



# Contingent movement and cooperation evolve under generalized reciprocity

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How cooperation and altruism among non-relatives can persist in the face of cheating remains a key puzzle in evolutionary biology. Although mechanisms such as direct and indirect reciprocity and limited movement have been put forward to explain such cooperation, they cannot explain cooperation among unfamiliar, highly mobile individuals. Here we show that cooperation may be evolutionarily stable if decisions taken to cooperate and to change group membership are both dependent on anonymous social experience (generalized reciprocity). We find that a win-stay, lose-shift rule (where shifting is either moving away from the group or changing tactics within the group after receiving defection) evolves in evolutionary simulations when group leaving is moderately costly (i.e. the current payoff to being alone is low, but still higher than that in a mutually defecting group, and new groups are rarely encountered). This leads to the establishment of widespread cooperation in the population. If the costs of group leaving are reduced, a similar group-leaving rule evolves in association with cooperation in pairs and exploitation of larger anonymous groups. We emphasize that mechanisms of assortment within populations are often behavioural decisions and should not be considered independently of the evolution of cooperation.

**Keywords:** mobility; positive assortment; altruism; free-rider

## 1. INTRODUCTION

Altruism can evolve under natural selection when groups are genotypically or phenotypically positively assorted, so that groups are non-random samples of the behavioural variation in the population. Under positive assortment, altruistic individuals are likely to help other altruists and, because between-group variation exceeds within-group variation, the effects of group membership and group success increase in importance in multi-level selection (Price 1970; Wilson & Dugatkin 1997). The formation of non-random groups commonly results from grouping with relatives (Hamilton 1963; Price 1970; Frank 1998) or from viscous movement, which leads to spatially structured populations (Nowak & May 1992; Killingback & Doebeli 1996; Brauchli *et al.* 1999; but see Hauert & Doebeli 2004). Positive phenotypic assortment of cooperation among partners may also result if individuals recognize cooperative individuals and adjust their behaviour so that cooperative individuals receive cooperation (direct or indirect reciprocity; Trivers 1971; Alexander 1986; Nowak & Sigmund 1998), if social transmission of behaviours changes the behavioural composition of groups after new members join (Wilson 2004), or from conformist transmission of behaviour (Koeslag & Terblanche 2003).

Many of these mechanisms imply substantial cognitive complexity, because cooperative individuals must be identified and remembered or behaviours must be copied among group members, mechanisms of kin recognition or strong limitations on movement. A simple way that positive phenotypic assortment could arise, even among highly mobile organisms of limited cognitive complexity, is if groups composed mainly of one phenotype (for instance,

cooperators) were more likely to persist than were groups composed of another phenotype (for instance, non-cooperators or ‘defectors’). For example, individuals that follow a simple habitat-selection rule of switching to the best available nearby patch can form either positively or negatively assorted groups when cooperation (in the form of restrained foraging) improves patch quality and defection reduces patch quality (Pepper & Smuts 2002). In such a case, foragers will be less likely to join and more likely to leave a group (i.e. the group of foragers on that patch) if it contains defectors. If individuals have the option of opting out of social interactions by playing a ‘loner’ strategy, altruism can invade a population of loners, because groups, should they form, remain small, while altruism is itself invaded by defectors (Hauert *et al.* 2002; Semmann *et al.* 2003). Because loners can invade a population of defectors, altruism can persist in a ‘rock–paper–scissors’ dynamic, with loner, altruist and defector tactics replacing one another cyclically (Hauert *et al.* 2002). Aktipis (2004) found that a simple ‘Walk Away’ rule, in which agents left groups after receiving defection, but not after receiving cooperation, could lead to positive assortment and cooperation. On the other hand, mobility between groups can hinder the evolution of cooperation, because cooperative groups are invaded by uncooperative, mobile ‘rovers’ or ‘free-riders’ (Dugatkin & Wilson 1991; Enquist & Leimar 1993).

Clearly, the behavioural rules that govern whether individuals join or leave groups can influence phenotypic assortment and the likelihood that altruism will evolve. However, movement is a decision that will itself be influenced by the probability of moving into or out of a cooperative environment. It is not necessarily clear whether the kinds of rules that would lead to the evolution of altruism will become established in a population of

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defectors. As mentioned earlier, the ability to move between groups can reward free-riding defectors, which could then prevent more cooperative strategies from becoming established, particularly if groups can grow larger than two.

