

Cooperation maintained by fitness adjustment

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ABSTRACT

Questions: Can cooperation be enhanced if players whose performance is higher than the mean are forced to pay an additional cost in each generation?

Mathematical methods: Analysis of replicator dynamics with mutation. The ESS distribution of cooperation level is obtained.

Key assumptions: Players engage in a cooperative dilemma game, and at the end of each generation those whose performance is higher than the mean are forced to pay an additional cost.

Conclusions: Without mutation, the entire population eventually conforms to a single cooperation level determined by the initial composition of the population. With mutation, there is an equilibrium distribution of cooperation, which has a peak at an intermediate level of cooperation. Whether it is institutionalized such as tax or just a social custom, fitness adjustment based ultimately on people's 'envy' is able to maintain cooperation.

Keywords: distribution of cooperation level, envy, evolution of cooperation, fitness adjustment, punishment.

1. INTRODUCTION

Emergence and maintenance of cooperation in humans and non-human animals has been a major theme in evolutionary ecology. Cooperative dilemmas, present in both biological and human social worlds (Hamilton, 1964; Wilson, 1975; Hammerstein and Hagen, 2005; Henrich, 2006; Camerer and Fehr, 2006), describe situations where individuals incur a cost to create benefit for the group or another individual. Examples include the alarm calls warning of predators, ants and bees stocking their community home, monkeys grooming each other, commuters taking public transportation to reduce traffic congestion, energy consumption, and environmental pollution, and governments adopting the Kyoto protocol to reduce global greenhouse gas emissions. Clearly, free-riders or defectors will profit and proliferate, and eventually altruism should disappear. Yet, altruism persists in many natural species. In fact, cooperation is the very fabric of many successful biological and human societies.

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There are many mechanisms to promote cooperation. Direct reciprocity (Trivers, 1971; Axelrod and Hamilton, 1981; Nowak and Sigmund, 1992) and indirect reciprocity (Nowak and Sigmund, 1998, 2005; Wedekind and Milinski, 2000; Ohtsuki and Iwasa, 2004, 2006), as well as kin selection and group selection, have played a major role in explaining the cooperative dilemma. Punishment (Fehr and Gächter, 2000; Boyd *et al.*, 2003) for defectors also leads to cooperative solutions, and this is perhaps more relevant to human societies. Of course, reward provides another incentive for cooperation, although reward is often more costly to mete out than punishment.

Gürerk *et al.* (2006) highlight the advantages of ‘sanctioning institutions’; their experiments show that humans prefer institutions that punish non-cooperators, even at a cost to the punishers. It has been concluded that ‘willingness to engage in costly punishment, even in one-shot situations, may be part of human psychology’ (Henrich *et al.*, 2006).

Recent experimental work has revealed that people have an emotional tendency to punish others who perform well. Henrich *et al.* (2006) observed that humans’ readiness to exert punishment increases as behaviour variance increases. In games conducted by Dawes *et al.* (2007):

subjects reduce and augment others’ incomes, at a personal cost. Furthermore, the size and frequency of income alterations are strongly influenced by inequality. Emotions towards top earners become increasingly negative as inequality increases, and those who express these emotions spend more to reduce above-average earners’ incomes and to increase below-average earners’ incomes. The results suggest that egalitarian motives affect income-altering behaviors, and may therefore be an important factor underlying the evolution of strong reciprocity and, hence, cooperation in humans.

‘Envy’ leads to the action that reduces the fitness of high scoring players, and might force the players to be more cooperative than in a society without this emotion. Just as it is natural for a free-rider to exploit an altruist and a defector to exploit a cooperator, it is equally natural for the weak to envy the strong, the have-nots to envy the haves. The former is regarded as rational behaviour but the latter as emotional. It was long believed that rational and emotional decisions are disparate. However, recent advances in neuroscience have revealed that humans’ ability to emote is intimately connected to the ability to make rational choices (Rolls, 1999). For example, a patient who lost his emotional faculties after a portion of his frontal lobe was removed suffered losses in his analytic abilities as well (Damasio, 1994). Sanctioning institutions in the society would be supported by people’s emotional tendency of envy to punish those who achieved a high gain.

In this paper, we study the dynamics of cooperation level in the framework of an evolutionary game theory, and seek the equilibrium distribution of cooperation level in the population. We consider a simple dilemma game played many times between random pairs of individuals. Towards the end of each generation, there is a session of fitness adjustment, and players who gain more than the population mean are forced to pay an additional cost. We examine mathematically the effect of such a fitness adjustment formalized as replicator dynamics (Taylor and Jonker, 1978; Hofbauer *et al.*, 1979).

We study in detail the case of mean-based fitness adjustment that penalizes those who are above the mean in fitness, and also alternative modes of fitness adjustment. We do not ask how the mode of adjustment is created or maintained. Instead, we focus on the cooperation level that is finally realized by the replicator dynamics in a population in the presence of fitness adjustment.

We find that when adjustment is weak, cooperation and altruism vanish, and the mean fitness of the population decreases. When adjustment is sufficiently strong, cooperation may persist and flourish, and the overall fitness of the population increases. When selection is error-free, we find that the entire population conforms to the same behaviour. In addition, if the initial population is more heterogeneous, then the cooperative effect of fitness adjustment is amplified when adjustment is strong and suppressed when adjustment is weak.

Taking mutation into consideration, we can derive mathematically the equilibrium distribution of strategies, which is a one-peak spectrum of behaviour. The higher the mutation rate, the lower the peak and higher the variation in behaviour. Under strong adjustment, mutation serves to suppress cooperation; under weak adjustment, mutation amplifies cooperation.

In Section 2, after introducing the basic game-theoretic model for the cooperative dilemma, we propose a model of fitness adjustment. In Section 3, we present analytic and simulation results. In Section 4, we present our results on two alternative modes of fitness adjustment. In Section 5, we summarize our findings and briefly discuss directions for further study.

2. THE MODEL

We first consider the simplest game between two players for a cooperative dilemma (Hauert and Doebeli, 2004). In this game, a cooperator incurs a cost c , and the recipient of a cooperator receives benefit b . When two cooperators interact, both receive net benefit $b - c$; a defector receives the highest payoff b when playing against a cooperator who bears the cost of $-c$; and mutual defection yields zero payoff to both parties. When benefit exceeds cost, the game resembles a Prisoner's dilemma game. We shall assume $b > c$ from now on.

Let the strategies be C and D , and the payoff matrix be given by Table 1(a).

Suppose a player's strategy can take mixed strategies of cooperation and defection. A player cooperates with probability s and defects with probability $1 - s$, where s is a continuous variable between 0 and 1.

A player with strategy s would receive from an opponent with strategy x payoff $bx - cs$, and in the same interaction the opponent receives payoff $bs - cx$. The s player receives $(b - c)(x - s)$ more than his opponent using strategy x , where $x > s$. Cooperative players are always exploited by less cooperative ones.

