

## The evolution of cooperation in mobile organisms

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**Abstract.** Current game theory models of cooperation based on reciprocity do not take into account the active switching of partners made possible by mobility. Since such situations cannot be understood by means of a repeated Prisoner's Dilemma game, new theory is developed which considers both a current partner and the access to other partners. It is shown that mobility seriously restricts the evolution of cooperation: an efficient free rider could move rapidly through a population of cooperative individuals, searching out victims to exploit. Properties of the social environment, such as population size and density, influence the search time for a free rider and thus the possibilities for the evolution of cooperation. Behavioural adaptations, such as initial suspiciousness towards strangers, and gossiping, may to some extent counteract the effects of mobility and favour cooperation. The possible importance of search time is illustrated by comparative data on the relationship between nest sharing and size of nest aggregations in sphecoid wasps.

Two decades have passed since Trivers (1971) presented his theory of reciprocal altruism. Examples of animals maintaining cooperative relationships based on reciprocity have been documented (Fischer 1980; Wilkinson 1984; Milinski 1987), but the general impression seems to be that there are fewer than expected (Packer 1986). Excluding humans, this relative scarcity is particularly striking for advanced organisms capable of recognizing and remembering many potential partners. Such organisms tend also to be highly mobile. Current theorizing about reciprocity (Axelrod & Hamilton 1981) has paid little attention to the active switching of partners made possible by mobility, although the problem has recently been dealt with by Friedman & Hammerstein (1991) and Dugatkin & Wilson (1991). Here, we suggest that mobility severely constrains the evolution of cooperation.

Although cooperation is a major behavioural phenomenon occurring in all groups of organisms, many opportunities for cooperation are not exploited. For instance, organisms often compete for resources instead of sharing them. It is well known that potential cooperative benefits are not sufficient for the evolutionary maintenance of cooperation. A cooperative population is vulnerable to invasion by non-cooperating (defecting) individuals, since the latter could benefit from

help offered by others without paying the cost of providing any help themselves.

Two explanations have been offered for the occurrence of cooperation: kinship (Hamilton 1964) and social control (Trivers 1971; Axelrod & Hamilton 1981). The idea of social control is that the social environment rewards or punishes individuals as a consequence of their behaviour. Compared with help between close kin, the evolution of cooperation between unrelated individuals and the mechanisms of social control are less well understood. Existing models, mainly based on the repeated Prisoner's Dilemma game, primarily apply to organisms that are sessile or unable to control the duration of stay with a companion (Axelrod & Hamilton 1981). An ability to choose between staying or leaving the present companion can, however, strongly influence the evolutionary stability of cooperation. Mobility permits strategies that efficiently exploit cooperating individuals. We use the term free rider for such strategies. A free rider moves around and uses cooperation offered by others but does not provide any help in return. When unmasked the free rider simply leaves and moves on, looking for other cooperative individuals to exploit. A cooperative strategy for mobile organisms will then need some type of defence against free riding.

In the following we present some models that illustrate the effects of mobility on the evolution of cooperation. First, the time a free rider needs to search for a new victim is shown to be of crucial importance: a short search time can prevent the evolution of cooperation. Second, a small population size, restricting the number of victims available to a free rider, is shown to favour cooperation. A number of behaviour patterns that may be viewed as social control, such as initial suspiciousness towards strangers and gossiping, also favour cooperation, and we attempt to quantify their effects. The evolutionary stability of a potentially costly mechanism of social control can, however, be problematic, and we address this issue in a model of the evolution of suspiciousness.

As an attempt to demonstrate empirically the importance of search time, we present comparative data of the relationship between frequency of nest sharing and size of nest aggregations in sphecoid wasps. Nest sharing is found to be rare in species with large aggregations, potentially indicating that short search times prevent the evolution of cooperation.

#### A MODEL OF COOPERATION IN MOBILE ORGANISMS

Introducing mobility leads to substantial modification of existing theory of cooperation. Apart from a consideration of interactions within a coalition, one must also take into account properties of the social environment, the most important being the time required to find a new coalition partner.