Here, we examine the simultaneous evolution of contingent group-leaving rules and conditional cooperation from a population of uncooperative individuals, rather than specifying group-leaving rules beforehand. At an evolutionary time-scale, Aviles (1999, 2002) modelled how group living and cooperation can interact to influence both the size of groups and the likelihood of cooperation. Recently, Le Galliard *et al.* (2005) modelled the simultaneous evolution of unconditional altruism and mobility in viscous populations. Aktipis (2004) examined how contingent movement could lead to positive assortment and cooperation, but did not examine how this might interact with group size, or examine alternative group-leaving rules that could be used in a population of interacting agents. There are also numerous models investigating how cooperation (usually in the form of by-product mutualism) can influence group size (Giraldeau & Caraco 2000). However, to our knowledge, ours is the first model to investigate the simultaneous evolution of conditional behavioural rules governing group leaving, group size and altruistic cooperation. We model a generalized reciprocity scenario, in which players do not identify individual cooperators and defectors, but base their decisions on their previous interaction in a group. Cooperation under generalized reciprocity means that individuals are more likely to cooperate with a potentially unfamiliar individual after having received cooperation from another than after having received defection. Evidence supporting cooperation via generalized reciprocity has been found in humans and rats (Yamagishi & Cook 1993; C. Rutte and M. Taborsky, unpublished data) and presents a challenge to our current understanding of the evolutionary mechanisms generating cooperative behaviour by selfish individuals (Pfeiffer *et al.* 2005).

We find that a win-stay, lose-shift rule (where shifting is either moving away from the group or changing tactics within the group after receiving defection), in which players either leave or defect if they have cooperated but received defection, often evolves even when mean group size is greater than two and players do not identify individual cooperators and defectors. This leads to the establishment of widespread cooperation in the population. In addition, non-cooperative strategies can evolve over a wide range of model parameters, even with similar group-leaving rules.

## 2. THE MODEL

We used a genetic algorithm to model the simultaneous evolution of group-leaving rules and altruism. A genetic algorithm uses biological evolution as a model for the solution of complex optimization problems (reviewed in Sumida *et al.* 1990). Individual strategies are vectors encoded on ‘chromosomes’. The fitness of different strategies is determined, in our case by using an agent-based simulation model, after which the fittest strategies are selected for reproduction. Occasional mutations and crossover events continually create new strategies. Despite the use of terms such as ‘chromosome’, ‘crossover’ and

‘mutation’, a genetic algorithm is merely a powerful optimization tool and makes no assumptions about the underlying genetics of traits being examined.

We used the classical simultaneous iterated Prisoner’s Dilemma payoff matrix. In most of our simulations, mutual cooperation ( $R$ ) yields a fitness payoff of 3, mutual defection ( $P$ ) yields a payoff of 1, an agent that defects but receives cooperation ( $T$ ) gains a payoff of 5, while one that cooperates but receives defection ( $S$ ) gains a payoff of 0. There is an additional payoff,  $A$  (‘alone’, the value of which was varied between 1 and 2, so that  $T > R > A \geq P > S$ ). When  $A > P$ , there is some cost of group living in the absence of cooperation. We assumed that group members interacted repeatedly within the group, did not know the previous moves of each partner, but did remember their own last action and their last action received from *any* group member.

In each generation of our simulations, each of  $N=500$  agents followed a behavioural policy specified on a 10-locus chromosome. The first five loci specified the likelihood of leaving the group upon entering it ( $L_A$ ) or when the last interaction within the current group was  $R$ ,  $T$ ,  $S$  or  $P$  ( $L_R$ ,  $L_T$ ,  $L_S$  and  $L_P$ ). The second 5 loci specified the likelihood of cooperating upon entering the group and the likelihood of cooperating after  $R$ ,  $T$ ,  $S$  or  $P$  ( $C_A$ ,  $C_R$ ,  $C_T$ ,  $C_S$  and  $C_P$ ). These probabilities could vary between 0.01 and 0.99. Thus, there was always some non-zero probability of leaving and staying and some non-zero probability of cooperating and defecting.

Agents began each generation alone. In each of  $\tau=200$  time-steps, solitary agents joined a randomly selected group or singleton with a probability,  $\alpha$  (the ‘encounter rate’), that was independent of their group-leaving and cooperative rules. There was no spatial structure to the model, so each group was equally likely to be chosen. The model structure is, therefore, analogous to that of a highly mobile, but group-living, organism. Group size could not exceed a maximum size ( $GS_{\max}$ ; usually 5). If an agent encountered a group of  $GS_{\max}$ , it randomly chose another group, or, if all groups were of size  $GS_{\max}$ , remained alone. Immediately after all solitary agents had the opportunity to join groups, all group members had the option of leaving their group according to the probabilities specified above (i.e. if their last interaction was mutual cooperation, they left with probability  $L_R$ ). Note that agents that had just joined the group could now leave before interacting with any other group members. Thus, it was possible for agents to almost never interact in groups (i.e. if  $L_A$  was high). All agents had an additional probability,  $\gamma$ , of leaving the group even if their genotype specified otherwise. This ‘intrinsic leaving rate’ meant that that even agents that never voluntarily left groups experienced several social situations over the course of the simulation and that there would always be some uncertainty about future group composition.