Here, we focus on infinitely large populations. Suppose at time t , $\rho_t(s)$ is the proportion of individuals using strategy s , i.e. $\rho_t(s)$ is the distribution of strategy space at time t . Suppose

Table 1. Payoff matrix for cooperative dilemma game

(a) Standard model			(b) Local pairwise fitness adjustment		
	C	D		C	D
C	$b - c$	$-c$	C	$b - c$	$-c$
D	b	0	D	$b - \frac{\alpha}{2}(b + c)$	0

each player interacts with a randomly chosen player in the population. Then, the payoff of player with strategy s at time t is given by

$$f_t(s) = b\bar{s}_t - cs, \quad (2.1)$$

where $\bar{s}_t = \int x\rho_t(x)dx$ is the mean strategy at time t . If the fitness is equal to the payoff, the mean fitness of the population at time t is given by

$$\bar{f}_t = \int f_t(x)\rho_t(x)dx = (b - c)\bar{s}_t, \quad (2.2)$$

which increases with the mean cooperation level $\bar{s}_t$.

Using the standard replicator dynamics formulation (Taylor and Jonker, 1978; Hofbauer *et al.*, 1979), if we assume that an individual's reproductive fitness is determined solely by their payoff from the game, then

$$\frac{d\rho_t(s)}{dt} = (f_t(s) - \bar{f}_t)\rho_t(s), \quad (2.3)$$

which leads to

$$\frac{d\bar{s}_t}{dt} = -c\sigma_t, \quad (2.4)$$

where σ_t is the variance of strategy space at time t . The proportion of those who are more altruistic than the mean is decreasing, while the proportion of those who defect more than the mean is increasing. The mean strategy $\bar{s}_t$ decreases monotonically and converges to the minimum value on the support of the initial distribution ρ_0 . In the end, as predicted, the entire population adopts the strategy of the least cooperative player among those in the initial population, and the population mean fitness is at its lowest.

Here, we introduce a fitness adjustment process incorporating the effects of envy. First, we let individuals interact with one another as before. Within a generation, players engage in a cooperation game with many players randomly chosen from the population. At the end of each generation, their fitness is not the same as their payoff; instead, the payoff of some individuals is discounted to determine the fitness.

2.1. The doctrine of the mean

Confucius said: The Superior Man actualizes the mean, the inferior man goes against it. The Superior Man actualizes the mean because he is always with it; the inferior man's contrariness is due to his heedlessness.

As the mode of modification of reproductive fitness, we use a form of mean-based adjustment, whereby only those whose game's payoffs are higher than the mean payoffs of the population have their reproductive fitness reduced. The magnitude of reduction is proportional to the excess payoffs. This adjustment scheme is supported by experiments conducted by Dawes *et al.* (2007).

This form of fitness adjustment is deeply rooted in the Confucian ideology in which mediocrity is considered a virtue. Is it better to be above the mean in any gauge of fitness, be it size, wealth, speed, strength, or whatever? A more colourful bird that is more attractive to mates might also be more visible to a bird of prey; a fatter goose is more likely to be

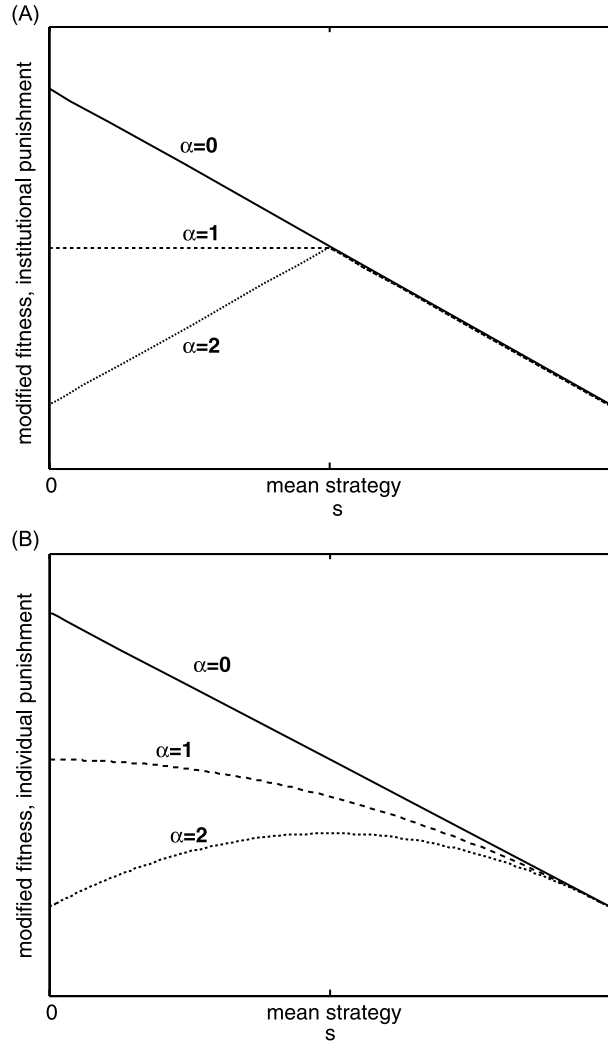


Fig. 1. Modified reproductive fitness under different levels of adjustment. (A) $\hat{f}(s)$, mean-based adjustment. (B) $\tilde{f}(s)$, individual-based adjustment. $\alpha = 0$, $\alpha = 1$, $\alpha = 2$ are indicated. The modified fitness for individual-based adjustment is based on a uniform distribution.

slaughtered. There is a price to be paid for being above average. In this model, an institution exists to police the players and force their cooperation.

We let the reproductive fitness of strategy s be

$$\hat{f}_i(s) = f_i(s) - \alpha \times \max(0, f_i(s) - \bar{f}_i). \quad (2.5)$$

Only those who are less cooperative and hence gain more than the mean are punished, and the strength of fitness adjustment is parametrized by α . The amount of adjustment on strategy $s < \bar{s}_i$ is proportional to $\bar{s}_i - s$; and the modified fitness function $\hat{f}_i(s)$ is a piecewise linear function of s (see Fig. 1A).

The mean reproductive fitness of the population is given by $\bar{f}_i = \int \hat{f}_i(x) \rho_i(x) dx$.

Now players reproduce according to their modified reproductive fitness. Again under frequency-dependent selection, the distribution of strategy space evolves according to

$$\frac{d\rho_t(s)}{dt} = (\hat{f}_t(s) - \bar{f}_t) \rho_t(s). \quad (2.6)$$

3. EQUILIBRIUM DISTRIBUTION

3.1. Without mutation

We are interested in the equilibrium solution to the replicator dynamics equation (2.6) with reproductive fitness modified by mean-based fitness adjustment.

Let $\bar{s}$ be the mean strategy and $\rho(s)$ the strategy distribution at equilibrium.

Proposition 1. *In the generic case, $\rho(s)$ is supported at $\bar{s}$ and is zero everywhere else. The value of $\bar{s}$ depends on the initial distribution $\rho_0(s)$ and the strength of fitness adjustment α . This is proved in Appendix A. Frequency-dependent selection acts to reduce the variance of strategies in the population to zero, and the entire population eventually adopts the same strategy determined by the initial conditions and fitness adjustment level.*

We also show in Appendix A that when $\alpha > 1$, there can be a degenerate case where $\rho(s)$ may be supported at two points.