This search time primarily depends on the density of individuals and on the speed with which an individual can move in the environment. To form a coalition an individual must also find someone who is not already fully engaged and is willing to be a partner, resulting in an effective search time  $S$  per coalition. Once a coalition is formed, it can be terminated by either partner; otherwise it lasts an expected time  $T$ . Coalitions can be lifelong, but may be shorter if they are terminated by causes other than death.

For interactions within a coalition two behavioural options, cooperate and defect, are available. The benefit of receiving help is  $b$  and the cost of giving help is  $c$ , per unit time. Hence, if both individuals cooperate their payoff is  $b - c$  per unit time. If neither individual cooperates they simply ignore each other and nothing is paid out. An animal that

exploits a cooperating individual receives  $b$  per unit time but pays no cost. We make no detailed assumption whether individuals take turns in helping each other or if cooperation occurs as joint actions; we simply assume that a defecting individual is detected at a certain rate.

A strategy is evolutionarily stable (an ESS), if it is favoured by selection when used by all but a small minority of individuals in a population. In mobile organisms, a simple strategy of conditional cooperation ( $C$ ) is to start by offering cooperation and to leave whenever a partner stops cooperating.

Let us now investigate when  $C$  is evolutionarily stable against a free rider strategy ( $FR$ ). With search time per coalition  $S$ , coalition time  $T$ , and payoff  $b - c$  per time unit when in coalition, the average utility of  $C$  per time unit in a population using  $C$  can be calculated. The formation and breaking up of coalitions are assumed to occur randomly at constant rates, so that  $S$  and  $T$  are expectations of exponentially distributed independent variables. With the expected lifetime  $L$ , the total utility  $U$  equals

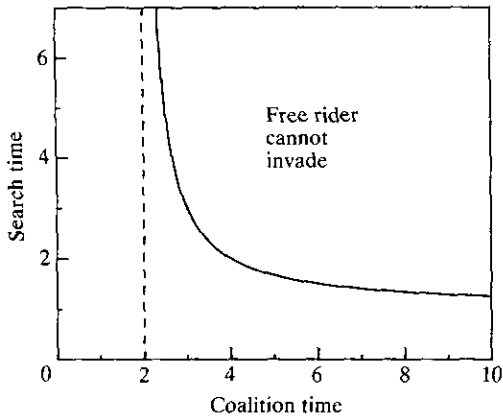
$$U(C,C) = (b - c) \frac{T}{S + T} L \quad (1)$$

Unconditional cooperation would receive the same payoff, so that conditional cooperation can at best be neutrally stable. The total utility for a free rider ( $FR$ ) exploiting a population of individuals using  $C$  equals

$$U(FR,C) = b \frac{1}{S + 1} L \quad (2)$$

where  $b$  is the payoff per time unit to exploit a cooperator. For simplicity, the time a free rider can exploit a conditional cooperator is set to 1 ( $T > 1$ ). The condition for evolutionary stability of  $C$  against a free rider,  $U(C,C) > U(FR,C)$ , shows that an increase in both coalition time and search time favours cooperation (Fig. 1). For long search times the condition approaches  $T > b/(b - c)$ . For smaller and more realistic values of  $S$  the condition is more restrictive,  $T > Sb/(S(b - c) - c)$  and for  $S \leq c/(b - c)$  cooperation is never evolutionarily stable.

Using the famous iterated Prisoner's Dilemma game it has been shown in economical game theory (Luce & Raiffa 1957; Shubik 1959) and in evolutionary game theory (Axelrod & Hamilton 1981) that, if individuals tend to interact with each other



**Figure 1.** The figure shows for which combinations of coalition time  $T$  and search time  $S$  conditional cooperation is stable against a free rider. The dashed line gives the condition for the cooperative Tit-for-Tat strategy in Axelrod & Hamilton's (1981) study and can be interpreted as the condition for evolutionary stability of cooperation in an organism unable to control coalition time. The benefit of receiving help  $b=2$  and the cost of giving help  $c=1$ , per unit time.

several times, conditionally cooperative strategies may withstand exploiting strategies. However, these models consider only behaviour within a pair of individuals and there is no alternative to the pair mate. In biology this type of situation may correspond to an organism that is sessile or, more generally, to an organism not able to control coalition time. By comparing the model by Axelrod & Hamilton with the results obtained in this paper we can get some insight into the differences between mobile and non-mobile organisms with respect to cooperation.

