

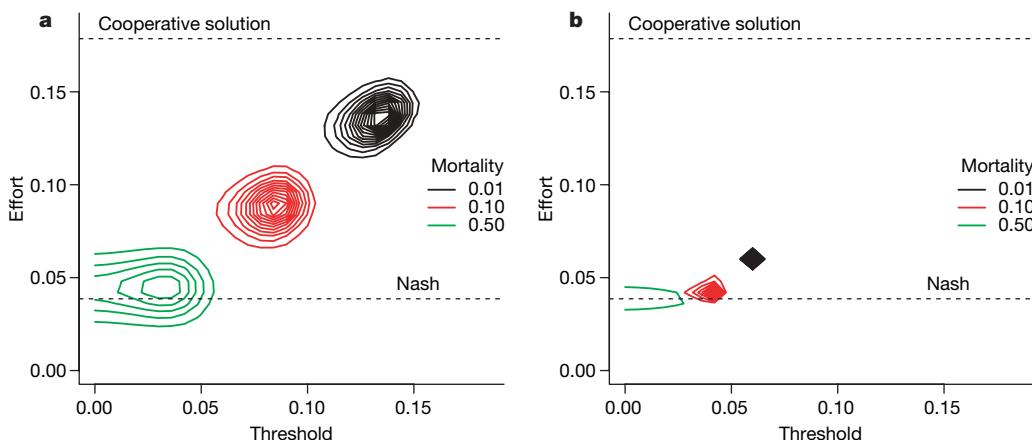
# The coevolution of choosiness and cooperation

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Explaining the rise and maintenance of cooperation is central to our understanding of biological systems<sup>1,2</sup> and human societies<sup>3,4</sup>. When an individual's cooperativeness is used by other individuals as a choice criterion, there can be competition to be more generous than others, a situation called competitive altruism<sup>5</sup>. The evolution of cooperation between non-relatives can then be driven by a positive feedback between increasing levels of cooperativeness and choosiness<sup>6</sup>. Here we use evolutionary simulations to show that, in a situation where individuals have the opportunity to engage in repeated pairwise interactions, the equilibrium degree of cooperativeness depends critically on the amount of behavioural variation that is being maintained in the population by processes such as mutation. Because our model does not invoke complex mechanisms such as negotiation behaviour, it can be applied to a wide range of species. The results suggest an important role of lifespan in the evolution of cooperation.

We consider an infinite population where, in each of a discrete series of time steps (rounds), pairs of individuals engage in a game that can be described as a social dilemma<sup>7</sup>. Each individual is characterized by two traits: a cooperativeness trait  $x$ , which specifies the amount of effort that the individual devotes to generating benefits available (at least in part) to its co-player; and a choosiness trait  $y$ , which specifies the minimum degree of cooperativeness that the focal individual is prepared to accept from its co-player. The traits  $x$  and  $y$  are genetically determined and are not adjusted in response to the co-player's behaviour. Thus, unlike in many models in which flexible effort adjustment is a key ingredient<sup>1,6,8</sup>, individuals in our model are consistent in their degree of cooperativeness. In each round, each individual receives a payoff  $W(x, x')$  that reflects its own effort,  $x$ , and

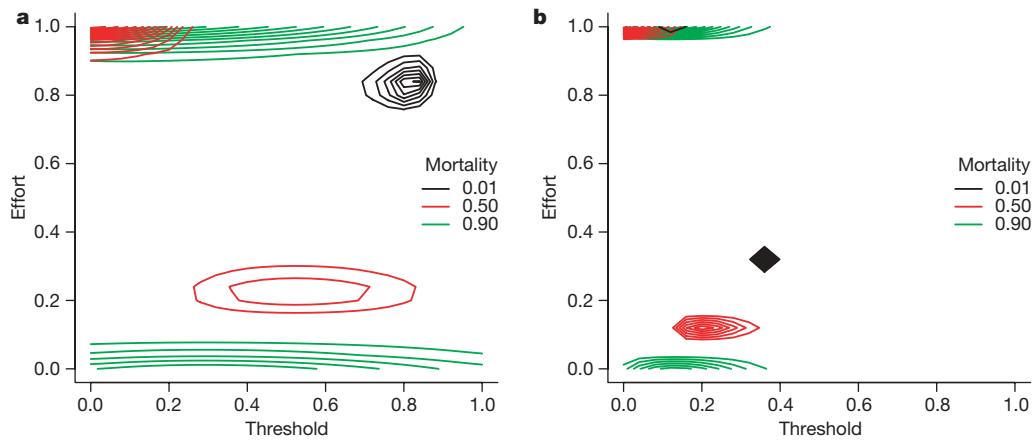
that of its co-player,  $x'$ . The payoff function (see below) is such that there is a conflict of interest between pair members, with each preferring the other to provide most of the total effort. Upon receiving their payoffs, pair members find out about each other's effort, and then incur some risk of mortality before entering the next round. If pair members are mutually acceptable (that is,  $x \geq y'$  and  $x' \geq y$ , where  $y'$  denotes the opposite player's choosiness), and if both survive, then they continue to interact with each other in the next round. Otherwise the pair break up and any survivors enter the pool of unpaired individuals, from which new pairs are randomly formed at the beginning of the next round. The breaking of pairs reflects the ability of mobile organisms to terminate unfavourable interactions by leaving<sup>9,10</sup>. We assume that finding a new co-player is costly, so that, in the first round of interacting with a new co-player, payoffs are reduced by a fixed amount  $S$ . On the other hand, because social interaction may not be the only way of generating payoffs, we assume that each individual also receives a fixed payoff component  $A$  in each round. Hence the total payoff is  $W(x, x') + A - S$  for an individual in a newly formed pair and  $W(x, x') + A$  for an individual in an established pair. We model reproduction as follows. Upon receiving a payoff in a given round, each individual produces offspring in numbers proportional to its payoff. Offspring are produced asexually, and so share the parental type in terms of  $x$  and  $y$ , subject to occasional small changes caused by mutation. (We have confirmed by additional computations that the results are similar if offspring are produced sexually; Supplementary Information.) Individuals that die are replaced by individuals selected at random from all offspring produced in the previous round; these replacements join the pool of unpaired individuals. (Computational details are given as Supplementary Information.)