Proposition 2. *If the initial strategy distribution $\rho_0(s)$ is symmetric with respect to $s = 1/2$, and the strength of adjustment α equals 2, then the strategy distribution $\rho_t(s)$ remains symmetric and $\bar{s}_t = 1/2$ for all time t . When the initial strategy distribution is symmetric, simulations show that, for $\alpha > 2$, $\bar{s}_t$ increases monotonically with respect to t , and for $\alpha < 2$, $\bar{s}_t$ decreases monotonically (see Fig. 2A). Therefore, under strong adjustment, the mean strategy increases, and hence the mean population fitness, $(b - c)\bar{s}_t$, also increases. Cooperation flourishes. Under weak adjustment, the mean strategy and mean population fitness decrease, and cooperation withers. The weaker the adjustment, the quicker cooperation evaporates.*

Simulation (Fig. 2A) shows that given a symmetric initial strategy distribution, as initial strategy variance σ_0 increases, the equilibrium mean strategy $\bar{s}$ increases for $\alpha > 2$, while $\bar{s}$ decreases for $\alpha < 2$. Therefore, greater initial variance amplifies the effect of fitness adjustment on the evolution of cooperation when the strength of adjustment α is high (i.e. above 2); greater initial variance suppresses the cooperative effect of fitness adjustment when α is small (i.e. below 2).

For an arbitrary initial strategy distribution, when $\alpha \leq 1$, we show in Appendix A that the cooperation level $\bar{s}_t$ decreases with time and approaches the minimum of the support of the initial distribution $\rho_0(s)$.

Proposition 3. *If $\alpha \leq 1$, modified reproductive success is decreasing with s , and the mean equilibrium strategy is the minimum value of the initial strategies. This implies that for weak adjustment, defection dominates and cooperation evaporates.*

For $\alpha > 1$, it is difficult to find $\bar{s}_t$ analytically. We have to rely on simulation (Fig. 2A) to find the evolutionary dynamics of cooperation level when fitness adjustment is imposed. Clearly, cooperation level $\bar{s}_t$ increases monotonically with the intensity of adjustment α .

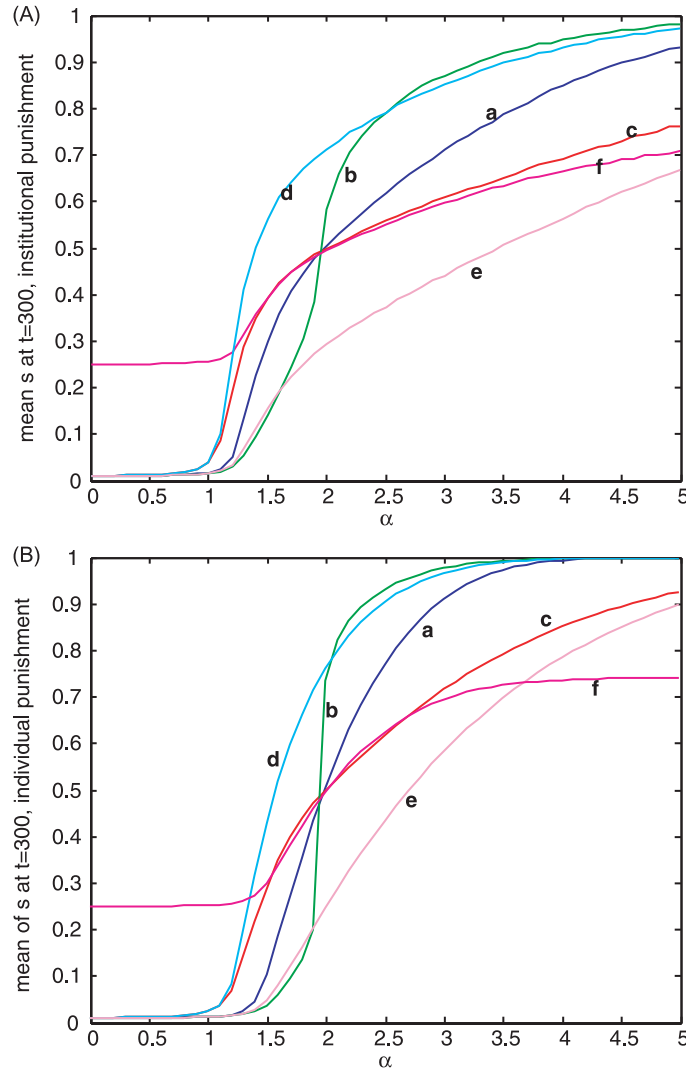


Fig. 2. Mean equilibrium strategy $\bar{s}$ as a function of the initial strategy distribution $\rho_0(s)$ and strength of adjustment α : (A) mean-based adjustment; (B) individual-based adjustment. The plots show the mean strategy at $t = 300$, $\bar{s}_{300}$, with initial distribution $\rho_0(s)$ given by: (a) 1, $\bar{s}_0 = 1/2$, $\sigma_0 = 1/12$; (b) $2 - 4s$ for $s \leq 1/2$ and $-2 + 4s$ for $s \geq 1/2$, $\bar{s}_0 = 1/2$, $\sigma_0 = 1/8$; (c) $4s$ for $s \leq 1/2$ and $4(1 - s)$ for $s \geq 1/2$, $\bar{s}_0 = 1/2$, $\sigma_0 = 1/24$; (d) $2s$, $\bar{s}_0 = 2/3$, $\sigma_0 = 1/18$; (e) $2 - 2s$, $\bar{s}_0 = 1/3$, $\sigma_0 = 1/18$; (f) 2 for $s \in [1/4, 3/4]$ and 0 elsewhere, $\bar{s}_0 = 1/2$, $\sigma_0 = 1/48$.

3.2. Two-strategy case

Let us consider the special case where only two strategies are possible initially. Namely,

$$\rho_0(s) = (1 - w)\delta(s - s_1) + w\delta(s - s_2). \quad (3.1)$$

Hence with probability w a player plays cooperative strategy s_2 and with probability $1 - w$ a player plays strategy s_1 , where $s_2 > s_1$. Instead of having a continuum of strategies, we have only two strategies. For all time, the strategy space will consist of s_1 and s_2 players.

In Appendix B, we prove that for $\alpha > 1/w$, $\bar{s}_t$ goes to s_2 as t increases, and for $\alpha < 1/w$, $\bar{s}_t$ goes to s_1 .

Proposition 4. *Cooperators can invade and take over a population of defectors if the strength of adjustment satisfies*

$$\alpha w > 1, \quad (3.2)$$

where w is the initial frequency of cooperators. If $\alpha w < 1$, then defectors take over the population eventually. Hence for cooperators to succeed, either w or α must be large.

For $\alpha = 1/w$, $\bar{s}_t$ remains $s_1 + w(s_2 - s_1)$ for all time.

3.3 With mutation

Without mutation, variance of the strategy space is depleted in the replicator dynamics, and conformity ensues. However, Darwinian evolution relies not just on selection, but also variation supplied by mutation. Biological or social replication includes errors that generate diversity. To make our fitness adjustment model more realistic, we consider the effects of mutation.

Suppose mutations occur at rate μ and mutants have a uniform distribution on $[0, 1]$. Some variance of traits is maintained in the population. The replicator dynamics equation becomes

$$\frac{d\rho_t(s)}{dt} = (\hat{f}_t(s) - \bar{f})\rho_t(s) + \mu(1 - \rho_t(s)). \quad (3.3)$$

According to the analysis in Appendix C, we can derive the equilibrium distribution $\rho(s)$ explicitly as

$$\rho(s) = \begin{cases} \frac{\mu}{\mu - C - c(\bar{s} - s)(1 - \alpha)} & s \leq \bar{s} \\ \frac{\mu}{\mu - C + c(s - \bar{s})} & s > \bar{s} \end{cases}, \quad (3.4)$$

where

$$C = \alpha c \int_0^{\bar{s}} (\bar{s} - s)\rho(s)ds. \quad (3.5)$$

$\rho(s)$ and $\bar{s}$ are independent of initial condition $\rho_0(s)$. Hence at equilibrium, the population includes individuals with different cooperation levels. The shape of the distribution depends on α .