Using our symbols, the stability condition for the conditionally cooperative strategy Tit for Tat (start by offering cooperation and after that mimic the behaviour of the partner) in Axelrod & Hamilton's game is the one given already for long search times:  $T > b/(b-c)$ . To see this, note that in the terminology used by Axelrod & Hamilton  $b-c$  is the reward for mutual cooperation,  $b$  the temptation to defect,  $-c$  the sucker's pay off, and the punishment for mutual defection is zero. Letting  $w$  be the probability of an additional round, Axelrod & Hamilton's two conditions for stability of cooperation both become  $w > c/b$ . Using the fact that  $T = 1/(1-w)$  we then obtain  $T > b/(b-c)$ .

A comparison shows that the condition for cooperation to be evolutionarily stable against exploiting strategies is more restrictive in mobile organisms

(see Fig. 1). The important difference is that, since a free rider can always 'move on' when unmasked, it is less sensitive to the normal duration of a coalition.

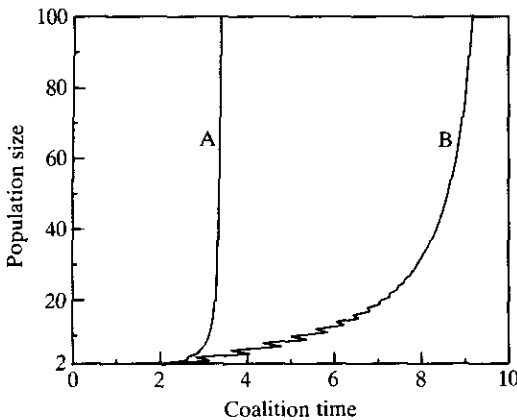
A conclusion from the iterated Prisoner's Dilemma game would be that cooperation is more likely when coalition time is long (the probability of repeated interactions is high) and that lack of cooperation is due to short coalition times. This condition may well apply to organisms unable to control coalition time. However, in mobile species with high capacity for control of coalition time, such as birds and mammals, coalitions can potentially form for long periods. The fact that cooperation is still uncommon among these species suggests that it is the potential for free riders to find victims at a high rate (short search time), rather than coalition time, that restricts the evolution of cooperation in many species (cf. Fig. 1).

### Small Populations

In the analysis given above we assumed that population size was infinite or very large and that encounters were random. However, individuals may sometimes live their whole lives or parts of their lives in rather small groups or populations with restricted possibilities of migration. If individuals remember defections and refuse to offer cooperation to defecting individuals in future interactions (we include this in the strategy C), the number of possible victims to a free rider becomes limited in smaller groups (in addition, a decrease in group size favours cooperation when accompanied by a decrease in density).

To model this we assume that the group has a certain size and that group members are replaced (e.g. through births and deaths) at a certain rate (Appendix I). Pure exploitation may not be the most efficient strategy to destabilize cooperation in small populations; often a strategy is more potent that starts with defection and, when search time reaches a certain level, switches to cooperative behaviour in some coalitions (Appendix II). Figure 2 shows when C is evolutionarily stable against such a strategy.

Number of individuals is sometimes discussed in a different context from the one given here. When more than two individuals cooperate together, i.e. a single coalition contains more than two individuals, game theory models have shown that the possibilities for cooperation decrease with the number of cooperating individuals (Boyd & Richerson 1988).