Once group composition was established, randomly selected dyads were generated by pairing up group members. If the group contained an odd number of members, one of these did not have a partner and received the same payoff as if it were alone for that time-step. However, this individual was considered to have remained in the group, and it remembered its last interaction there. Once paired, each dyad played a round of PD, with each player’s probabilities of  $C$  specified by its genotype, and

Table 1. The median (interquartile range) probabilities of leaving ( $L_i$ ) and cooperating ( $C_i$ ) when the previous interaction experienced was  $i=A, R, S, T$  or  $P$ . (Results are displayed for the four behavioural rules that emerged in evolutionary simulations: (a) always leave, (b) rarely leave, (c) suspicious generalized PAVLOV, (d) trusting generalized PAVLOV. Rules were assigned using PROC CLUSTER in SPSS 11.0.)

agent's last move	joining ( $A$ )	cooperating		defecting	
		cooperation ( $R$ )	defection ( $S$ )	cooperation ( $T$ )	defection ( $P$ )
<i>probability of leaving</i>					
always leave	0.94 (0.89–0.97)	0.39 (0.14–0.74)	0.37 (0.23–0.69)	0.45 (0.12–0.67)	0.34 (0.17–0.54)
rarely leave	0.01 (0.01–0.02)	0.58 (0.32–0.84)	0.08 (0.05–0.14)	0.04 (0.02–0.06)	0.01 (0.01–0.02)
suspicious generalized PAVLOV	0.01 (0.01–0.02)	0.01 (0.01–0.02)	0.96 (0.91–0.98)	0.02 (0.01–0.03)	0.01 (0.01–0.02)
trusting generalized PAVLOV	0.01 (0.01–0.01)	0.01 (0.01–0.01)	0.18 (0.05–0.47)	0.04 (0.02–0.07)	0.04 (0.02–0.20)
<i>probability of cooperating</i>					
always leave	0.16 (0.07–0.22)	0.48 (0.30–0.78)	0.40 (0.19–0.67)	0.18 (0.10–0.51)	0.15 (0.06–0.24)
rarely leave	0.01 (0.01–0.02)	0.60 (0.39–0.76)	0.03 (0.02–0.03)	0.03 (0.02–0.03)	0.01 (0.01–0.02)
suspicious generalized PAVLOV	0.01 (0.01–0.01)	0.97 (0.95–0.98)	0.14 (0.04–0.25)	0.04 (0.02–0.07)	0.73 (0.57–0.80)
trusting generalized PAVLOV	0.99 (0.98–0.99)	0.99 (0.98–0.99)	0.04 (0.02–0.08)	0.05 (0.02–0.11)	0.62 (0.50–0.71)

<sup>a</sup> Partner in current round may be a different individual.

players received  $R$ ,  $T$ ,  $S$  or  $P$  accordingly. Lone agents and those without partners received  $A$ .

After  $\tau$  time-steps, agents reproduced according to their accumulated payoffs over the entire simulation ( $w$ ), relative to those of the entire population. Reproduction occurred as follows: all agents were ranked according to payoff and the 25% with the highest payoffs were chosen for reproduction ('reproductives'). Note that the proportion chosen for reproduction influenced the time to reach equilibrium, but not the equilibrium itself. These then replicated according to their relative payoff (i.e. reproductive  $j$  produced  $Nw_j/(N_{\text{rep}}\bar{w}_{\text{rep}})$  offspring rounded to the nearest integer, where  $N_{\text{rep}}$  was the number of reproductives and  $\bar{w}_{\text{rep}}$  was the average fitness of a reproductive) to produce  $N$  new agents ('offspring'). Because of rounding, there could be more or fewer than  $N$  offspring produced. If more, reproductives were ranked according to fitness, and excess offspring were removed sequentially, starting with those of the lowest ranked reproductive, until there were  $N$  offspring. If fewer than  $N$  offspring were produced, an additional offspring was assigned to each reproductive, beginning with the highest ranked, until the population size again equalled  $N$ .

Offspring faithfully copied the chromosome of their parent agent, with an  $\epsilon=0.01$  probability of mutation at each locus. If a mutation occurred, the allele at that locus was replaced with a random value between 0.01 and 0.99. After replication, each offspring paired up with a randomly selected partner offspring. Crossover between partner chromosomes occurred with a probability of 0.2, at a randomly selected locus between 1 and 10; that locus and everything following it were exchanged with the partner chromosome. In extensive preliminary simulations, we found that these mutation and crossover rates allowed equilibria to be reached fairly quickly (i.e. within 5000 generations). In our sensitivity analysis, small changes in these rates did not influence equilibrium values (I. M. Hamilton and M. Taborsky, unpublished modelling

results). The  $N$  resultant offspring were then entered into the simulation as described earlier.

### 3. RESULTS

#### (a) Contingent movement and cooperation

In the absence of differential group-leaving, cooperation should be less likely in larger groups of anonymous individuals (Kollock 1998; Gaube 2001). In our simulations, when group-leaving rules were set beforehand (ranging from  $L_i=0$  to  $L_i=0.225$ , same regardless of last move and partner's last move), cooperation (in the form of  $C_A$  and  $C_R$  both  $\approx 0.99$ ) evolved within 2000 generations in only 2 out of 48 simulations covering the same parameter space as in table 2. In all other simulations, players never cooperated upon joining a group or upon mutual defection, so cooperation could not become established.