For $\alpha < 1$, $\rho(s)$ is strictly decreasing everywhere (Fig. 3A). Therefore, when fitness adjustment is weak, the proportion of s players decreases as s increases. There are more defectors than cooperators.

For $\alpha = 1$, ρ is constant over $[0, \bar{s}]$. It decreases monotonically with s over the interval $[\bar{s}, 1]$ (Fig. 3B).

For $\alpha > 1$, we find that ρ attains its maximum at its mean $\bar{s}$ (Figs. 3C, D).

We prove in Appendix C the following proposition on the limit of small mutation rate.

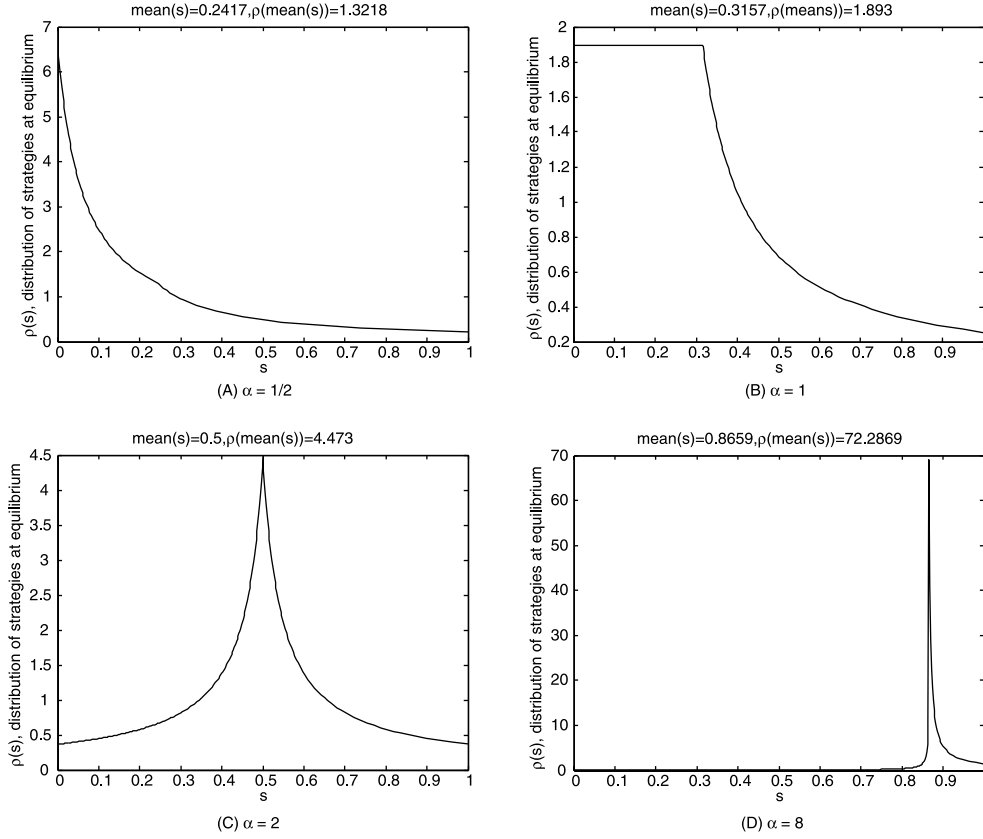


Fig. 3. Mean equilibrium strategy distribution $\rho(s)$ as a function of $s \in [0, 1]$ under different levels α of mean-based adjustment when the global mutation rate μ is 0.2.

Proposition 5. *Under mean-based fitness adjustment of strength α , when global mutation rate $\mu \rightarrow 0$, the equilibrium distribution $\rho(s)$ approximates a δ -function at mean equilibrium strategy $\bar{s} = 0$ when $\alpha \leq 1$; $\rho(s)$ approximates a δ -function at mean equilibrium strategy $\bar{s} = 1 - 1/\alpha$ when $\alpha > 1$. Simulation (Fig. 4) indicates that, at equilibrium, the peak height of the distribution $\rho(\bar{s})$ decreases monotonically as the mutation rate increases; the equilibrium distribution is more evenly spread out and has a greater variance.*

When $\alpha > 2$, as mutation rate increases, $\bar{s}$ also decreases monotonically and remains above $1/2$; when $\alpha < 2$, $\bar{s}$ increases monotonically and remains below $1/2$. Therefore, under strong adjustment ($\alpha > 2$), mutation deters the rise of altruism; under weak adjustment ($\alpha < 2$), mutation enhances cooperation.

3.4 Local mutation

We can also consider the dynamics when mutants are not evenly distributed but they are similar to their parents. This is ‘local mutation’.

$$\frac{d\rho_t(s)}{dt} = (\hat{f}_t(s) - \bar{f}_t) \rho_t(s) + \int_0^1 K(s, x) \rho_t(x) dx, \quad (3.6)$$

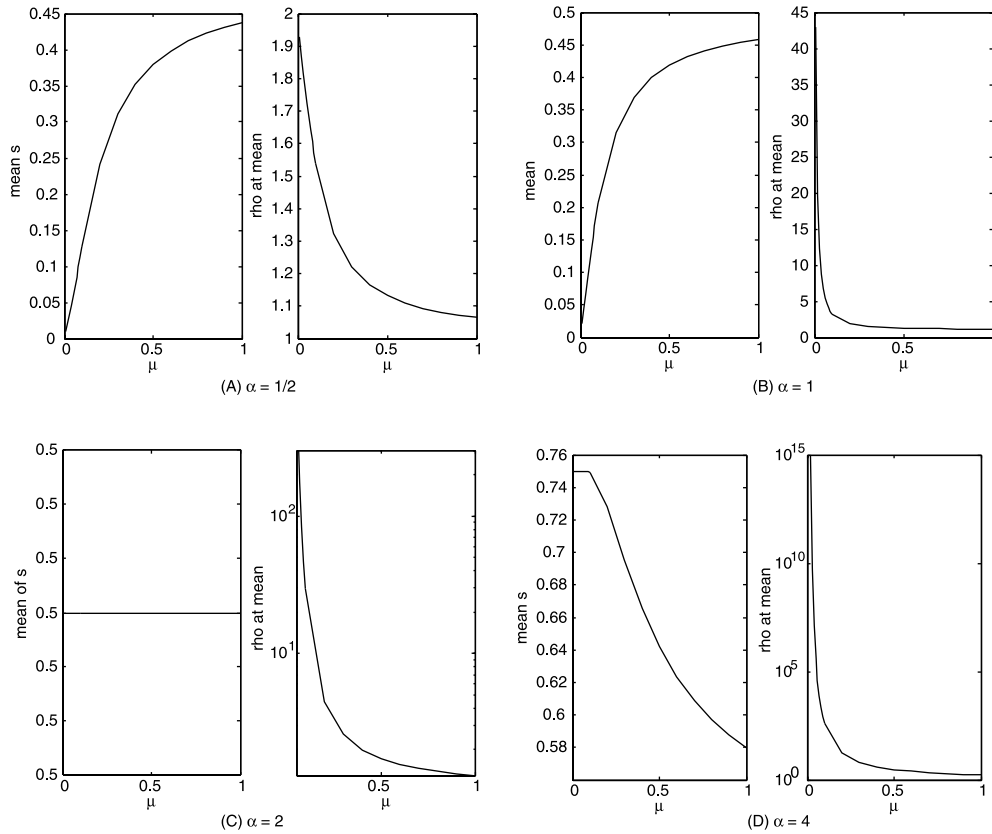


Fig. 4. The values of mean equilibrium strategy $\bar{s}$ and mean equilibrium strategy distribution at $\bar{s}$, $\rho(\bar{s})$, as functions of mutation rate μ under different levels α of mean-based adjustment. In each part, $\bar{s}$ is plotted on the left and $\rho(\bar{s})$ on the right.