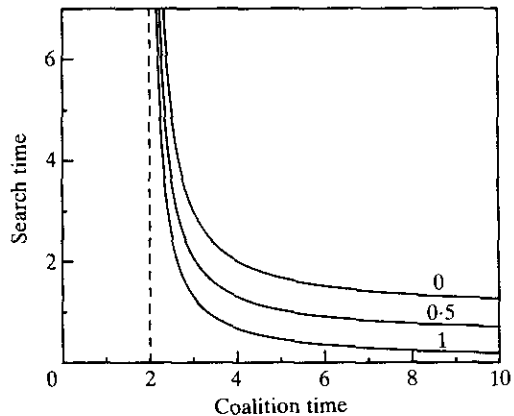
**Figure 2.** The stability of cooperation in finite populations. The area to the left of a curve shows combinations of population size  $N$  and coalition time  $S$  for which conditional cooperation can be invaded by an exploitative strategy. Curve A refers to a case with lower density and curve B to a case with higher density (Appendix II). The irregularities in the curves are caused by effects of odd and even numbers on the possibilities of forming coalitions. The benefit of receiving help  $b=2$  and the cost of giving help  $c=1$ , per unit time.

### DEFENCES AGAINST FREE RIDERS

The success of a free rider could be further reduced if cooperative individuals used more refined social control than considered so far. Such strategies would either enhance the detection of a free rider so that its average gain per potential victim decreases or slows down the rate at which the free rider meets potential victims.

When analysing small populations we have already assumed that a cooperating individual learns about a free rider when it does not reciprocate. In addition, individuals could be suspicious towards strangers and could try to assess potential partners in some way before offering cooperation. Initial suspiciousness also causes a free rider to have to wait longer for each reward, and thus decreases the encounter rate of potential victims (Friedman & Hammerstein 1991). Synchronization of interactions among coalitions has similar effects (Knowlton 1979).

A cooperating individual could also decrease each investment in cooperation and compensate by increasing the number of interactions and thus detect non-reciprocating individuals at a lower cost. This has been referred to as trading (Fischer 1980; Friedman & Hammerstein 1991). Information about potential partners could also come from



**Figure 3.** The effect of suspiciousness on the evolutionary stability of cooperation against a free rider. The area above a curve shows combinations of coalition time  $T$  and search time  $S$  for which free riding cannot invade conditional cooperation. The curves are labelled with the duration of suspiciousness. The benefit of receiving help  $b=2$  and the cost of giving help  $c=1$ , per unit time.

observations of interactions between other individuals or from gossiping (Paine 1967; Trivers 1971; Alexander 1987).

To gain some insight into the effect of defences against free riders we analyse suspiciousness and gossiping in some detail.

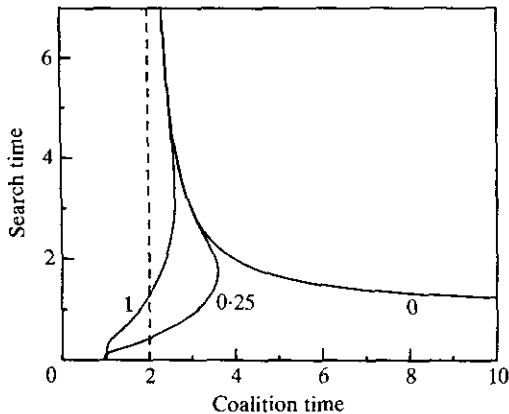
### Suspiciousness

To study suspiciousness we extend our first model so that cooperative players are suspicious for a fixed time before offering cooperation (Appendix III). This has negative consequences for both cooperating individuals and free riders (see also the section on selection for social control below). The total reward from interacting with a partner or a victim decreases since an association might be terminated before any help is offered. In addition, a free rider has to stay for longer with each victim and so is disadvantaged (Fig. 3).

Qualitatively, suspiciousness has a strong effect when it forces a free rider to spend a time greater than  $b/(b-c)$  on each victim (compare the condition for sessile organisms given above).

### Gossiping

Our analyses suggest that the opportunity for cooperative behaviour is less in mobile than in sessile organisms. How, then, can the impressive



**Figure 4.** The effect of gossiping on the evolutionary stability of cooperation. The area to the right of a curve shows combinations of coalition time  $T$  and search time  $S$  for which exploitative strategies cannot invade conditional cooperation. The three curves represent no gossiping, gossip transmitted to 25% (0.25), and to all (1.0) individuals encountered. The benefit of receiving help  $b=2$  and the cost of giving help  $c=1$  and the population size  $N=100$ .

amount and diversity of cooperation between unrelated individuals in humans be explained? We suggest that information about prospective partners is available to a greater extent in humans than in other animals. The human language is unique as a means to share information efficiently. Exchange of information about the capacity of other individuals, and their morals, is a human characteristic. The extent of gossiping in many societies has led anthropologists to regard it as one of the most important social and cultural phenomena (Gluckman 1963; Paine 1967).