**Figure 1 | Equilibrium frequency distribution of trait combinations in the continuous snowdrift game with accelerating costs.** Contour lines connect trait combinations that occur with equal frequency. Results for three levels of mortality  $M$  are shown for simulations using (a) high mutation rate ( $\mu = 0.05$ ) and (b) low mutation rate ( $\mu = 0.001$ ). Dashed lines indicate the

Nash solution (0.0386) and the cooperative solution (0.179). Payoff function:  $W(x, x') = B(x + x') - C(x)$ , with  $B(x + x') = \frac{x+x'}{1+x+x'}$  and  $C(x) = 0.8(x + x^2)$ . Other parameters (see Supplementary Information): maximum effort value,  $x_{\max} = 0.18$ ;  $A = 0.01$ ;  $S = 0.01$ .

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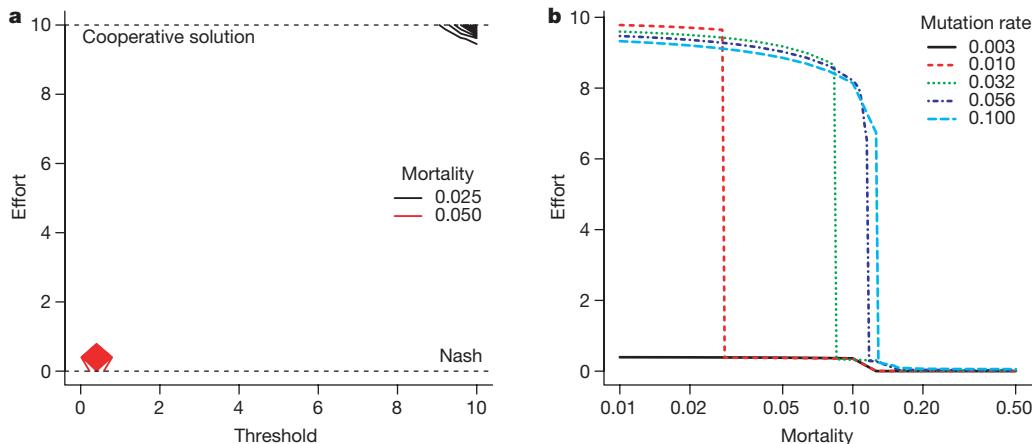
**Figure 2 | Continuous snowdrift game with decelerating costs.** Results for three levels of mortality  $M$  are shown for simulations using (a) high mutation rate ( $\mu = 0.005$ ) and (b) low mutation rate ( $\mu = 0.0001$ ). Payoff function:  $W(x, x') = B(x + x') - C(x)$ , with

We use two benchmark solutions to judge the observed degree of cooperation: the (non-cooperative) ‘Nash solution’, which corresponds to the expected behaviour if individuals are maximizing their payoff in one-off interactions<sup>11,12</sup>; and the ‘cooperative solution’, which corresponds to the expected behaviour if payoffs to pairs rather than to individuals are being maximized<sup>12,13</sup>.

For the sake of generality, we consider two types of payoff function that conform to alternative paradigms for the study of cooperation: the continuous prisoner’s dilemma game<sup>8</sup>, and the continuous snowdrift game<sup>14</sup>. In the continuous prisoner’s dilemma, individuals incur a cost  $C(x)$  that depends on their own effort, while gaining a benefit  $B(x')$  that depends on their co-player’s effort. In the continuous snowdrift game, individuals also incur a cost  $C(x)$  that depends on their own effort, but gain a benefit  $B(x + x')$  that depends on the summed effort of both co-players. The resulting payoff functions are of the forms  $W(x, x') = B(x') - C(x)$  and  $W(x, x') = B(x + x') - C(x)$ , respectively. The important difference here is that in the continuous prisoner’s dilemma, the Nash solution is always to invest zero effort<sup>8</sup>, whereas this is not the case in the continuous snowdrift game. Here we consider a version of the continuous prisoner’s dilemma with linear cost and benefit functions, which, because of its simplicity, allows us to obtain some analytical results. We first consider a version of the continuous snowdrift game with saturating benefit and accelerating cost functions, because similar cases may be common in nature (for

example, in the context of parental care for offspring<sup>11,15</sup>, or of vigilance in the face of predation risk<sup>16</sup>); here the Nash effort is greater than zero but lower than the cooperative solution (Fig. 1). For details on the payoff functions used, see figure legends and Supplementary Fig. 1.