where

$$K(s, x) = \begin{cases} \mu(1 - 2\varepsilon\delta(s - x)) & |s - x| \leq \varepsilon \\ 0 & |x - s| > \varepsilon \end{cases}. \quad (3.7)$$

A strategy s can only mutate to another in its ε -neighbourhood. Note that when s is close to the boundary, 0 or 1, its mutant's abundance given by equation (3.7) must be adjusted to account for the fact that the mutant's strategy is constrained within the $[0, 1]$ -interval.

If the initial strategy distribution is symmetric, and $\alpha = 2$, we can show that $\bar{s}_t = 1/2$ for all time t , and $\rho(s)$ is a one-peaked distribution with its maximum at $1/2$.

In general, we cannot solve analytically for $\rho(s)$ and $\bar{s}$.

Figure 5 shows that the equilibrium distribution has much smaller variance under local mutation ($\varepsilon = 0.1$) than under global mutation.

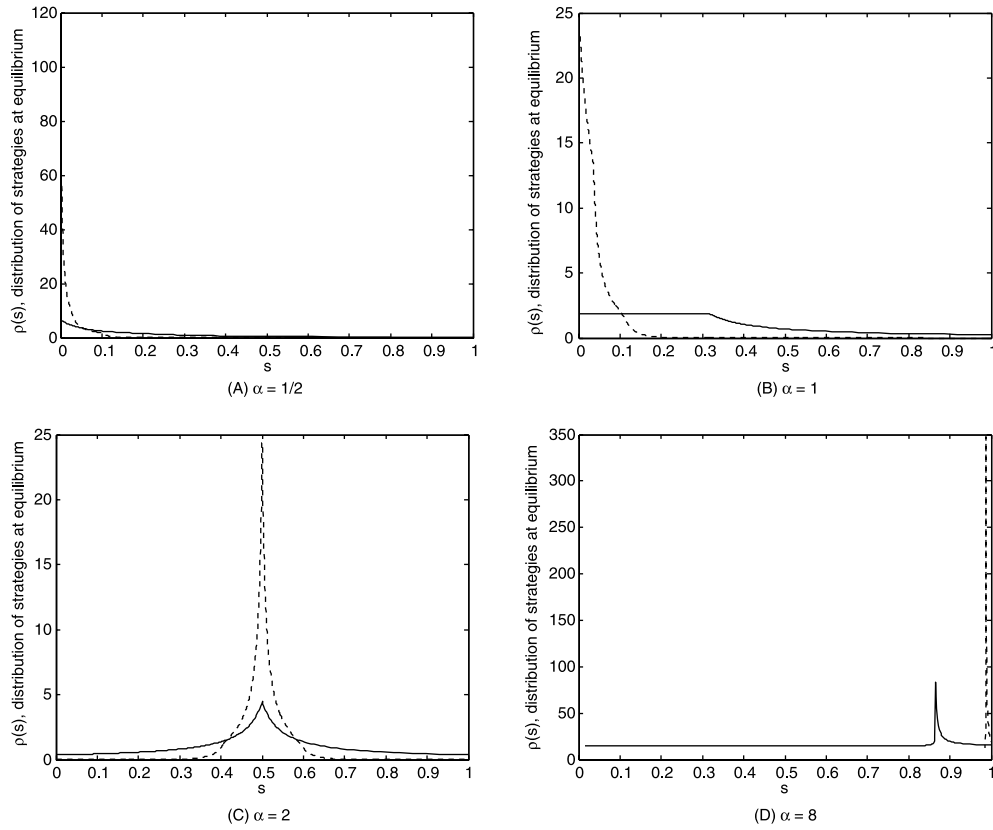


Fig. 5. Mean equilibrium strategy distribution $p(s)$ under different levels α of mean-based adjustment when the mutation rate μ is 0.2. Global mutation (analytic result): solid lines. Local mutation (simulation result, with $\varepsilon = 0.1$ and $\rho_0(s) = 1$ for all s): dashed lines.

4. ALTERNATIVE MODES OF FITNESS ADJUSTMENT

Now we consider two alternative modes of fitness modification: the first is frequency-dependent individual-based adjustment, where a player punishes anyone who is less cooperative; and the second is frequency-independent, where a fixed fitness adjustment regimen is established.

4.1 Individual-based adjustment

In individual-based adjustment, players with a fitness smaller than the population mean are also requested to pay a cost, considering the number of players with even lower fitness.

We let the modified reproductive fitness of strategy s become

$$\tilde{f}_t(s) = f_t(s) - \alpha \int_s^1 c(x-s) \rho_t(x) dx. \quad (4.1)$$

Here, adjustment operates on all players instead of those who are above the mean, and the magnitude of adjustment is proportional to the difference in the cooperation level. In a

sense, each player can punish those who are less cooperative than himself (i.e. those with a higher payoff). The amount of adjustment on a player with strategy s decreases non-linearly as s increases; and the modified fitness here $\tilde{f}_i(s)$ is a non-linear function of s (see Fig. 1B).

Again we let players reproduce according to their modified reproductive fitness.

$$\frac{d\rho_t(s)}{dt} = (\tilde{f}_i(s) - \bar{\tilde{f}}_t) \rho_t(s). \quad (4.2)$$

Propositions 1, 2, 3, and 4 of Section 3 on mean-based adjustment also hold true under individual-based adjustment. We prove these in Appendices B and D.

As in the case of mean-based fitness adjustment, for $\alpha \leq 1$ we find that $\bar{s}_t$ decreases with time t , and $\bar{s}_t$ decreases to the minimum of the support of the initial strategy distribution $\rho_0(s)$. For $\alpha > 1$, analytic solutions are not possible and we rely on simulation to find $\bar{s}$ (see Fig. 2B). The equilibrium distribution $\rho(s)$ is a δ -function centred at some $\bar{s}$ that depends on the initial strategy distribution and α .

Simulation (Fig. 6) shows that given the same initial strategy distribution and same strength of adjustment α , individual-based adjustment promotes cooperation more than mean-based adjustment when adjustment is strong. In contrast, mean-based adjustment promotes cooperation more than individual-based adjustment when adjustment is weak.