Gossiping counteracts free riding by allowing information (that a particular individual is unreliable and should not be interacted with) to spread through a group. We have modelled a finite population where gossip is exchanged when individuals meet (Appendix IV). The results show that gossiping is very potent in decreasing the success of a free rider. The condition for evolutionary stability of cooperation comes close to that for non-mobile organisms. With gossiping cooperation can be stable even in very dense populations (Fig. 4).

### SELECTION FOR SOCIAL CONTROL

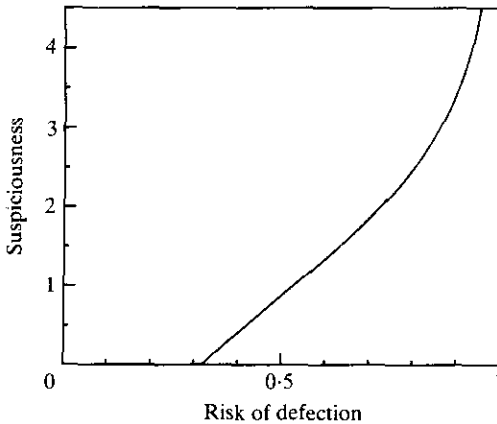
So far we have investigated the evolutionary stability of cooperation only against strategies trying to exploit cooperation. We have not considered

how a particular cooperative strategy could be maintained in the presence of other cooperative strategies. In fact, cooperative strategies that are difficult to exploit tend to be costly in terms of less efficient cooperation and will thus not be evolutionarily stable against more unconditional cooperation (this problem also existed in the first model in this paper in the less severe form of neutral stability of cooperation). The conclusion is that evolutionary stability against exploiting strategies is a necessary but not sufficient condition for a cooperative evolutionarily stable strategy. In addition one must show how a defence against defection can be maintained when less conditional cooperative strategies are possible. In fact, evolutionary stability of cooperation requires that exploitation occurs to some extent. Although this may sound like a paradox, costly defences against exploitation cannot be selected and thus maintained if defection never occurs.

In most models of cooperation, the populations dealt with are homogeneous. However, a more realistic situation is that some individuals benefit more from exploitation than from cooperation. This may be related to the individual itself or to the situation. For instance, it may pay to exploit a new partner if you already have a coalition partner, if you are strong, if you are just migrating through an area, or if the new partner is particularly easy to exploit.

To get some quantitative insight we ask how much suspiciousness will be maintained in a heterogeneous population if, when initiating a coalition, there is a certain risk that the new partner subsequently defects (Appendix V). In our example we assume that the assessment of a partner is not related to whether an individual has yet offered cooperation or not. A situation of this kind occurs when individuals that already have a partner show interest in forming a coalition but subsequently defect. For instance, in monogamous birds females must assess the mating status of potential males in order to avoid already mated males and, as a consequence, poor male assistance in parental care. By spending time with a male a female may, for example, be able to detect his mate if he already has one. In the example in Fig. 5, with a risk greater than 40% of initiating a coalition with a non-cooperative individual substantial suspiciousness will be maintained (compare Figs 5 and 3).

Concerning gossiping, there might be a cost in the form of time spent exchanging information.



**Figure 5.** Evolutionarily stable degree of suspiciousness as a function of the risk that a new partner will defect rather than cooperate. The benefit of receiving help  $b=2$ , the cost of giving help  $c=1$  and the coalition time  $T=5$ .

With a non-negligible chance of encountering a free rider, it could be advantageous for an individual to spend time receiving information. Further, if the individual needs to provide information in order to receive (trading of gossip), it could also be advantageous to spend time providing information.