The traditional approach to analysing evolutionary games is to identify evolutionarily stable strategies, which, if used by almost all individuals in a population, cannot be invaded by any mutant strategy<sup>17</sup>. In our model, an obvious candidate evolutionarily stable strategy in this sense is a strategy that involves neither cooperation (beyond the Nash effort) nor choosiness. (We show that this is in fact the only evolutionarily stable strategy in the continuous prisoner’s dilemma case; Supplementary Information.) This strategy is stable because, in a population where virtually all individuals are the same, nothing can be gained by being choosy. Without the risk of being dismissed by a co-player, however, there is no incentive for individuals to invest more than the Nash effort. This situation changes profoundly if significant variation is maintained in the population by processes such as mutation. Now the dismissal of uncooperative individuals can be advantageous, because more cooperative co-players are available to be found. This implies that cooperative individuals, by not being dismissed, enjoy an advantage. As the average level of cooperativeness in the population increases, so does the optimal threshold value below which relatively uncooperative individuals are dismissed. This in turn favours even higher levels of cooperativeness.



**Figure 3 | Continuous prisoner’s dilemma.** a, Equilibrium frequency distribution of trait combinations for two levels of mortality  $M$ . Contour lines connect trait combinations that occur with equal frequency. The Nash solution is  $x = 0$  and the cooperative solution is  $x_{\max}$ . Mutation rate:

$\mu = 0.01$ . b, Population mean effort at equilibrium, plotted against mortality for five different mutation rates  $\mu$ . Payoff function:  $W(x, x') = B(x') - C(x)$ , with  $B(x') = 5x'$  and  $C(x) = x$ . Other parameters: maximum effort value,  $x_{\max} = 10$ ;  $A = 1$ ;  $S = 0.001$ .

Depending on the type of payoff function used, this positive feedback can drive cooperativeness up to intermediate levels (Figs 1 and 2), or even up to the cooperative solution (Fig. 3).

A high mutation rate can increase the equilibrium degree of co-operation in our model (Figs 1 and 2) and/or broaden the conditions under which cooperation arises (Fig. 3). This is because it enhances the amount of behavioural variation, which is the substrate on which choosiness, and hence cooperation, thrives in our model (Box 1). Whenever the average cooperativeness exceeds the Nash solution, a positive correlation between an individual's choosiness and cooperativeness arises (noticeable in Fig. 1a). This is because 'paradoxical' trait combinations yield particularly low payoffs: individuals with low choosiness but high effort tend to get exploited by their co-players; individuals with high choosiness but low effort waste their time searching for better co-players, which are, however, unlikely to accept them. The positive correlation between choosiness and cooperativeness leads to a positive assortment between cooperative types – an essential feature of all mechanisms that promote cooperation<sup>18,19</sup>. High mortality counteracts the evolution of cooperation by reducing the equilibrium degree of cooperation (Fig. 1), and/or by restricting the conditions under which cooperation can arise (Fig. 3b). This can be explained as follows. The benefits of being both choosy and cooperative arise when mutually acceptable co-players find each other. This usually requires a period of searching, during which costs arise both in terms of *S* and in terms of being exploited by less cooperative individuals. If the cooperative associations thus formed are soon disrupted by mortality, then establishing them is not worth the associated costs (Box 1). Cooperation is, however, slower to evolve from non-cooperative starting conditions when lifespan is long (Supplementary Fig. 2).

As well as considering the continuous snowdrift game with accelerating costs, we also consider a version with decelerating costs. This version is applicable in situations where the initiation of cooperative acts is more costly than subsequent increases in cooperative investments. For example, if bacteria secrete enzymes into the environment that can be used to digest nutrients and are therefore a public good, costs for turning on the relevant genetic machinery may be high compared with subsequent increases in enzyme production<sup>14</sup>. This form of cost has been shown to produce disruptive evolution of cooperative and non-cooperative individuals in one-shot games<sup>14</sup>; thus there is no pure stable state here that meets our definition of a Nash solution. At high mortality, repeated interactions are unlikely, so that the situation is like a one-shot game, yielding a bimodal distribution of cooperative and uncooperative types (Fig. 2). Under low mortality, however, uncooperative types are put at a disadvantage because they are likely to be dismissed in every round; given sufficient mutation (Fig. 2a, but see Fig. 2b), this can lead to a unimodal distribution of cooperative types.

The rise of cooperation in our model hinges on the existence of consistent individual differences in cooperativeness. In our model, genetic variation is responsible for differences. However, reproductive success in our model depends only on the phenotypic composition of the population. Thus, as long as some of the available variation is heritable, the direction of selection (that is, the sign of the covariance between reproductive success and a given trait) would be the same if differences were largely non-heritable ( $cf^{20}$ ).

The importance of low mortality for the evolution of choosiness has been noted before<sup>21,22</sup>, though in a context of mate choice rather than cooperation. In our model, this combines with the additional effect that low mortality, by allowing for long series of interactions, offers a long-term perspective that can trump the short-term incentive for defection. The latter effect is analogous to findings that in the iterated prisoner's dilemma, cooperative strategies are only successful if there is a low probability that any given iteration is the last<sup>1</sup>.