When group-leaving probabilities were allowed to evolve, all simulations converged upon one of four distinct rules, usually in less than 1000 generations, and always within 5000 generations, and these rules persisted until at least  $5 \times 10^5$  generations (the longest that simulations were run). Rules were assigned using PROC CLUSTER in SPSS v. 11.0. Increasing the number of clusters did not yield any qualitatively different rules. Nearly all agents in a population used similar rules, although there was some variation in the specific contingent probabilities of cooperation and group-leaving within a population. The rule that was established in a population depended on the encounter rate,  $\alpha$ , intrinsic leaving rate,  $\gamma$ , and the payoff of being alone,  $A$  (table 2).

Two of these rules were always non-cooperative and the average payoff in the population was exactly the same as the payoff to solitary agents. Because  $A \geq P$ , members of groups of mutual defectors could always do as well or better by leaving the group, and should do so until the payoffs to grouping and being alone are equal. The first non-cooperative rule, which we call 'Always Leave',

specified that group members almost always left immediately after joining a group, and often left after any other interaction (table 1). The probabilities of cooperation after any interaction were high, but this probably reflects the rarity of opportunities for cooperation and lack of selection on these traits (table 1). The payoff received by group members was generally slightly less than that received when alone (figure 1a); however, groups were small (figure 1b) and very rare (figure 1c). This rule was associated with high intrinsic group intrinsic leaving rates,  $\gamma$ , and a relatively high payoff for being alone ( $A > P$ ; table 2). The failure of cooperation to become established is intuitive. The high intrinsic leaving rate led to high group instability because agents were likely to leave groups coincidentally and a large number of solitary agents were available to join groups. Under such conditions, cooperators have little expectation that group structure will remain consistent. This should lead to mutual defection; however, because  $A > P$ , players could do better by leaving the group altogether than they could by remaining in a group of mutual defectors.

In the second non-cooperative rule, which we call ‘Rarely Leave’, group members rarely left the group except after experiencing mutual cooperation (table 1). They also almost never cooperated, again except after mutual cooperation (table 1). Since agents always defected upon joining the group, mutual cooperation (and thus, leaving or cooperating) was very rare, and the high values of these probabilities probably reflects the fact that they were rarely exposed to selection. Group sizes were large (figure 1b) and most agents spent most of their time in groups (figure 1c) when the population played Rarely Leave. The payoff to group members was the same as the payoff to solitary agents (figure 1a). This rule was found when  $A = P$ , except at low encounter rates when trusting generalized PAVLOV (see below) sometimes became established (table 2).

The other two rules were, in terms of cooperativeness, forms of PAVLOV (or ‘win-stay, lose-shift’; Nowak & Sigmund 1993) in which group members almost always cooperated upon receiving  $R$  (mutual cooperation), and commonly cooperated after receiving  $P$  (mutual defection; table 1). The two rules differed in whether new group members cooperated on the first round.

In the first of these rules, which we call ‘suspicious generalized PAVLOV’, players defected on the first round. If they were paired with another solitary player playing suspicious generalized PAVLOV, they would both immediately defect. However, as long as they remained as a pair, they would cooperate on the next round. Thus, cooperation could become established in pairs. However, if a third player joined the group, it would be able to exploit both cooperators in turn, driving them from the group. Nevertheless, the average payoff in groups exceeded that of solitary agents (figure 1a) or that expected in mutually defecting pairs ( $P=1$ ). This rule was associated with a typical group size slightly larger than 2 (figure 1b) and a very high probability of leaving upon receiving  $S$  (cooperating but receiving defection) but almost never otherwise (table 1). Cooperation could become established, as most groups were pairs (figure 2a), with a large proportion of solitary agents (who would probably eventually cooperate if they joined). However, groups of all sizes contained a high frequency of