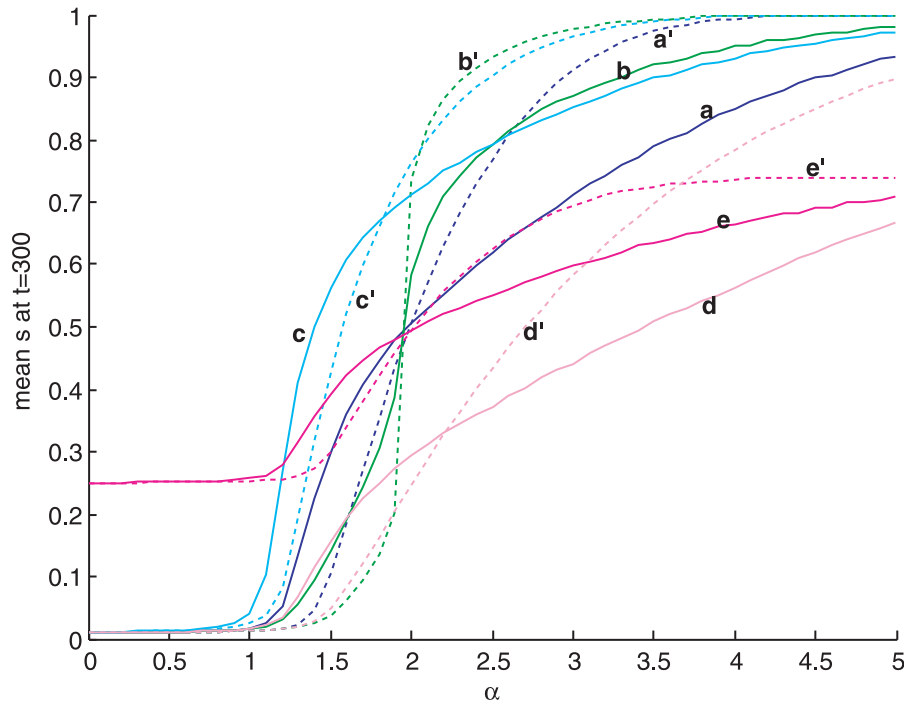


Fig. 6. Comparison of mean equilibrium strategies $\bar{s}$ as a function of strength of adjustment α given different initial distributions $\rho_0(s)$ for mean-based and individual-based adjustment. Mean-based adjustment: solid lines; individual-based adjustment: dashed lines. The plots show the mean strategy at $t = 300$, $\bar{s}_{300}$, with initial distribution $\rho_0(s)$ given by (a,a') 1; (b,b') $2 - 4s$ for $s \leq 1/2$ and $-2 + 4s$ for $s \geq 1/2$; (c,c') $2s$; (d,d') $2 - 2s$; (e,e') 2 for $s \in [1/4, 3/4]$ and 0 elsewhere.

4.2 Frequency-independent adjustment

In the frequency-independent adjustment model, we define the modified reproductive fitness of strategy s by

$$\check{f}_t(s) = f_t(s) - \alpha\beta(s). \quad (4.3)$$

$\beta(s)$ is a decreasing function of s that is independent of the composition of the population. Under replicator dynamics,

$$\frac{d\rho_t(s)}{dt} = (\check{f}_t(s) - \bar{\check{f}}_t)\rho_t(s), \quad \frac{d\bar{s}_t}{dt} = -c\sigma_t + \alpha\bar{s}_t\bar{\beta}_t - \alpha \int_0^1 s\beta(s)\rho_t(s)ds, \quad (4.4)$$

where $\bar{\beta}_t = \int_0^1 \beta(s)\rho_t(s)ds$. For example, when $\beta(s)$ is constant, equations (4.4) reduce to equations (2.3) and (2.4). The mean cooperation level decreases until everyone adopts the least cooperative strategy.

When $\beta(s) = a_1s + a_2$ is a linear function of s , we find that

$$\frac{d\bar{s}_t}{dt} = -(c + a_1\alpha)\sigma_t. \quad (4.5)$$

In particular, when adjustment is inversely proportional to cooperation level and the strength of adjustment is sufficiently strong ($a_1 < 0$ and $\alpha > -c/a_1$), the mean cooperation level increases until everyone adopts the most cooperative strategy.

If we again assume a mutation rate of μ and that mutants are uniformly distributed on the strategy space $[0, 1]$, the equilibrium distribution of cooperation level $\rho(s)$ is given by

$$\rho(s) = \frac{\mu}{\mu + cs + \alpha\beta(s) - K}, \quad K = \alpha\bar{\beta} + c\bar{s}, \quad (4.6)$$

where

$$\bar{\beta} = \int_0^1 \beta(s)\rho(s)ds \quad (4.7)$$

and

$$\bar{s} = \int_0^1 s\rho(s)ds. \quad (4.8)$$

Since $\int_0^1 \rho(s) = 1$, we can determine K numerically and hence find $\bar{s}$ and $\bar{\beta}$.

As an example, we consider the case where $\beta(s)$ is linear, $\beta(s) = a_1s + a_2$, then

$$\rho(s) = \frac{\mu}{\mu + (c + \alpha a_1)(s - \bar{s})}, \quad \bar{s} = \frac{\mu}{c + \alpha a_1} - \frac{1}{\exp((c + \alpha a_1)/\mu) - 1}, \quad \rho(\bar{s}) = 1. \quad (4.9)$$

If $a_1 < 0$ and $\alpha > c/(-a_1)$, then $\rho(s)$ is increasing in s ; otherwise, $\rho(s)$ is decreasing with respect to s .

For general adjustment function $\beta(s)$, if α is sufficiently small, $\rho(s)$ will be decreasing in s ; if α is sufficiently large, $\rho(s)$ will be increasing in s . If $\beta(s)$ is a concave function, $\rho(s)$ can attain two peaks at $s = 0$ and $s = 1$, where the population consists of mostly cooperators and defectors. If $\beta(s)$ is convex, then $\rho(s)$ can attain a peak at an intermediate value of s , and the population consists mostly of players with a mixed strategy.

5. DISCUSSION

Variance exists in every aspect of biological and social phenomena. It can be manifested in size, shape, colour, age, behaviour, wealth or prestige, which confers fitness to the relevant species. Together with variance comes inevitably envy, particularly in human societies. Those who are less successful in whatever measure of fitness are envious of those who are more successful. When success is achieved through non-cooperative actions, animosity in addition to envy arises. Envy and resentment can manifest themselves in punishment.

It is important to note that envy is directed at those with higher fitness, whether it is achieved legitimately or not, whereas general punishment is directed at those who acted illegitimately, whether they have high fitness or not. Regardless of whether the motive for punishment is emotional or rational, punishment fosters the evolution of cooperation and is therefore advantageous to the development of a community and society. Emotion and reason are both integral to behavioural dynamics, and hence they are both maintained by evolution.

We have discussed the effect of fitness adjustment on the maintenance of cooperation. Fitness adjustment is strongly supported by empirical evidence (Henrich *et al.*, 2006; Dawes *et al.*, 2007); it can be institutionalized such as tax or just a social custom. They are likely to be based on envy. Without any mutation in the replicator dynamics, we show that in the generic case the equilibrium distribution of strategy space $\rho(s)$ is a δ -function centred at a single value $\bar{s}$. Everyone conforms to the same strategy $\bar{s}$. Therefore, without variance supplied by recurrent mutation, the variance of the strategy in the population decreases to zero. Frequency-dependent natural selection acts to reduce the variance of the strategy space. $\rho(s)$ and $\bar{s}$ depend on the initial strategy distribution of the population $\rho_0(s)$ and the strength of adjustment α (see Fig. 2). In the special case when only two discrete strategies are present, the more cooperative strategy can invade and replace the other strategy if the product of its initial frequency and the intensity of adjustment is greater than one.