Like models of direct reciprocity based on behaviourally flexible cooperativeness<sup>1,8</sup>, our model generates a situation in which current cooperation is rewarded by the prospect of future cooperation. This

is mediated by the possibility of ostracizing uncooperative individuals ( $cf^{6,23,24}$ ), which we have modelled as being based on an evolving trait rather than on a fixed parameter or strategy. Note that for this form of ostracism to work, individuals do not need to be able to remember and compare the behaviour of multiple population members (unlike<sup>6,24</sup>).

Consistent with previous results<sup>6,23,24</sup>, our model predicts that the evolution and maintenance of cooperation can critically depend on the ability to stop interacting with relatively uncooperative individuals. This is in line with findings of divorce behaviour that depends on partner quality in birds<sup>25,26</sup> and fish<sup>27</sup> with bi-parental care, where an individual's contribution to the cooperative task of breeding can be an important aspect of partner quality<sup>26</sup>. Even humans, despite being far more sophisticated than the players in our model, show increased (and relatively constant) levels of cooperativeness in an experimental setting where they can establish optional long-term relations<sup>28</sup>, thus strengthening the case that our model encapsulates

### Box 1 | Optimal choosiness

In a single round of the game, an individual that expends effort  $x$  receives payoff  $W(x, x')$  when its partner's effort is  $x'$ . Here we consider the special case of the continuous prisoner's dilemma for which

$$W(x, x') = bx' - C(x) \quad (1)$$

where  $C(x)$  is a strictly increasing function of  $x$ , and  $b$  is a positive constant. For this payoff the Nash effort in a single round is the minimum effort  $x^* = 0$ .

Consider a population in which the efforts of members of the pool of single individuals are distributed with probability density function  $f(x)$  and mean  $\bar{x}$ . Then (see Supplementary Information) an individual that is never dismissed by others should dismiss its partner if and only if its partner's effort is below  $y^*$ , where

$$y^* = \bar{x} - (S/b) + \beta \int_{y^*}^{\infty} (x' - y^*) f(x') dx' \quad (2)$$

where  $\beta = (1 - M)^2 / [M(2 - M)]$  is a decreasing function of the mortality  $M$ , and  $S$  is the search cost. Individuals that are dismissed by some co-players have a lower optimal threshold (Supplementary Information). From equation (2) it is easy to show that  $y^*$  increases as  $S$  and  $M$  decrease (Supplementary Information).

It can be shown (Supplementary Information) that if all population members behave optimally then all expend the minimum effort  $x^* = 0$ . Thus complete non-cooperation is evolutionarily stable unless effects such as mutation maintain a significant amount of non-adaptive variation in the population. Equation (2) provides an intuitive explanation of this result. If we assume a monomorphic population with all individuals expending effort  $\bar{x}$ , then equation (2) reduces to  $y^* = \bar{x} - S/(b(1 + \beta)) < \bar{x}$ . If all individuals adopt this optimal threshold and  $\bar{x} > 0$ , it pays to reduce effort below  $\bar{x}$  because this can be done without incurring the risk of being dismissed.

So how much variation is necessary for cooperation to evolve? We expect mean effort to evolve so that it is greater than most acceptance thresholds (so ensuring the cost of dismissal is not paid). Thus cooperation should evolve when  $y^*$  exceeds the mean effort in the population. Approximating this mean by  $\bar{x}$ , equation (2) predicts cooperation to evolve when the variation, as measured by

$$\Delta = \sqrt{\int_{-\infty}^{\infty} |x' - \bar{x}|^2 f(x') dx'} \quad (\text{the mean absolute deviation of effort from the population mean}), \text{ is sufficiently high:}$$

$$\Delta > \frac{2S}{\beta b} \quad (3)$$

Equivalently, the mortality rate must be sufficiently low:

$$M < 1 - \sqrt{\frac{2S}{2S + b\Delta}} \quad (4)$$

Because  $\bar{x}$  (the mean among single individuals) is typically less than the overall population mean, these are minimal criteria.

a general principle. Because of both the widespread ability of animals to exert some form of choice among their conspecifics<sup>29</sup>, and accumulating evidence for the ubiquity of consistent behavioural differences between individuals<sup>30</sup>, we believe that the interacting effects of choice and variation (differing in biological detail across species, but following similar logic) may be among the most important reasons for the evolution of cooperation in nature.

Received 15 October; accepted 6 November 2007.

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**Supplementary Information** is linked to the online version of the paper at [www.nature.com/nature](http://www.nature.com/nature).