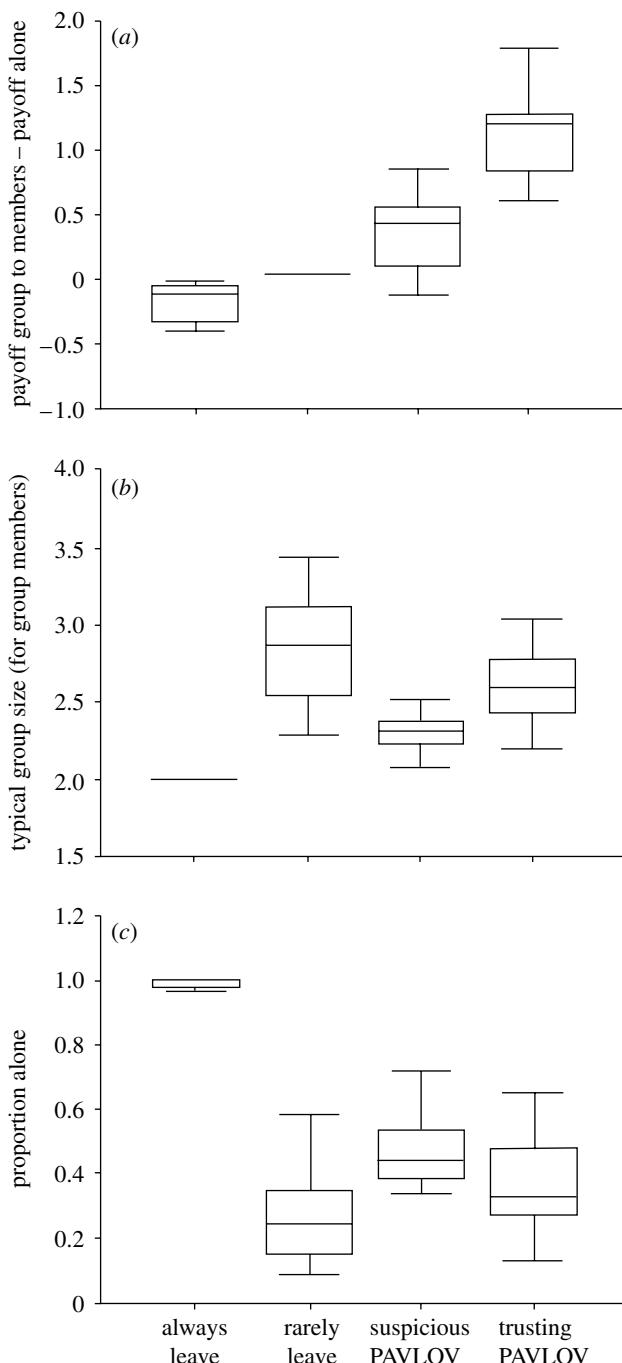


Figure 1. The effects of group-leaving and cooperative rules on (a) mean payoff to group members relative to those that are alone, (b) typical group size and (c) the proportion of the population found in groups. Rules were assigned using PROC CLUSTER in SPSS v. 11.0. Boxes represent the interquartile range, with the central line representing the median; bars represent the range.

individuals that had either recently received defection or had recently defected (figure 2a).

In ‘trusting generalized PAVLOV’, group members cooperated on the first round, and continued to cooperate in later rounds (table 1). This led to a high average payoff for group members (figure 1a), which approached that of mutual cooperation, and large groups (although not as large as in Rarely Leave; figures 1b and 2b). This cooperative rule was also associated with leaving after receiving  $S$ , but with a relatively low probability compared with suspicious generalized PAVLOV (see table 1). Agents

Table 2. Effects of model parameters on group-leaving rules.

(All evolved group-leaving rules could be classified into four distinct clusters using PROC CLUSTER in SPSS v. 11.0. Here, we show the percentage of simulations that resulted in each of these rules for each combination of independent variables.)

payoff when alone ( $A$ )	intrinsic leaving rate ( $\gamma$ )	encounter rate ( $\alpha$ )	always leave	rarely leave	suspicious generalized PAVLOV	trusting generalized PAVLOV
1.0	0.01	0.05	0.0	0.0	0.0	100.0
		0.15	0.0	100.0	0.0	0.0
		0.25	0.0	100.0	0.0	0.0
	0.03	0.05	0.0	100.0	0.0	0.0
		0.15	0.0	100.0	0.0	0.0
		0.25	0.0	100.0	0.0	0.0
	0.05	0.05	0.0	100.0	0.0	0.0
		0.15	0.0	100.0	0.0	0.0
		0.25	0.0	100.0	0.0	0.0
	1.5	0.05	0.0	0.0	0.0	100.0
		0.15	0.0	0.0	0.0	100.0
		0.25	0.0	0.0	100.0	0.0
		0.05	0.0	0.0	0.0	100.0
		0.15	0.0	0.0	0.0	100.0
		0.25	25.0	0.0	50.0	25.0
2.0	0.01	0.05	0.0	0.0	0.0	100.0
		0.15	0.0	0.0	100.0	0.0
		0.25	0.0	0.0	100.0	0.0
	0.03	0.05	25.0	0.0	25.0	50.0
		0.15	0.0	0.0	100.0	0.0
		0.25	75.0	0.0	0.0	25.0
	0.05	0.05	50.0	0.0	0.0	50.0
		0.15	25.0	0.0	75.0	0.0
		0.25	100.0	0.0	0.0	0.0

also left with a probability  $>0.01$  after receiving  $T$  or  $P$ , although, because all new group members cooperated initially, these states were rare (figure 2b). Trusting generalized PAVLOV occurred at lower encounter rates and lower payoffs to being alone (in other words, a lower incentive to leave the group) than suspicious generalized PAVLOV (table 2). Under trusting generalized PAVLOV, groups as large as  $GS_{max}$  (five individuals) were present and these still were mainly composed of cooperating agents (the proportion of  $R$ , or agents that had just experienced mutual cooperation was high; figure 2b). Indeed, the proportion of group members that had recently experienced cooperation tended to increase with group size (figure 2b).

Increasing  $GS_{max}$  to 10 had little effect on typical group sizes, group-leaving rules and cooperation. Interestingly, increasing  $R$  and  $T$  (to 6 and 8, respectively) also had little effect on the output of the model, even though, in the absence of differential group-leaving, doing so led to a dramatic increase in the proportion of simulations in which cooperation became established within 2000 generations (I. M. Hamilton and M. Taborsky, unpublished modelling results).

