 1986. End behaviour sequences of finite Prisoner's Dilemma supergames. *J. Econ. Behav. Organiz.*, **7**: 47–70.
- Sommer, K. and Hölldobler, B. 1995. Colony founding by queen association and determinants of reduction in queen number in the ant *Lasius niger*. *Anim. Behav.*, **50**: 287–294.
- Taylor, P.D. 1992a. Altruism in viscous populations – an inclusive fitness model. *Evol. Ecol.*, **6**: 352–356.
- Taylor, P.D. 1992b. Inclusive fitness in a homogeneous environment. *Proc. R. Soc. Lond. B*, **249**: 299–302.
- Trunzer, B., Heinze, J. and Hölldobler, B. 1998. Cooperative colony founding and experimental primary polygyny in the ponerine ant *Pachycondyla villosa*. *Insectes Sociaux*, **45**: 267–276.
- Tschinkel, W.R. 1992a. Brood raiding in the fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae): laboratory and field observations. *Ann. Entomol. Soc. Am.*, **85**: 638–646.
- Tschinkel, W.R. 1992b. The population dynamics of founding and incipient colonies of the fire ant, *Solenopsis invicta*, and their relation to brood raiding. *Ecol. Entomol.*, **17**: 179–188.
- West Eberhard, M.J. 1981. Intragroup selection and the evolution of insect societies. In *Natural Selection and Social Behavior* (D. Alexander and D.W. Tinkle, eds.), pp. 3–17. New York: Chiron Press.
- Wheeler, W.M. 1917. Notes on the marriage flights of some Sonoran ants. *Psyche*, **24**: 177–180.
- Williams, G.C. 1966. *Adaptation and Natural Selection*. Princeton, NJ: Princeton University Press.
- Wilson, D.S. 1979. Structured demes and trait-group variation. *Am. Nat.*, **113**: 606–610.
- Wilson, D.S. 1983. The group selection controversy: history and current status. *Annu. Rev. Ecol. Syst.*, **14**: 159–187.
- Wilson, D.S. 1990. Weak altruism, strong group selection. *Oikos*, **59**: 135–140.
- Wilson, D.S. and Dugatkin, L.A. 1991. Nepotism vs tit-for-tat, or, why should you be nice to your rotten brother? *Evol. Ecol.*, **5**: 291–299.
- Wilson, D.S. and Dugatkin, L.A. 1997. Group selection and assortative interactions. *Am. Nat.*, **149**: 336–351.
- Wilson, D.S., Pollock, G.B. and Dugatkin, L.A. 1992. Can altruism evolve in purely viscous populations? *Evol. Ecol.* **6**: 331–341.
- Wilson, J.B. 1987. Group selection in plant populations. *Theor. Appl. Genet.*, **74**: 493–502.