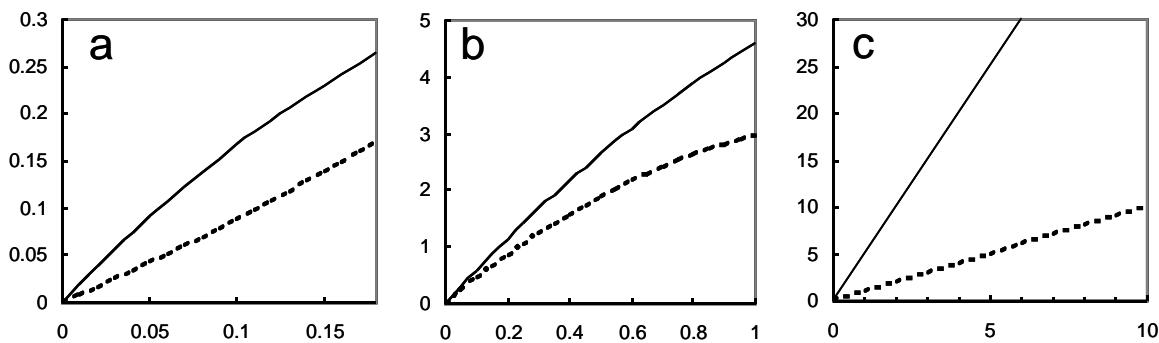
**Acknowledgements** We thank O. Leimar and four anonymous referees for comments on a previous version of this paper. Z.B. was supported by a grant from the Biotechnology and Biological Sciences Research Council to A.I.H. and J.M.M. L.F. was supported by the Deutsche Forschungsgemeinschaft.

**Author Contributions** Based on an idea by J.M.M., the concept for this paper was developed in discussions among all authors. J.M.M. also formulated the material in Box 1 and most of the Supplementary Information; Z.B. performed the computations and prepared the figures; A.I.H. surveyed the literature; L.F. had the main responsibility for writing the paper.

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## SUPPLEMENTARY INFORMATION

## 1. Supplementary Figure 1



Supplementary Figure 1: Benefit  $B(\cdot)$  (solid line) and cost  $C(\cdot)$  (dashed line) functions

as used in our model. a: Continuous snowdrift game with accelerating costs.

$$B(x + x') = \frac{x + x'}{1 + x + x'} \quad (\text{here shown for the special case where } x' = x) \text{ and}$$

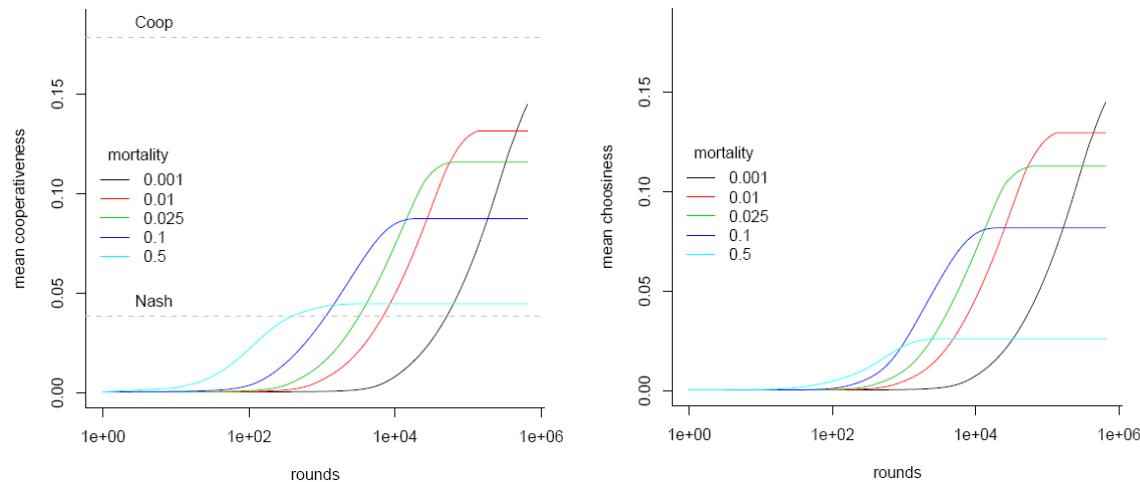
$C(x) = 0.8(x + x^2)$ . b: Continuous snowdrift game with decelerating costs (as used in

Figure 1A of Doebeli et al. 2004).  $B(x + x') = -1.4(x + x')^2 + 6(x + x')$  (shown for  $x' = x$ )

and  $C(x) = -1.6x^2 + 4.56x$ . c: Continuous prisoner's dilemma.  $B(x') = 5x'$

and  $C(x) = x$ .

## 2. Supplementary Figure 2



Supplementary Figure 2: Effect of mortality on the equilibrium degree of cooperativeness

(a) and choosiness (b), and on the time needed to reach these equilibria in our simulations. Payoff function as in Supplementary Figure 1a, with parameters:  $x_{\max}=0.18$ ;  $A=0.01$ ;  $S=0.01$ .

### 3. Model description

The population cycle can be divided into five non-overlapping stages.

**Stage 1:** Any individuals that are single pair up, so that all individuals are paired at the start of Stage 2.

**Stage 2:** Each population member plays one round of the game with the current co-player, receiving a reward.

**Stage 3:** Each population member produces offspring asexually, with reproductive success proportional to the reward in Stage 2. Offspring inherit parental type with mutation.

**Stage 4:** Each individual decides whether to dismiss the current co-player.

**Stage 5:** Mortality acts. Adult mortality is density independent. Juvenile mortality is density dependent and acts to restore the original population size.

After stage 5, stage 1 occurs again, and so on. In our computations we start with a population in which individuals have minimum effort levels and minimum levels of choosiness. The above cycle is then repeated until the composition of the population settles down; that is until it is the same on successive cycles. The details of how these five stages are implemented are as follows.