### (b) Contingent movement and assortment

We used a similar simulation model to measure ‘genotypic’ (i.e. decision rule) and phenotypic assortment in populations following three of the four group-leaving rules. We did not repeat this procedure for the fourth rule Always Leave, because groups would be exceedingly rare, and calculation of the genotypic and phenotypic

correlation among group members would not be informative. For each simulation, we assigned the same group-leaving rule to all 500 members of the population (based on the median probability of leaving for each rule; table 1), and did not allow these to evolve. Tendencies to cooperate ( $C_i$ ) were chosen from a normal distribution derived from the mean and standard deviation of  $C_i$  that we found associated with that rule in the above simulations (table 1; note that most probabilities of cooperation were roughly normally distributed). We then allowed agents to interact over 200 time-steps, and recorded the cooperative rule played by the partner (if any) of each agent in each time-step. In a second set of simulations, we recorded the proportion of group interactions in which the focal agent cooperated, and the proportion of interactions in which the focal agent received cooperation.

We randomly selected 50 focal agents from the population for each of 50 simulations for each group-leaving rule that we examined. We analysed results for each group-leaving rule, and for genotypic and phenotypic assortment, independently. To find genotypic assortment coefficients, we used PROC MIXED in SPSS v. 11.0, with simulation as a random factor,  $C_R$ , the probability of cooperating after mutual cooperation, as a covariate and the mean value of partners’  $C_R$  as the dependent variable. We used the standardized slope ( $\beta$ ) of the regression line of partners’  $C_R$  on the focal agents’  $C_R$  as our measure of assortedness. To find phenotypic assortment, we employed a similar procedure, with the proportion of interactions in which cooperation was received as the

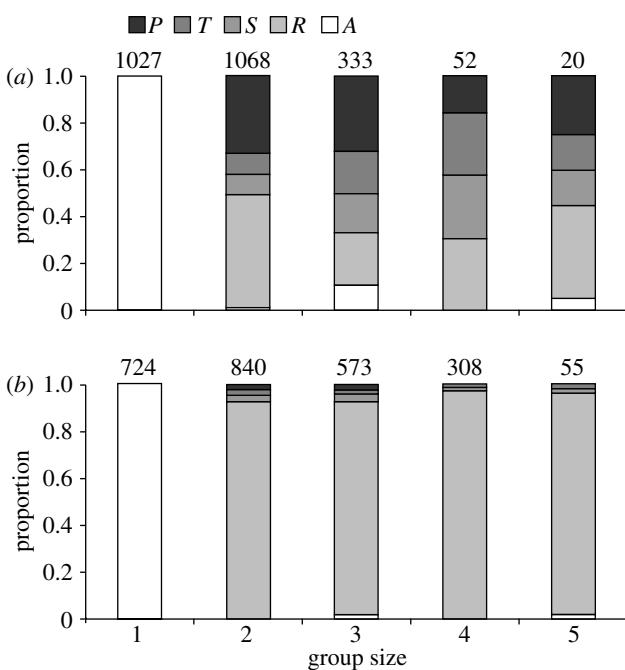


Figure 2. Group size and frequency of cooperation for groups established under (a) suspicious generalized PAVLOV and (b) trusting generalized PAVLOV. Shown are the results from five replicate populations of 500 agents in which that rule was established. Shading denotes the proportion of cases in which the last remembered interaction within the group was  $A$ ,  $R$ ,  $S$ ,  $T$  or  $P$ , respectively; groups characterized by high frequencies of cooperation would have a high proportion of agents that had most recently experienced  $R$ .

Table 3. Mean ( $\pm$ s.e.) assortment coefficients for three of the four behavioural rules that emerged in evolutionary simulations.

(The fourth rule was not included because groups were extremely rare. Genotypic (or decision-rule) assortment is the standardized slope of the regression line of partners' probability of cooperating after mutual cooperation ( $C_R$ ) upon the focal agent's  $C_R$ . Phenotypic assortment is the standardized slope of the regression line of the proportion of interactions in which cooperation was received against the proportion of interactions in which the focal agent cooperated.)

group-leaving rule	genotypic assortment coefficient ( $\pm$ s.e.)	phenotypic assortment coefficient ( $\pm$ s.e.)
rarely leave	0.014 ( $\pm$ 0.022)	0.065 ( $\pm$ 0.072)
suspicious generalized PAVLOV	0.134 ( $\pm$ 0.013)	0.245 ( $\pm$ 0.022)
trusting generalized PAVLOV	0.206 ( $\pm$ 0.016)	0.524 ( $\pm$ 0.017)

dependent variable, and the proportion of interactions in which cooperation was given as the covariate.

As shown in table 3, the group-leaving rules associated with suspicious and trusting generalized PAVLOV led to values of assortment for  $C_R$  (genotypic assortment), and for cooperative phenotypes, that were greater than random. In contrast, under Rarely Leave, there was neither genotypic nor phenotypic assortment of cooperators.