If the initial strategy distribution $\rho_0(s)$ is symmetric with respect to $s = 1/2$, then for $\alpha = 2$ the strategy distribution will remain symmetric for all time, i.e. $\rho_t(s)$ is symmetric with respect to $s = 1/2$ and hence $\bar{s}_t = 1/2$ for all t . In particular, if initially the strategy space of the population has a normal distribution centred at $s = 1/2$, as is often the case in nature, then eventually everyone should play with strategy $s = 1/2$.

We see from the simulation (Fig. 2) that given a symmetric initial strategy distribution, as initial variance σ_0 increases, the equilibrium mean strategy $\bar{s}$ increases for $\alpha > 2$ whereas it decreases for $\alpha < 2$. Therefore, greater initial variance amplifies the effect of fitness adjustment on the evolution of cooperation when the strength of adjustment α is high (i.e. above 2); in contrast, greater initial variance suppresses the cooperative effect of adjustment when α is small (i.e. below 2).

Figure 6 shows that much like the initial variance of strategy space, compared with mean-based adjustment, individual-based adjustment amplifies the cooperative effect of strong adjustment, and suppresses the cooperative effect of weak adjustment.

For an arbitrary initial strategy distribution, when $\alpha \leq 1$, we find that $\bar{s}_t$ decreases to the minimum of the support of $\rho_0(s)$ in both adjustment models. Therefore, for weak adjustment, defection dominates and cooperation evaporates.

For $\alpha > 1$, it is difficult to find $\bar{s}$ analytically. We have to rely on simulation (Fig. 2) to find the evolutionary dynamics of cooperation level when adjustment is imposed.

Without mutation, variance of the strategy space is depleted in the replicator dynamics, and conformity ensues. Mutation is an integral part of Darwinian evolution. With mutation, we have not only diversity but also progress.

If we consider global mutation in the mean-based fitness adjustment model, we can solve for $\rho(s)$ and $\bar{s}$ analytically, and they are independent of initial condition $\rho_0(s)$.

Mutation adds diversity to the equilibrium distribution of strategy space. The greater the mutation, the higher the variance in the equilibrium strategy distribution. On the other hand, mutation suppresses the cooperative effect of strong adjustment and amplifies the cooperative effect of weak adjustment.

We can think of alternative modes of fitness modification. We have only considered fitness adjustment as a consequence of envy, but not reward as a consequence of empathy. If we impose mean-based adjustment and reward, where we increase the fitness of low payoff players and decrease the fitness of high payoff players, the reproductive fitness of each player at time t becomes

$$\hat{f}_t(s) = f_t(s) - \alpha(f_t(s) - \bar{f}_t).$$

We find that independent of the initial distribution, if $\alpha > 1$ the entire population will adopt the most cooperative strategy, whereas if $\alpha < 1$ the entire population will adopt the least cooperative strategy. There is no possibility of the evolution of intermediate cooperation. Hence non-linearity caused by the maximum operation in equation (2.5) is needed to produce the equilibrium population with an intermediate level of cooperation.

Another modification is adjustment given by the opponent of the game. The payoff matrix is modified and becomes Table 1(b). Here α is the strength of pairwise adjustment on the local level.

D is a Nash equilibrium strategy, and C is Nash as well if and only if

$$\alpha > \frac{2c}{b+c}. \quad (5.1)$$

When equation (5.1) holds, the game becomes bi-stable. The basin of attraction for C is given by $s = 2c/(a(b+c))$. Hence, as c decreases or α increases, the cooperative strategy C has a larger basin of attraction. Here again there is no possibility of the evolution of an intermediate level of cooperation.

Many questions remain to be explored in the future. It would also be interesting to study stochastic models of our adjustment mechanism in finite populations.

We have not considered the effects of costs associated with fitness adjustment, particularly in the case of individual-based adjustment. In a future paper, we will derive the optimal adjustment that achieves the maximal level of cooperation without unduly diminishing the overall welfare of a community. When costs of punishment are involved, both cooperators and defectors arise who punish or do not punish. This requires much more involved and detailed analysis and is a suitable topic of future study.

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APPENDIX A: MEAN-BASED ADJUSTMENT

In the case of mean-based fitness adjustment, the modified reproductive fitness is given by equation (2.5), which becomes

$$\hat{f}_t(s) = \begin{cases} b\bar{s} - cs & s \geq \bar{s}_t \\ (b - \alpha c)\bar{s} + (\alpha - 1)cs & s < \bar{s}_t \end{cases} \quad (\text{A1})$$

Proof of Proposition 1. The equilibrium distribution $\rho(x)$ must satisfy $d\rho(x)/dt = 0$ for all x . If $\rho(s) \neq 0$ for some s , then equation (2.6) implies that $\hat{f}(s) = \hat{f}$.

When $\alpha < 1$, equation (A1) shows that $\hat{f}(x)$ is decreasing with x everywhere, so s must equal $\bar{s}$. ρ is supported at only one value, $\bar{s}$, and $\rho(s) = \delta(s - \bar{s})$.

When $\alpha = 1$, ρ must be non-zero only on the interval $[0, \bar{s}]$ where $\hat{f}$ is constant. Since $\int_0^{\bar{s}} \rho(x) dx = 1$ and $\int_0^{\bar{s}} s\rho(x) dx = \bar{s}$, ρ must be entirely supported at $\bar{s}$, modulo some subsets of $[0, \bar{s}]$ of measure zero.

When $\alpha > 1$, $\hat{f}$ attains its maximum at $\bar{s}$. Either ρ is supported at $\bar{s}$ only as in the case $\alpha < 1$. Or if the support of the initial distribution ρ_0 is disconnected, then ρ may be supported at two points, s_1 and s_2 , i.e. $\rho(s) = w\delta(s - s_1) + (1 - w)\delta(s - s_2)$, and $s_1 < \bar{s} < s_2$. Since $\hat{f}(s_1) = \hat{f}(s_2) = \hat{f}$, we have $(s_2 - s_1) = \alpha(\bar{s} - s_1)$. From $\bar{s} = ws_1 + (1 - w)s_2$, we deduce $\alpha(1 - w) = 1$. Hence

$$\rho(s) = \left(1 - \frac{1}{\alpha}\right)\delta(s - s_1) + \frac{1}{\alpha}\delta(s - s_2), \quad (\alpha - 1)(\bar{s} - s_1) = (s_2 - \bar{s}).$$

However, this case is unstable. As we shall see in Appendix B, if the probability of $s_2 \neq 1/\alpha$, then $\rho(s)$ will be supported entirely at either s_1 or s_2 .

Proof of Proposition 2. If $\alpha = 2$ and $\rho_t(s) = \rho_t(1 - s)$ for some t , we have $\bar{s}_t = 1/2$, $d\rho_t(s)/dt = d\rho_t(1 - s)/dt$. Hence, $\bar{s}_{t'} = 1/2$ for all $t' > t$.

Proof of Proposition 3. For $\alpha \leq 1$, we can show that $d\bar{s}_t/dt < 0$, so $\bar{s}_t$ decreases monotonically with time. Furthermore, as $d\hat{f}_t(s)/ds \leq 0$, we can show that $\bar{s}$ must take the value of the minimum of the support of the initial distribution ρ_0 .