## EMPIRICAL DATA AND DISCUSSION

Our models show that inability to control coalition time favours cooperation. This result contrasts with earlier opinions (Axelrod & Hamilton 1981) in suggesting that cooperation should be more common in primitive organisms, which typically are less mobile. In fact, cooperation appears to be widely distributed over all kingdoms of organisms rather than particularly associated with vertebrates and insects. This is most clearly seen for interspecific cooperation (Boucher et al. 1982; the systematic distribution of mutualism seems better known, probably because it is easier to detect). For instance, most higher plants, including mosses and ferns, cooperate with fungi (mycorrhizae), and many other fungi are lichenized.

### Effects of Search Time in Sphecoid Wasps

For mobile species, our models predict that increasing search time favours cooperation. We have addressed this issue in a comparative study of nest sharing in solitary wasps.

Females of solitary wasps build nests, often in the soil, and provision cells within the nest with food for the offspring. After egg laying the cell is sealed off and no further parental care occurs (e.g. Evans 1966). Asocial behaviour is common and includes usurpation of nests, stealing of prey, and cuckoo behaviour (Brockmann & Dawkins 1979). Females are often seen searching and entering other females' nests (Brockmann & Dawkins 1979). Interestingly, cooperation between females also occurs. In most groups of solitary wasps and bees there are species where two or more females share a nest (Michener 1974; Brockmann & Dawkins 1979). Nest sharing has several potential benefits, including joint nest building and joint defence against both intraspecific and interspecific parasitism. It also entails a problem, since a female accepting conspecifics in her nest becomes more susceptible to intraspecific parasitism.

Solitary wasps often nest in dense aggregations with up to several hundred individuals. According to the theory developed in this paper one would expect parasitic behaviour to be more profitable when it is easy to find potential victims, and thus cooperation to be less likely. Aggregated nesting is likely to make search time short for two reasons: aggregations are easy to find and many potential victims are readily available within an aggregation. We collected data from the literature for one group of solitary wasps, Sphecidae (for literature on nest sharing in sphecoid wasps contact us or see Brockmann & Dawkins 1979 and Evans & Hook 1986), where nest sharing has been observed in at least 79 species distributed over six subfamilies and 31 genera. Using data on the frequency of nest sharing in relation to aggregation size, we find, as predicted, that nest sharing is virtually absent among highly aggregated species (Fig. 6). To avoid misunderstandings we want to point out that search time is not an exclusive explanation and that search time together with other factors (e.g. benefit and cost of cooperation, coalition time and kinship) determine the evolutionary outcome. Further empirical studies are needed to sort out the relative importance of these factors.

### Examples of Social Control

A number of observations indicate that a coalition ends or changes when it is unproductive for one or both partners. Many ants form mutualistic relationships with lycaenid butterfly larvae, in



been observed in several species (Dunbar 1988). In some species a significant part of the day (over 10% of daylight time) is spent grooming (Dunbar 1988). In a comparison across species, the amount of grooming was positively correlated with typical group size (Dunbar 1988), indicating that a stronger defence against exploitation is maintained in larger groups.

(4) Simultaneous hermaphrodites tend to have complex and time consuming mating behaviour, which may substantially decrease the success of a pure male strategy. Observations include complicated courtship or transfer of sperm, accurate synchronization among spawning pairs, egg trading, long-term pair bonding, and fusing together for life (Hyman 1951; Edwards & Lofty 1972; Fischer 1980; Tompa et al. 1984; Pearse et al. 1987; Sella 1988).

(5) In monogamous mating systems males are potential free riders and females potential victims. Females are usually described as coy and ready to reproduce only after a period of courtship and attachment. This period may allow the female to assess male quality and intentions. In some species, such as pigeons, the female lays two very small eggs at each breeding attempt but repeats this several times during a season, instead of making one heavy investment.

(6) Synchronous reproduction occurs in monogamous fish and birds. An interesting result from some bird species is that the degree of synchrony seems to increase in larger colonies (Gochfeld 1980), where the risk of exploitation is presumably greater.

