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The Paradox of Cooperation Benefits

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Abstract

It seems obvious that as the benefits of cooperation increase, the share of cooperators in the population should also increase. It is well known that positive assortment between cooperative types, for instance in spatially structured populations, provide better conditions for the evolution of cooperation than complete mixing. This study demonstrates that, assuming positive assortment, under most conditions higher cooperation benefits also increase the share of cooperators. On the other hand, under a specified range of payoff values, when at least two payoff parameters are modified, the reverse is true. The conditions for this paradox are determined for two-person social dilemmas: the Prisoner's Dilemma, the Hawks and Doves game, and the Stag Hunt game, assuming global selection and positive assortment.

Keywords: altruism, evolution of cooperation, spatially structured social dilemmas, Price equation, Prisoner's Dilemma, Hawks and Doves, Stag Hunt

1. Introduction

Cooperation in single-shot two-person social dilemmas is a difficult puzzle that has attracted many theorists. If the interaction is not repeated, there is no place for reciprocity, reputation, image scoring or other similar mechanisms that sustain cooperation. Without doubt, the possibilities for the evolution of cooperation are very limited in single-shot social dilemma situations with complete mixing (random interactions), i.e., when

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individuals are paired with a partner from all possible actors with uniform probability. In social dilemmas, cooperators can be exploited by defectors, which leads to the extinction of cooperation in evolutionary terms.

The exception is the Hawks and Doves game, in which in evolutionary equilibrium, cooperators (doves) establish a share in the population (Maynard Smith, 1982). In the Hawks and Doves game (Table .1), increasing the payoffs for mutual cooperation (R) will increase the proportion of cooperators at equilibrium (cf. Maynard Smith, 1982). A smaller temptation payoff (T), a smaller payoff for mutual defection (P), and a higher sucker's payoff (S) will also increase the proportion of cooperators in evolutionary equilibrium. Hence, the role of cooperation benefits is clear: an increase always contributes to a larger share of cooperators in the population. Similarly, larger benefits for defection (hawks) will always decrease the share of unconditional cooperators in the population.

INSERT TABLE .1 HERE

In all social dilemmas, when cooperators are more likely to meet each other than by pure chance, the benefits of cooperation go also more likely to cooperators. This is a segmentation effect that can make cooperation a viable strategy (Becker, 1976; Axelrod and Hamilton, 1981; Queller, 1985; Bowles and Gintis, 1998; Doebeli and Hauert, 2005). For instance, cooperators are more likely to meet other cooperators if interaction and reproduction takes place in a spatial structure or in a social network (Ohtsuki et al, 2006; Wang et al, 2008). In most social dilemmas, the introduction of a spatial arrangement modifies equilibrium conditions in favor of cooperation (Doebeli and Hauert, 2005). A spatial structure promotes cooperation also in the mostly studied Prisoner's Dilemma (Nowak and May, 1992, 1993; Hubermann and Glance, 1993; Nowak et al, 1994).

In contrast with the spatial Prisoner's Dilemma, a spatial structure has no positive effect in the Hawks and Doves game if local interaction is coupled with local competition for reproduction (Doebeli and Hauert, 2005).

Population viscosity, where neighbors compete with each other to occupy nearby spaces for their offspring, unsurprisingly has a drawback for segmented clusters of cooperators. The counterpoint of positive assortment and local competition in viscous populations has been well studied (Taylor, 1992a,b; Wilson et al, 1992; Queller, 1994; van Baalen and Rand, 1998; Doebeli and Hauert, 2005; Grafen and Archetti, 2008). Despite the

relevance of this problem, a necessary first step to investigate effects of cooperation benefits on the share of cooperators with positive assortment is to neglect local competition and assume (for the sake of simplicity) selection at a global level.

Hamilton's rule (1964), which has been the basis for one of the most important explanations of the evolution of altruism, can be used to determine the effect of cooperation benefits assuming positive assortment. If α denotes the frequency to which the benefits of altruism accrue to other altruists rather than to average population members, b denotes the benefits of altruism to the partner and c indicates the cost to the altruist, then altruists will increase their share if their inclusive fitness $\alpha b - c$ is greater than zero. Clearly, an increase in benefits b will always make it more likely that this requirement of Hamilton's rule is met, indicating that larger cooperation benefits always increase the proportion of cooperators in the population.

The general result of Ohtsuki et al (2006) is very similar to Hamilton's rule (Grafen, 2007). They show that when interaction is not random, but determined by social networks, natural selection favors cooperation. The rule of thumb is that the benefit of the altruistic act b , divided by cost c , should exceed the average number of neighbors k , which means $b/c > k$. This result holds for all type of graphs, including cycles, spatial lattices, other regular graphs, random and scale-free networks. This result also implies that increasing the benefits (b) of cooperation in a given structure will always support the survival of cooperators.