APPENDIX B: TWO-STRATEGY CASE

Let us consider the special case where the initial condition is given by equation (3.1). The strategy distribution $\rho_t(s)$ is completely determined by the mean strategy $\bar{s}_t$.

$$\rho_t(s) = \frac{s_2 - \bar{s}_t}{s_2 - s_1}\delta(s - s_1) + \frac{\bar{s}_t - s_1}{s_2 - s_1}\delta(s - s_2). \quad (\text{B1})$$

Under both mean-based and individual-based adjustment, we can derive the following:

$$\frac{d\bar{s}_t}{dt} \propto (\bar{s}_t - s_1)(\bar{s}_t - s_2)(s_2 - \alpha\bar{s}_t + (\alpha - 1)s_1). \quad (\text{B2})$$

Given the initial mean strategy $\bar{s}_0 = s_1 + w(s_2 - s_1)$, it follows that for $\alpha > 1/w$, $\bar{s}_t$ goes to s_2 as t increases, and for $\alpha < 1/w$, $\bar{s}_t$ goes to s_1 . For $\alpha = 1/w$, $\bar{s}_t$ remains $s_1 + w(s_2 - s_1)$ for all time. Therefore, we have shown Proposition 4.

APPENDIX C: MUTATION

We now consider replicator dynamics with mutation. Suppose that mutations occur at rate μ and mutants have a uniform distribution on $[0, 1]$. The replicator dynamics equation with mean-based fitness adjustment becomes equation (3.3).

At equilibrium, the strategy distribution $\rho(s)$ and mean strategy $\bar{s}$ are given by equations (3.4) and (3.5). Since $\rho(\bar{s}) = \mu/(\mu - C) \geq 0$, we have $C < \mu$.

The conditions $\int_0^1 \rho(s) ds = 1$ and equation (3.5) give us two equations for two unknowns C and $\bar{s}$, from which we can solve for C and $\bar{s}$.

$$\frac{c(\alpha - 1)}{\mu} = \log\left(1 + \frac{c\bar{s}(\alpha - 1)}{\mu - C}\right) + (\alpha - 1)\log\left(1 + \frac{c(1 - \bar{s})}{\mu - C}\right)$$

$$C = \alpha \left[\frac{\mu\bar{s}}{(\alpha - 1)} - \frac{\mu(\mu - C)}{c(\alpha - 1)^2} \log\left(1 + \frac{c\bar{s}(\alpha - 1)}{\mu - C}\right) \right]$$

After some lengthy calculations, we find that

$$\bar{s} = \frac{\exp(z) - 1}{\frac{c(\alpha - 1)}{\mu} + \frac{\alpha}{\alpha - 1} E(z)}, \quad C = \mu - \frac{c}{\frac{c}{\mu} + \frac{\alpha}{(\alpha - 1)^2} E(z)}, \quad \rho(\bar{s}) = 1 + \frac{\alpha\mu}{c(\alpha - 1)^2} E(z) \quad (C1)$$

where z is a solution to the equation

$$E(z) = (\alpha - 1)^2 E\left(\frac{c}{\mu} - \frac{z}{\alpha - 1}\right), \quad (C2)$$

and $E(z) = \exp(z) - z - 1$.

Proof of Proposition 5. First we consider the case when $\alpha > 1$. As $\mu \rightarrow 0$, z increases as well and is bounded from above by $c(\alpha - 1)/\mu$, and $\exp(z) \gg c/\mu$. From equation (C1) we can conclude that $\bar{s} \rightarrow 1 - 1/\alpha$ and $\rho(\bar{s}) \gg 1$.

If $\alpha < 1$, from equation (C2) we can check that z must be less than 0. As $\mu \rightarrow 0$, z decreases and is bounded from below by $c(\alpha - 1)/\mu$. As $\mu \rightarrow 0$, z decreases and remains above $c(\alpha - 1)/\mu$. From equation (C1) we see that $\bar{s} \rightarrow 0$ and $\rho(\bar{s}) \gg 1$.

When $\alpha = 1$, we calculate that

$$\bar{s} = \frac{\frac{c}{\mu} - z}{\frac{c}{\mu} - z + \exp(z) - 1}, \quad C = \mu - \frac{c}{\frac{c}{\mu} - z + \exp(z) - 1}, \quad \rho(\bar{s}) = 1 + \frac{\mu}{c} E(z) \quad (C3)$$

where z satisfies the equation

$$2cE(z) = \left(z - \frac{c}{\mu}\right)^2. \quad (C4)$$

Again, as $\mu \rightarrow 0$, z grows and is bounded from above by c/μ . Furthermore, $\bar{s} \rightarrow 0$ and $\rho(\bar{s}) \gg 1$.

As $\mu \rightarrow 0$, equation (3.4) shows that $\rho(s) \rightarrow 0$ for $s \neq \bar{s}$. Hence the equilibrium distribution $\rho(s)$ approximates a δ -function at $\bar{s}$.

In the special case $\alpha = 2$, we find that $z = c/(2\mu)$. $\bar{s} = 1/2$ and $\rho(\bar{s}) = 2\mu(\exp(c/2\mu) - 1)/c$. $\rho(\bar{s})$ decreases monotonically as μ increases, and as $\mu \rightarrow 0$, $\rho(\bar{s}) \rightarrow \infty$.

APPENDIX D: INDIVIDUAL-BASED ADJUSTMENT

In the case of individual-based adjustment, the modified reproductive fitness is $\tilde{f}_t(s)$, where

$$\tilde{f}_t(s) = f_t(s) - \alpha c(\bar{s}_t - s) + \alpha c \int_0^s (x - s) \rho_t(x) dx. \quad (D1)$$

Proof of Proposition 1 (individual-based adjustment). Using the following relation

$$\frac{d}{ds} \int_{x=0}^s s \rho_t(x) dx = s \rho_t(s) + \int_{x=0}^s \rho_t(x) dx,$$

we have

$$\frac{d\tilde{f}_t(s)}{ds} \propto (\alpha - 1) - \alpha \int_{x=0}^s \rho_t(x) dx. \quad (D2)$$

Using similar arguments as in Appendix A, we can prove Proposition 1 for individual-based adjustment.

We also check that Proposition 2 holds under individual-based adjustment.

Proof of Proposition 3 (individual-based adjustment). Equation (D2) shows that for $\alpha \leq 1$, we have $d\tilde{f}_t(s)/ds \leq 0$.

By introducing mutation into the individual-based adjustment model, whereby mutations occur at rate μ and mutants have a uniform distribution on $[0, 1]$, the replicator dynamics equation becomes

$$\frac{d\rho_t(s)}{dt} = (\tilde{f}_t(s) - \bar{f}) \rho_t(s) + \mu(1 - \rho_t(s)). \quad (D3)$$

At equilibrium, the frequency distribution of strategy space $\rho(s)$ is given by

$$\frac{\mu}{\rho(s)} = \mu + c(s - \bar{s}) + \alpha c \int_{x=s}^1 (x - s) \rho(x) dx + \alpha c \int_{y=0}^1 \int_{x=0}^y (x - y) \rho(x) \rho(y) dx dy \quad (D4)$$

We will not be able to solve for $\rho(s)$ and $\bar{s}$ explicitly.

If ρ is smooth at s , then

$$\frac{d\rho(s)}{ds} \propto \alpha \int_{x=s}^1 \rho(x) dx - 1. \quad (D5)$$

Hence for $\alpha < 1$, the equilibrium distribution $\rho(s)$ is a decreasing function.

For $\alpha > 1$, define s_0 to be where $\rho(s)$ attains its maximum value. Equation (D5) shows that s_0 satisfies the condition

$$\int_{x=s_0}^1 \rho(x) dx = \frac{1}{\alpha}. \quad (D6)$$