#### 4. DISCUSSION

Contingent movement often evolved in our simulations, and, when it did, it was associated with positive behavioural assortment and some degree of cooperation in the population. We found that a highly cooperative strategy, trusting generalized PAVLOV, could evolve under a 'generalized reciprocity' scenario despite the lack of individual recognition, spatial structure or social transmission of cooperative rules. However, allowing group-leaving rules to evolve did not necessarily yield contingent movement or highly cooperative groups. Over a wide range of parameters groups were not stable (Always Leave), consistently uncooperative (Rarely Leave) or, despite following a similar group-leaving rule as trusting generalized PAVLOV, employed a strategy that mixed cooperation and exploitation (suspicious generalized PAVLOV).

Assumptions about the likelihood and costliness of movement among groups, both voluntary and involuntary, strongly influenced the predictions of the model. Whenever intrinsic leaving rates were sufficiently low, a win-stay, lose-shift rule for group leaving was established. However, similar group-leaving rules could be associated with exploitation or cooperation, depending on the relative costliness of leaving the group. When new groups were difficult to find and the payoff to being alone ( $A$ ) was relatively low, the highly cooperative trusting generalized PAVLOV rule was established. On the other hand, when new groups could more easily be found and the payoff to being alone was relatively high, a similar group-leaving rule was associated with a suspicious strategy that could establish cooperation in pairs, but could also exploit cooperative groups. Under a win-stay, lose-shift movement rule, a free-riding cheater would rapidly find itself on its own, after having exploited and driven away other group members. However, when the probability of finding a new group is high, or the payoff to being alone high, the net cost of being abandoned is fairly low.

Cooperation only evolved when the payoff to being alone was higher than (or, when the likelihood of encountering a new group was very low, equal to) that experienced under mutual defection. Otherwise, groups formed randomly and never broke up (even though some group members might have done better if they had left and found a more cooperative group). Consequently, there was no phenotypic assortment in the population (table 3: Rarely Leave), groups were probably too large for direct reciprocity to be important, and cooperation did not evolve.

The win-stay, lose-shift rules (suspicious and trusting generalized PAVLOV) were associated with positive genotypic and phenotypic assortment (table 3). That is, agents that cooperated upon receiving mutual cooperation were more likely to associate with agents that used similar rules than expected by chance. Agents that cooperated frequently tended to be associated with others that cooperated frequently. Because mutually cooperative groups would experience greater fitness gains than non-cooperative groups or singletons, cooperation could flourish because of the effects of between-group selection (Wilson & Dugatkin 1997).

The most cooperative strategy (trusting generalized PAVLOV) was associated with relatively large group sizes. In populations using trusting generalized PAVLOV

strategy, the proportion of cooperators even increased slightly with group size (the proportion of interactions that were mutually cooperative in figure 2b increases). This finding is the opposite of that generally expected when group sizes are set beforehand (Pfeiffer *et al.* 2005; reviewed in Kollock 1998). In that case, larger groups should allow greater opportunities for invasion by cheaters (Packer & Rutman 1988; Kollock 1998; Gaube 2001), although experimental results in a generalized reciprocity game suggest this is not necessarily so (e.g. Yamagishi & Cook 1993). In our model, the conditional group-leaving rules that evolved resulted in the dissolution of groups invaded by conditional cheaters (as would commonly occur in suspicious generalized PAVLOV). Unless  $A=P$ , unconditionally uncooperative agents would do better by being alone than by grouping, so groups of these did not form. Therefore, neither conditional nor unconditional cheaters would be expected in large groups when contingent group-leaving was established. The largest groups found in any of our simulations were, however, associated with a non-cooperative strategy. When group-leaving was rare and unconditional (table 2, Rarely Leave; i.e. no win-stay, lose-shift scenario), larger groups were not associated with more cooperative strategies.

Although, in our model, group formation was random, we suggest that players using a more complex decision rule could use group size as a cue to the likelihood of receiving cooperation, which may influence their decisions to join and to cooperate initially. Because, under win-stay, lose-shift, the very existence of larger groups implies cooperation, the best decisions of a potential joiner may differ between groups likely to include only highly cooperative individuals (large groups) and those less likely to (small groups). Thus, potential joiners to groups of different sizes may be able to use this information when deciding whether to join and whether to cooperate with or, conversely, to exploit these groups.

In contrast with such rather complex agents, however, the rules that evolved in our model are attractive because they do not require complex cognitive capacities on the part of players. Individuals only need to keep track of their most recent experience (including their own behaviour) and whether they are in a group. Importantly, they do not need to, and, indeed are assumed not to, keep track of the identity of partners. Simple group-leaving rules may be particularly important in highly mobile populations, in which each individual could potentially interact with all others in the population and, therefore, assortment is unlikely in the absence of such behavioural mechanisms. Thus, simple contingent movement rules provide a simple behavioural mechanism that could explain positive assortment and cooperation in highly mobile organisms with limited cognitive complexity.