On the other hand, Németh and Takács (2007) demonstrated in a simulation study that assuming spatial interaction and global selection, altruism benefits might have a paradoxical effect on the proportion of altruists. They investigated a knowledge transfer interaction, in which passing knowledge is costly and an altruistic help cannot be reciprocated because knowledge is dichotomous and cannot be lost. They showed that altruists gain a share in the population, but this share decreases as the value of knowledge in terms of extended lifetime increases. This study highlights that it is misleading to draw too early conclusions from intuition and from Hamilton's rule and conclude that increased cooperation benefits always result in a larger share of contributors. On the contrary, as a major contribution of this study, with a simple analysis, we intend to show that such paradoxes occur for all types of social dilemma games. With a thorough and systematic analysis of games with positive assortment, we

will demonstrate under what conditions one can find paradoxical effects of cooperation benefits. Our findings not only imply that an investment in extending cooperation benefits might backfire at a medium level of positive assortment, but also that less investment in cooperation benefits can contribute to more cooperation when individuals of the same genotype meet more frequently than by chance.

1.1. The use of the Price equation

The starting point of our analysis is the Price equation (Price, 1970) that has been used in its simple and general form for a wide range of evolutionary phenomena (Frank, 1995; van Veelen, 2005), including a rederivation of Hamilton's rule (Grafen, 1985; Queller, 1985). We will use several simplifications as we consider a haploid population interacting in pairs, where the genetic component of cooperation is at a single locus with two possible values: cooperation and defection. We will use the Price equation first without payoff restrictions to determine under what conditions (1) defection or (2) cooperation is an evolutionary stable strategy (Maynard Smith and Price, 1973) and under what conditions there is a (3) mixed equilibrium of defectors and cooperators.

Consider two groups: cooperators and defectors, having characteristics $z_1 = 1$ and $z_2 = 0$. As the characteristic values do not change from the parent to the child generation ($\Delta z_i = 0$), we can use the simplified Price equation:

$$w\Delta z = \text{cov}(w_i, z_i)$$

where z_i are the characteristic values of different groups of the population, w_i are their absolute fitness (per capita number of offspring), z is the average characteristic value, and w is the average fitness.

That in our special case can be further transformed to:

$$w\Delta z = z(1 - z)(w_1 - w_2) \quad (1)$$

1.1.1. Equilibrium

At equilibrium, $\Delta z = 0$, which gives three different solutions:

1. $z = 0$. The equilibrium proportion of cooperators is zero.
2. $z = 1$. The equilibrium proportion of defectors is zero.

3. $w_1 = w_2$. A mixed equilibrium of cooperators and defectors. At this point, the average number of offspring of both cooperators and of defectors are the same, which means that population ratios do not change, hence the equilibrium. This equilibrium only exists if $0 < z^* < 1$, where z^* is the equilibrium proportion of cooperators for the solution $w_1(z) = w_2(z)$.

1.1.2. Stability

Let us take the partial derivative of equation (1) over z :

$$\frac{\partial w}{\partial z} \Delta z + w \frac{\partial \Delta z}{\partial z} = \frac{\partial(z - z^2)}{\partial z} (w_1 - w_2) + z(1 - z) \left(\frac{\partial w_1}{\partial z} - \frac{\partial w_2}{\partial z} \right)$$

At equilibrium we can simplify to:

$$\frac{\partial \Delta z}{\partial z} = (1 - 2z) \frac{w_1 - w_2}{w} + \frac{z(1 - z)}{w} \left(\frac{\partial w_1}{\partial z} - \frac{\partial w_2}{\partial z} \right)$$

An equilibrium is stable if

$$\frac{\partial \Delta z}{\partial z} < 0.$$

Now we can take a look at the three equilibria again:

1. $z = 0$

$$\frac{\partial \Delta z}{\partial z} = \frac{w_1 - w_2}{w} < 0$$

So this equilibrium is stable if $w_1 < w_2$. A cooperator cannot penetrate the population because his or her fitness falls below the fitness of defectors. This means that defection is an evolutionary stable strategy (ESS).

2. $z = 1$

$$\frac{\partial \Delta z}{\partial z} = -\frac{w_1 - w_2}{w} < 0$$

So this equilibrium is stable if $w_1 > w_2$. This means that cooperation is an ESS.

3. $w_1 = w_2$

$$\frac{\partial \Delta z}{\partial z} = \frac{z(1 - z)}{w} \left(\frac{\partial w_1}{\partial z} - \frac{\partial w_2}{\partial z} \right) < 0$$

So this equilibrium is stable if $\frac{\partial w_1}{\partial z} < \frac{\partial w_2}{\partial z}$. If the ratio of cooperators increases, their fitness falls below the fitness of defectors, so their ratio decreases back. Similarly, if the ratio of cooperators decreases, their fitness exceeds the fitness of defectors, so their ratio increases back.