Although we envisage effort and choosiness as continuous traits, for computational reasons we map pairs of traits onto a  $(G + 1) \times (G + 1)$  grid. Specifically the effort levels of individuals fall into one of the  $G + 1$  discrete classes  $i = 0, 1, \dots, G$ , where an individual in effort class  $i$  has effort level  $(i/G)x_{\max}$ , where  $x_{\max}$  is the maximum level of effort allowed. Similarly the choosiness levels of individuals fall into the one of the  $G + 1$  discrete classes  $j = 0, 1, \dots, G$ , where an individual in choosiness class  $j$  has choosiness level  $(j/G)x_{\max}$ . We refer to an individual as  $(i, j)$  if its effort class is  $i$  and its choosiness class is  $j$ . The computation in Figure 1 is based on  $G = 30$ , that for Figure 2 on  $G = 25$ .

We are concerned with a large (essentially infinite) population that has the same size,  $N$ , at the start of each cycle. This population is sufficiently large so that stochastic effects due to small population size can be ignored. In that sense we use the variable  $N$  for didactical reasons only; results are independent of the value of  $N$  used. Consider the population structure at the beginning of Stage 1 on some cycle. At this time some individuals may have remained paired from the last population cycle and some are single. The number of  $(i, j)$  population members that are already paired to a  $(k, l)$  individual is  $NP(i, j; k, l)$  and the number of single  $(i, j)$  individuals is  $Nu(i, j)$ , where  $P$  and  $u$  are the proportions of individuals in the population that are in these respective categories. The proportion of  $(i, j)$  individuals in the population is thus

$$\rho(i, j) = \sum_{k=0}^G \sum_{l=0}^G P(i, j; k, l) + u(i, j). \quad (\text{A1})$$

Below we specify how this population structure determines the population structure at the beginning of Stage 1 in the next cycle.

### Pairing of single individuals

In Stage 1, single individuals pair up at random. Specifically, let  $N_s = N \sum_{i=0}^G \sum_{j=0}^G u(i, j)$  be the total number of single individuals at the start of Stage 1. Then the number of  $(i, j)$  individuals in a newly formed pair with a  $(k, l)$  individual at the end of Stage 1 is  $NQ(i, j; k, l)$  where  $Q(i, j; k, l) = u(i, j)u(k, l)N / N_s$ . Thus

$$Q(i, j; k, l) = u(i, j)u(k, l) / \left( \sum_{m=0}^G \sum_{n=0}^G u(m, n) \right). \quad (\text{A2})$$

### Payoffs in the round of the game

During the focal round of the game there are  $NP(i, j; k, l)$   $(i, j)$  individuals with a  $(k, l)$  co-player retained from the last round and  $NQ(i, j; k, l)$   $(i, j)$  individuals with a new  $(k, l)$  co-player. Thus the total payoff to all  $(i, j)$  individuals is  $Nr(i, j)$  where

$$r(i, j) = \sum_{k=0}^G \sum_{l=0}^G P(i, j; k, l)[W(i, k) + A] + \sum_{k=0}^G \sum_{l=0}^G Q(i, j; k, l)[W(i, k) + A - S]. \quad (\text{A3})$$

As stated in the main text,  $S$  in this equation is the cost associated with searching for a new co-player, and  $A$  is a fixed payoff component that is independent of the game.

### Reproduction

We assume that the mean number of offspring produced by an individual is proportional to the payoff the individual received in the round of the game. Thus the total number of offspring produced by all  $(i, j)$  individuals is  $RNr(i, j)$ , where  $R$  is the constant of proportionality.

Because of mutation not all offspring are the same type as their parent. Specifically we assume that if the parent is in effort class  $i$  then each offspring is in effort class  $k$  with probability  $m(k | i)$ . Similarly, if the parent is in choosiness class  $j$  then each offspring is in choosiness class  $l$  with probability  $m(l | j)$ . Mutation is assumed to act independently at the effort and choosiness loci. Thus an offspring of an  $(i, j)$  individual is  $(k, l)$  with probability  $m(k | i)m(l | j)$ . The total number of  $(k, l)$  offspring produced by all population members is therefore equal to  $RNv(k, l)$  where

$$v(k,l) = \sum_{i=0}^G \sum_{j=0}^G r(i,j)m(k|i)m(l|j) \quad (\text{A4})$$

The total number of surviving offspring equals  $RNV$ , where

$$V = \sum_{k=0}^G \sum_{l=0}^G v(k,l). \quad (\text{A5})$$

Computations are based on mutation to an adjacent class with probability  $\mu$ . Specifically, for  $1 \leq i \leq G-1$

$$m(i-1|i) = m(i+1|i) = \mu/2$$

and

$$m(i|i) = 1 - \mu.$$

To deal with edge effects, we set

$$m(1|0) = m(G-1|G) = \mu/2$$

and

$$m(0|0) = m(G|G) = 1 - \mu/2.$$

### Co-player dismissal

Individuals  $(i, j)$  and  $(k, l)$  are mutually acceptable, and hence do not dismiss each other, if and only if  $i \geq l$  and  $k \geq j$ . Note that, if individuals of a pair were mutually acceptable in the previous cycle, then they are still acceptable in the current cycle.