Both generalized PAVLOV strategies, which could lead to cooperation, only evolved when group-leaving was conditional, that is, agents often left upon receiving  $S$ , but rarely did so otherwise. In natural groups, members commonly leave when the payoff to grouping is low. For example, pholcid spiders have been found to use a win-stay, lose-shift strategy when deciding whether to share a web with another. If success on a shared web was experimentally increased, spiders were more likely to stay at that web (Jakob 2004). Similarly, in cleaner fish-client interactions, client fish were more likely to leave

cleaners that had cheated by nipping them (e.g. Bshary & Schaffer 2002). Although these examples are unlikely to conform to the Prisoner's Dilemma game as modelled here, they do suggest that an individual's history of success in a group will influence its decision to stay there.

### (a) Comparison with other models

In general, we found that the effects of mobility on grouping were not simple. Contingent movement may allow cooperation to evolve, or it may result in a mix of cooperative groups and exploitation. Highly mobile agents (e.g. those with intrinsically high encounter and intrinsic leaving rates) may not group at all. Previous modelling results, in which group-leaving rules were specified beforehand, have also found that mobility can either increase or decrease cooperation. As in our model, in the model by Hauert *et al.* (2002), mobility kept groups relatively small. However, in our study, more cooperative strategies were found associated with larger groups (figures 1b and 2). This difference probably has to do with the choice of conditional versus unconditional strategies; the unconditionally cooperative strategies used in Hauert *et al.* (2002) are vulnerable to exploitation, whereas the conditionally cooperative strategies and contingent movement rules that evolved in our model lead to the formation of 'conspiracies of cooperators' (Aktipis 2004) that gain from mutual cooperation and can punish defectors by abandoning them. Pepper & Smuts (2002) found that mobility could either increase or decrease assortiveness of cooperators. In their model, however, cooperative tendency and the tendency to move were unconditional and could not evolve. Cooperation was the prudent exploitation of a shared prey population, and positive assortment was found when the growth rate of prey was relatively low. This may be because the search time for a non-depleted patch is lower when the growth rate of prey is high. Search time influences the success of free-riding strategies. As found by Enquist & Leimar (1993) and in our model, a free-riding strategy (e.g. suspicious generalized PAVLOV) cannot invade when either search time or expected time in the group are large. This corresponds to conditions in our model where the payoff to leaving groups was relatively low.

Recently, Le Galliard *et al.* (2005) modelled the simultaneous evolution of mobility and altruism. When allowed to evolve separately, altruism was associated with low mobility. However, when allowed to evolve simultaneously, altruism and mobility could be positively or negatively correlated, depending on life history traits and constraints on mobility. For example, increases in habitat connectivity could lead to a decline in both mobility and altruism by reducing habitat saturation and the kin-selected benefits of altruism. Surprisingly, in their model, increasing costs of mobility could promote increases in both altruism and mobility through effects on local aggregation, except when costs were very high or very low. Our model differs in that movement and altruism were conditional upon the phenotype of other group members and that the immediate costs and benefits of group living did not depend on group or neighbourhood size. Furthermore, in our model, we assumed very high habitat connectivity (i.e. any agent could join any group smaller than  $GS_{max}$ ). Nevertheless, we found that extensive cooperation evolved alongside mobile strategies

in many of our simulations, suggesting an important role for conditional behaviours in stabilizing cooperation even under environmental conditions hostile to the spread of altruism. In contrast to the model of Le Galliard *et al.* (2005), we found a negative correlation between cooperation and mobility over most of the range of mobility costs examined. Although agents using either suspicious or trusting generalized PAVLOV would move if cheated, movement rates at equilibrium were lower for the more cooperative trusting generalized PAVLOV, as implied by the relatively larger group sizes associated with this strategy (figure 1). At the highest costs of mobility examined, there was a positive correlation between mobility and cooperation; the more mobile trusting generalized PAVLOV strategy was more cooperative than the less mobile Rarely Leave strategy. This difference between the models may arise in part because habitat saturation was relatively unimportant in our model; even in populations using Rarely Leave, few groups were sufficiently large that new members could not join (figure 1b).

There are similarities between trusting generalized PAVLOV and Aktipis's Walk Away strategy (Aktipis 2004), in which agents walk away from a dyad if they have received defection. In Aktipis's model, as in ours, contingent movement was associated with positive phenotypic assortment and the evolution of cooperation. Our model demonstrates that such a group-leaving rule can evolve in concert with the evolution of cooperative strategies, and that a walk-away type rule can evolve in groups larger than two. Our trusting generalized PAVLOV strategy also differs from the 'win-stay, lose-move' rule employed in Aktipis's agent-based simulations, in that agents using trusting generalized PAVLOV will not always leave after defection. They will remain after mutual defection and, even in the case of S, often remain in the group (with a probability  $> 0.01$ ), and switch to defection instead.

Finally, we suggest that other characteristics of Prisoner's Dilemma-type games may also be under the control of players. For example, it is well established that limited dispersal can lead to assortative population structure and cooperation (Nowak & May 1992; Ferriere & Michod 1995; Killingback & Doebeli 1996; Brauchli *et al.* 1999; Pepper & Smuts 2002; Hauert & Doebeli 2004). However, dispersal distance and direction are, to some degree, under the control of dispersers. Therefore, additional insights into the behaviour of viscous populations might be gained by incorporating flexible dispersal decisions into such models.

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