1.2. ESS in social dilemmas

When looking at replicator dynamics based on reproductive fitness, defection is the evolutionary stable strategy (ESS) in the Prisoner's Dilemma, and it is also an ESS in the Stag Hunt game (Maynard Smith, 1982; Doebeli and Hauert, 2005). On the other hand, in the Hawks and Doves game, replicator dynamics converge to a mixed stable equilibrium at which both cooperation and defections strategies are present (Maynard Smith, 1982). These textbook results are displayed in Figure .1a-c for comparison.

INSERT FIGURE .1 HERE

2. Populations with positive assortment

2.1. General equilibrium conditions

Let us now study populations in which the interaction probability of two individuals of the same genotype might be different from the probability of interacting with an average individual. Let us denote the fitness of individuals with genotype G interacting with another individual with genotype H by w_{GH} . We will denote the level of positive assortment by α . This is the probability that an average individual interacts with another individual of its own genotype instead of with a randomly selected partner (Cavalli-Sforza and Feldman, 1981). Thus $\alpha = 0$ means random interaction or complete mixing, in which individuals of the same genotype only meet each other, as expected, based on their share in the population, and $\alpha = 1$ means that individuals meet only members of their own genotype. The average fitness of cooperators and defectors are given as:

$$w_1 = \alpha w_{CC} + (1 - \alpha)[z w_{CC} + (1 - z) w_{CD}]$$

$$w_2 = \alpha w_{DD} + (1 - \alpha)[z w_{DC} + (1 - z) w_{DD}]$$

Using the classical notations $P = w_{DD}$, $R = w_{CC}$, $S = w_{CD}$, $T = w_{DC}$:

$$w_1 = \alpha R + (1 - \alpha)[z R + (1 - z) S]$$

$$w_2 = \alpha P + (1 - \alpha)[z T + (1 - z) P]$$

The three equilibria in this case are:

1. $z = 0$ is stable if $\alpha(R - S) < P - S$.

2. $z = 1$ is stable if $\alpha(T - P) > T - R$.
3. $z^* = \frac{P - \alpha R - (1 - \alpha)S}{(1 - \alpha)(R + P - S - T)}$ exists if $0 < z^* < 1$ and is stable if $R - S < T - P$.

These comply with the results of Bergstrom (2003).

2.2. Prisoner's Dilemma with positive assortment

The three equilibria in the Prisoner's Dilemma with positive assortment with $T > R > P > S$ payoffs are:

1. $z = 0$ is stable if $\alpha < \frac{P - S}{R - S}$.
2. $z = 1$ is stable if $\alpha > \frac{T - R}{T - P}$.
3. $z^* = \frac{P - \alpha R - (1 - \alpha)S}{(1 - \alpha)(R + P - S - T)}$ exists if $\frac{P - S}{R - S} \leq \alpha \leq \frac{T - R}{T - P}$ and is stable if $R - S < T - P$. ($z^*|_{\alpha = \frac{P - S}{R - S}} = 0$; $z^*|_{\alpha = \frac{T - R}{T - P}} = 1$; $\frac{\partial z^*}{\partial \alpha} > 0$)

In the Prisoner's Dilemma with positive assortment, close to complete mixing ($\alpha < \frac{P - S}{R - S}$) all cooperators die out, and close to perfect assortment ($\alpha > \frac{T - R}{T - P}$) all defectors die out. For intermediate cases of $\frac{P - S}{R - S} \leq \alpha \leq \frac{T - R}{T - P}$ we have a stable mixed equilibrium with z monotonously rising from 0 to 1 as α is rising from $\frac{P - S}{R - S}$ to $\frac{T - R}{T - P}$ (cf. Figure .2).

INSERT FIGURE .2 HERE

It is interesting to note that a homogenous population of cooperators is an evolutionary stable equilibrium when positive assortment is above a threshold level of $\frac{T - R}{T - P}$. This is also one of the two thresholds that the continuation probability has to exceed in the iterated Prisoner's Dilemma for a trigger strategy Tit for Tat (TFT) being an equilibrium (Axelrod, 1984). The similarity is more than pure resemblance: in both cases, the condition describes the minimum probability that a cooperator interacts with another cooperator.

In the single-shot Prisoner's Dilemma in an evolutionary horizon, if $\frac{P - S}{R - S} > \frac{T - R}{T - P}$, then the mixed equilibrium is unstable and above the critical value of z^* , the population evolves to full cooperation, and below the critical value of z^* , the population evolves to full defection (cf. Figure .3).