### Risk of Exploitation in Cooperative Behaviour

Costly social control will not be maintained in evolution unless there is a real risk of exploitation. Indeed, careful observation of situations where cooperation occurs shows that individuals are not invariably cooperative (Boucher et al. 1982). For instance, monogamy is a form of reproductive cooperation and it has been observed in an increasing number of monogamous bird species that males regularly court and try to copulate with females without offering, for instance, protection or paternal care. In fact, such behaviour has been offered as an explanation for polygyny in some species of birds (von Haartman 1969). Studies of hermaphroditic polychaetes and fish have shown that individuals that for some reason do not carry unfertilized eggs still take part in courtship (Fischer 1980; Sella 1988). Even tight relationships, such as between fungi and higher plants (mycorrhiza), algae and fungi (lichens), or algae and cnidarians, are not invariably mutualistic (Henry 1966).

### Conclusions

In this paper we have shown that mobility seriously restricts the possibility for cooperation to evolve. Our models suggest that population characteristics such as density could strongly influence the stability of cooperation. Many of these aspects have yet to be fully explored both theoretically and empirically. We also emphasize that the maintenance of social control requires both cooperation and exploitation.

## APPENDIX I

For a finite population, we use the following life-history model. Interactions take place in a group of  $N$  individuals that are replaced at the rate  $\nu$  (per individual; expected duration of stay becomes  $L = 1/\nu$ ). Unpaired individuals find each other at the rate  $\mu$  (per searching pair). A coalition of two cooperators breaks up when either is replaced (thus, the coalition time is  $T = 1/2\nu$ ). A free rider—conditional cooperator coalition additionally breaks up when the free rider is detected; the time scale is set so that the expected duration becomes unity (implies  $T > 1$ ). After a sufficient amount of time, the formation and breaking up of coalitions results in a statistical equilibrium, entailing a distribution of the number of individuals engaged in coalitions. For a population of conditional cooperators in such a statistical equilibrium, the probability,  $p$ , that a random individual is not in coalition is easy to compute numerically. The equation  $p = S/(S + T)$  then defines  $S$ , the search time per coalition.

## APPENDIX II

Consider a population (Appendix I) using the strategy  $C$  in statistical equilibrium. We wish to determine an optimal strategy for a newly introduced individual. Let us keep  $N$  and  $\mu$  fixed. For long coalition times

$T$ ,  $C$  will be optimal, but below a limiting  $T'$ , some exploitative strategy,  $I$ , will do better. The strategy  $I$  could be to defect in all coalitions, but one must also consider possibilities such as defecting in the first coalition and then cooperating in following coalitions, etc. At coalition time  $T'$ ,  $C$  and  $I$  are equally good. To determine  $I$ , and thus  $T'$ , one needs to do dynamic programming, which is prohibitively difficult in this situation. We conjecture that  $I$  will be to defect in the first coalition and to cooperate in following coalitions. We have used this  $I$  to compute the limiting  $T'$  for Fig. 2 numerically. We used  $\mu = 1/(N - 1)$  as low density and  $\mu = 7/(N - 1)$  as high density. Note that both for  $N = 2$  and very large  $N$ , all exploitative strategies  $I$  will yield the same  $T'$ . This follows for  $N = 2$  from the fact that replacement of the other individual represents a renewal of the original situation. For very large  $N$ , on the other hand, previous partners will not encounter each other again. Thus, an error in our conjecture would mean only small changes to Fig. 2 (since both ends of the curves are determined).

APPENDIX III

Let  $\tau$  be the exponentially distributed coalition time (with expectation  $T$ ). With time of suspiciousness equal to  $x$ , the relevant payoffs become

$$U(C,C) = (b - c) \frac{\Pr(\tau \geq x)T}{S + T} L \text{ and}$$

$$U(FR,C) = b \frac{\Pr(\tau \geq x) \times 1}{S + \Pr(\tau < x)E(\tau | \tau < x) + \Pr(\tau \geq x)(x + 1)} L$$

where  $\Pr$  denotes probability and  $E$  denotes expectation.