### Mortality

Each adult (an individual that has previously bred) dies before Stage 1 of the next cycle with probability  $M$ . Thus the number of  $(i, j)$  individuals that remain paired to a  $(k, l)$  co-player at the start of Stage 1 of the next cycle is  $NP'(i, j; k, l)$  where

$$P'(i, j; k, l) = (1-M)^2[P(i, j; k, l) + Q(i, j; k, l)I(i, j; k, l)], \quad (\text{A6})$$

where  $I(i, j; k, l) = 1$  if both  $i \geq l$  and  $k \geq j$ , and  $I(i, j; k, l) = 0$  otherwise. The number of single  $(i, j)$  adults at the start of Stage 1 of the next cycle is the number of surviving

$(i, j)$  individuals from the initial Stage 1 minus the number surviving that are in pairs. Thus this number is  $Na(i, j)$  where

$$a(i, j) = (1 - M)\rho(i, j) - \sum_{k=0}^G \sum_{l=0}^G P'(i, j; k, l). \quad (\text{A7})$$

Juvenile survival is density dependent; we assume that the number of offspring that survive to the start of the new Stage 1 is exactly  $NM$ , ensuring the new population has total size  $N$  at this time. Thus the total number of single  $(i, j)$  individuals at the start of the new Stage 1 is  $Nu'(i, j)$  where

$$u'(i, j) = a(i, j) + Mv(i, j)/V. \quad (\text{A8})$$

Equations (A1) - (A8) determine the quantities  $u'(..)$  and  $P'(..;..)$  in terms of  $u(.)$  and  $P(.,.;.)$ . Note that in this calculation the constants  $N$  and  $R$  play no part – they are included in the model description to clarify the procedure.

### Sexual reproduction

Although Figs. 1-3 are based on the assumption of asexual reproduction, similar results can be obtained if offspring are produced sexually by diploid organisms (not shown). We have modelled this by an individual-based simulation in a finite-size population, in which individuals have two chromosomes, carrying twenty alleles each. On each chromosome alleles are arranged in two groups of ten alleles, which code the individual's cooperativeness and choosiness, respectively. Alleles can take the values of 0, 1 and 2. By summing up these values across all alleles (on both chromosomes) that code a given trait, we obtain an individual's 'total allele score' for that trait. The total allele score can take integer values between 0 and 40, thus providing a 41-step grid on which trait values are then mapped as in the asexual model described above. Individuals behave as outlined above (stage 1-5), except that in stage 3, sexual reproduction occurs. Individual are modelled as hermaphrodites which mate exactly once in the female role and on average once in the male role. In the female role, an individual chooses a randomly selected mate. On mating it produces two offspring (recombination, mutation occur here), which enter the pool of young individuals from which the dead individuals are replaced. The probability that an offspring is recruited, replacing an individual that has died, is proportional to the mother's payoff from the game. The mean total number of recruits left by an individual is thus proportional to the individual's game payoff (from the female role) plus a constant (from the male role).

## 4. Supplementary analysis of optimal acceptance thresholds

### Notation

$W(x, x')$  = payoff in a single round to an individual with effort value  $x$  when co-player has effort value  $x'$ .

$S > 0$ , the cost of searching for a new co-player, measured as a loss in payoff in the next round.

$M$  = between round mortality

$f(x)$  = probability density function giving the distribution of efforts amongst single individuals in the pool.

### **Optimal acceptance threshold (in terms of payoff)**

We first focus on the optimal choosiness strategy of an individual that has effort value  $x$  and is never dismissed.

To simplify notation we set  $r(x') = W(x, x')$ . Our aim is to find the value  $R^*$  such that it is optimal for the individual to dismiss a co-player with effort value  $x'$  if and only if  $r(x') < R^*$ .

Consider the focal individual just after receiving its payoff in a given round. Suppose that at this time the current co-player has effort value  $x'$ .

Let  $D$  = expected future total payoff if the focal individual dismisses its co-player now and behaves optimally in the future.

Let  $V(x')$  = expected future total payoff given the focal individual never dismisses the current co-player, but behaves optimally if the current co-player dies.

Then it is optimal to dismiss a co-player if and only if  $V(x') < D$ . The dynamic programming equations for  $D$  and  $V$  are

$$D = (1 - M) \int_{-\infty}^{\infty} \{r(x') - S + \max[V(x'), D]\} f(x') dx' \quad (\text{A9})$$

and

$$V(x') = (1 - M)^2 [r(x') + V(x')] + MD. \quad (\text{A10})$$

To solve these equations we subtract  $D$  from both sides of equation (A9). After some rearrangement this gives

$$\frac{M}{1 - M} D = \bar{r} - S + \int_{-\infty}^{\infty} \max[V(x') - D, 0] f(x') dx', \quad (\text{A11})$$

where

$$\bar{r} = \int_{-\infty}^{\infty} r(x') f(x') dx'$$

is the mean payoff with a randomly selected pool member. We can also rewrite equation (A10) as

$$V(x') - D = \beta(r(x') - R^*), \quad (\text{A12})$$

where

$$\beta = \frac{(1 - M)^2}{1 - (1 - M)^2}$$

and

$$R^* = \frac{M}{1 - M} D. \quad (\text{A13})$$

Note that  $V(x') < D$  if and only if  $r(x') < R^*$ . Thus  $R^*$  is the minimum reward that an individual of effort  $x$  requires in a round to make it optimal to retain the current co-player. From equations (A11) – (A13) the threshold  $R^*$  satisfies

$$R^* = \bar{r} - S + \beta \int_{r(x')=R^*}^{\infty} (r(x') - R^*) f(x') dx', \quad (\text{A14})$$

where the integral in equation (A14) is over the values of  $x'$  for which  $r(x') \geq R^*$ .

This gives the optimal threshold for an individual that is never dismissed. If an individual with effort value  $x$  is dismissed by some population members, then this individual has a lower  $D$  than that given above (since the individual has less choice in terms of potential long-term co-players). By equation (A13),  $R^*$  is then also less for this individual.

## Dependence on parameters

To investigate the dependence of  $R^*$  on the parameters  $S$  and  $M$  we define the function  $H$  by

$$H(R) = R - \bar{r} + S - \beta \int_{r(x')=R}^{\infty} (r(x') - R) f(x') dx'.$$

Then

$$H'(R) = 1 + \beta \int_{r(x')=R}^{\infty} f(x') dx'.$$

Thus  $H$  is strictly increasing and the equation  $H(R) = 0$  has a unique solution at  $R = R^*$ . Since  $H(R)$  increases with increasing  $S$  for fixed  $R$  we see that increasing  $S$  decreases  $R^*$ . Similarly increasing  $\beta$  increases  $R^*$ . Thus since  $\beta$  increases as  $M$  decreases,  $R^*$  increases as  $M$  decreases.

### Additive payoffs

We now consider the special case in which  $W$  can be expressed as

$$W(x, x') = bx' - C(x), \quad (\text{A15})$$

where  $C$  is any function of  $x$  and  $b$  is a positive constant. In this special case the dismissal criterion,  $r(x') < R^*$ , is equivalent to  $x' < y^*$  where  $y^*$  satisfies

$$y^* = \bar{x} - (S/b) + \beta \int_{y^*}^{\infty} (x' - y^*) f(x') dx' \quad (\text{A16}),$$

and where  $\bar{x}$  is the mean value of effort among individuals that are single at the beginning of a round.

Thus all individuals that are never dismissed have the same optimal acceptance threshold. Since individuals that are dismissed by some co-players have a lower optimal threshold, all population members have an optimal threshold that is no greater than  $y^*$ .

### Evolutionary stability

We assume the additive payoff of the form (A15) where  $C(x)$  is a strictly increasing function of  $x$ . Our version of the continuous prisoner's dilemma is of this form. Effort values are constrained to lie in the range  $[0, \infty)$ . The Nash effort in a single round is  $x^* = 0$ . We consider a population in which each population member is behaving optimally given the behaviour of the others. We show that at this ESS the effort in the repeated

game is  $x = 0$  for all population members. Thus at evolutionary stability with no mutation, all individuals are playing the Nash effort on each round.

Note that equation (A16) holds in this case, but  $y^*$  may be negative. This just means that no co-player is dismissed. To analyse the ESS we first note that since all population members are behaving optimally they all have divorce thresholds no greater than  $y^*$  given by equation (A16). Thus if an individual has effort value  $x$ , where  $x \geq y^*$ , then this individual is never divorced. Now compare two individuals with efforts  $x_1$  and  $x_2$ , where  $y^* \leq x_1 < x_2$ . Then neither of these individuals will ever be dismissed by their co-player. They must also have the same divorce threshold  $y^*$ . Thus on average both receive the same contribution towards their payoffs from their co-players (the  $bx'$  term in equation (A15)) and pay the same search costs. Thus the individual with effort  $x_1$  has a payoff that exceeds that of the individual with effort  $x_2$  by  $C(x_2) - C(x_1)$  per round. Since the function  $C$  is strictly increasing the former individual has a higher total lifetime payoff than the latter. It follows that any individual with effort greater than  $\max(0, y^*)$  cannot be optimal. Thus the effort of all population members must lie in the range  $[0, \max(0, y^*)]$ .

Now suppose that  $y^* > 0$ . By the above  $f(y) = 0$  for  $y > y^*$ . Thus the integral on the right hand side of equation (A16) is 0. Furthermore we must also have  $\bar{x} \leq y^*$ . Thus equation (A16) implies that  $y^* \leq y^* - (S/k)$ : a contradiction. It follows that  $y^* = 0$ , and hence  $x = 0$  for all population members.

### Evolution of increased effort

Because we expect mean effort to evolve so that it is greater than most acceptance thresholds (so ensuring the cost of being dismissed is not paid), we are interested in the conditions under which  $y^*$  exceeds the mean effort in the population. We approximate this mean effort by  $\bar{x}$ , the mean effort among individual that are single at the beginning of a round.

Define the function  $h$  by

$$h(v) = v - \bar{x} + (S/b) - \beta \int_v^\infty (x' - v) f(x') dx'.$$

Then, as for the case of  $H$  above,  $h$  is a strictly increasing function. By equation (A16)  $x' = y^*$  is the unique solution of the equation  $h(y) = 0$ . Thus  $y^* > \bar{x}$  if and only if  $h(\bar{x}) < 0$ ; i.e.

$$S/b < \beta \int_{\bar{x}}^\infty (x' - \bar{x}) f(x') dx'.$$

This can be re-expressed to obtain (B3) and (B4) in the box of the main text.