APPENDIX IV

We want to determine the best strategy for an individual  $A$  that is introduced into a group of gossiping conditional cooperators. Let  $q$  be the proportion of the group willing to interact with  $A$  (i.e. the proportion that has not received information or observed that  $A$  is unreliable). We need several simplifying assumptions about our life-history model (Appendix I). The proportion  $q$  varies gradually and deterministically with time and is used as the state variable in dynamic programming. With  $S$  the search time for a conditional cooperator, let  $s(q) = S/q$  be the search time for  $A$ , expressing that it takes proportionally longer for  $A$  to find a partner when only part of the group is willing to interact. The payoffs per unit time if  $A$  cooperates ( $U_c$ ) and defects ( $U_d$ ) are put to

$$U_c(q) = (b - c) \frac{T}{s(q) + T} \text{ and } U_d(q) = b \frac{1}{s(q) + 1}$$

(compare equations 1 and 2). Let  $z(q)$  ( $0 \leq z \leq 1$ ) be the strategy (control variable) for  $A$ , where  $z = 0$  means cooperate,  $z = 1$  defect, and intermediate values represent a mixture. The rate of payoff at state  $q$  and strategy  $z$  is

$$u(q,z) = (1 - z)U_c(q) + zU_d(q)$$

The dynamics of the state variable is taken to be

$$\dot{q}(q,z) = \alpha(q) - z\beta(q)$$

The function  $\beta$  represents partners of  $A$  that observe defection

$$\beta(q) = \frac{\gamma}{s(q) + 1} \frac{1}{N - 1}$$

where  $\gamma$  is the rate of detection of a free rider in a free rider–conditional cooperator coalition (we have assumed in Appendix I that  $\gamma + 2\nu = 1$ ) and  $N$  is the group size. The function  $\alpha$  is given by

$$\alpha(q) = \nu(1 - q) - k(1 - q)q$$

where the first term represents replacement of informed group members and the second the spread of gossip. The parameter  $k$  regulates the intensity of gossip. It seems natural to relate  $k$  to a rate,  $1/(Sp)$ , of encountering other group members, where  $p = S/(S + T)$  is the proportion of the group not in a coalition. We have used  $k = K/(Sp) = K(S + T)/S^2$ . If  $K = 1$ , gossip is transmitted at every meeting between group members.

Since  $A$  is replaced at the rate  $\nu$ , the optimal strategy  $z(q)$  and the corresponding utility  $U(q)$  is given by

$$U(q(t)) = \max_{z(\cdot)} \int_t^\infty e^{-\nu\tau} u(q(\tau), z(q(\tau))) d\tau$$

At  $t = 0$ , when  $A$  is introduced, we have  $q = 1$ . We wish to determine whether the optimal  $z(1)$  corresponds to cooperation or defection. With the dynamics for  $q$ , one gets the dynamic programming equation

$$\nu U(q) = \max_z \{u(q, z) + \dot{q}(q, z)U'(q)\}$$

To make Fig. 4, we solved this equation numerically with parameter values  $b = 2$ ,  $c = 1$ ,  $N = 100$ , and  $K = 0$ , 0.25 and 1, respectively.

## APPENDIX V

Let  $a$  be the risk of being defected against. When two individuals with differing degrees of suspiciousness (say  $x$  and  $x_0$ ) meet, we assume that they start cooperating after a time that is between  $x$  and  $x_0$  and rather close to the smaller of the two. Denote this time by  $H(x, x_0)$ . The utility of suspiciousness  $x$  in a population using suspiciousness  $x_0$  is then given by

$$U(x, x_0) = (1 - a)\Pr[\tau \geq H(x, x_0)]T(b - c) - a\Pr[\tau_d \geq H(x, \infty)]c$$

where  $\tau$  is the exponentially distributed coalition time with expectation  $T$  and  $\tau_d$  the coalition time (with expectation 1) for the case when the partner defects (note that a defecting partner has ‘infinite’ suspiciousness).

An example of a function  $H$  that fulfils our requirements is given by

$$H(x, x_0) = \frac{\sqrt[k]{2xx_0}}{\sqrt[k]{x^k + x_0^k}}$$

We used this function with  $k = 10$  to make Fig. 5.

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