INSERT FIGURE .3 HERE

2.3. Hawks and Doves with positive assortment

The three equilibria in the Hawks and Doves game with positive assortment with $T > R > S > P$ payoffs are:

1. $z = 0$ is never stable.
2. $z = 1$ is stable if $\alpha > \frac{T-R}{T-P}$.
3. $z^* = \frac{P-\alpha R-(1-\alpha)S}{(1-\alpha)(R+P-S-T)}$ exists if $\alpha \leq \frac{T-R}{T-P}$ and is always stable.
 $(0 < z^*|_{\alpha=0} = \frac{S-P}{S-P+T-R} < 1; z^*|_{\alpha=\frac{T-R}{T-P}} = 1; \frac{\partial z^*}{\partial \alpha} > 0)$

In the Hawks and Doves game with positive assortment, close to perfect assortment ($\alpha > \frac{T-R}{T-P}$), all defectors die out. For $\alpha \leq \frac{T-R}{T-P}$, there is a stable mixed equilibrium with z monotonously rising from $\frac{S-P}{S-P+T-R}$ to 1 as α is increasing from 0 to $\frac{T-R}{T-P}$ (cf. Figure .4).

INSERT FIGURE .4 HERE

2.4. Stag Hunt with positive assortment

The three equilibria in the Stag Hunt game with positive assortment with $R > T > P > S$ payoffs are:

1. $z = 0$ is stable if $\alpha < \frac{P-S}{R-S}$.
2. $z = 1$ is always stable.
3. $z^* = \frac{P-\alpha R-(1-\alpha)S}{(1-\alpha)(R+P-S-T)}$ exists if $\alpha \leq \frac{P-S}{R-S}$ and is never stable.
 $(0 < z^*|_{\alpha=0} = \frac{P-S}{P-S+R-T} < 1; z^*|_{\alpha=\frac{P-S}{R-S}} = 0; \frac{\partial z^*}{\partial \alpha} < 0)$

The mixed equilibrium in the Stag Hunt game with positive assortment exists if $\alpha \leq \frac{P-S}{R-S}$ but it is not stable. A tiny move below the equilibrium point results in all cooperators dying out. Similarly, a tiny move above the equilibrium point has the consequence that all defectors die out. Besides, if $\alpha \geq \frac{P-S}{R-S}$ then only full cooperation is an ESS; otherwise both full cooperation and full defection are stable equilibria (cf. Figure .5).

INSERT FIGURE .5 HERE

3. The Price of Cooperation

3.1. General guidelines of a comparative analysis

In this section, we determine the conditions under which increasing the benefits of cooperation results in fewer cooperators at equilibrium; or

decreasing the benefits of cooperation results in an increase in more cooperators at equilibrium in social dilemmas with positive assortment. As the effects of changing a single parameter are trivial, we highlight that paradoxes occur when two (or more) payoffs are modified.

3.2. Prisoner's Dilemma with positive assortment

3.2.1. Boundary conditions (Prisoner's Dilemma)

We do not find any surprises when analyzing the effect of changes in single parameter values of the Prisoner's Dilemma with positive assortment on the proportion of cooperators at equilibrium. As one can already directly imply from the payoff matrix (Table .1), an increase in R or S are beneficial for cooperation and an increase in T or P are beneficial for defection. Hence, the effects of the change in single payoff parameters on z^* are trivial. For instance, when the reward for mutual cooperation R is increased, the proportion of cooperators in the mixed ESS of the Prisoner's Dilemma with positive assortment also increases. Paradoxes might occur however, when at least two parameter values, one that favors cooperation and one that favors defection (for instance, R and T) are modified at the same time. In case $\Delta T > \Delta R$, where we intuitively would expect the decrease of cooperators in ESS, the proportion of cooperators actually rises in a certain range of α (an example is shown in Figure .6).

INSERT FIGURE .6 HERE

One can see from Figure .2 that a mixed equilibrium is ESS in the Prisoner's Dilemma with positive assortment for $\frac{P-S}{R-S} \leq \alpha \leq \frac{T-R}{T-P}$. Let us now introduce the notation $\alpha_L = \frac{P-S}{R-S}$ and $\alpha_H = \frac{T-R}{T-P}$ for the boundaries. The effects of single payoff parameters on the boundaries are self-explanatory and help us to determine the conditions under which paradoxes occur. For this, at least two parameters should change at the same time. Table .2 shows all possible pairs of parameter changes which may cause a paradox. In Appendix I, all cases denoted with an asterisk in Table .2 are explored.

INSERT TABLE .2 HERE

Consider the case when the temptation reward T is increased. This clearly favors defection, because it has an unambiguous impact on z^* (see previous section) and also on α_H . Let us also increase at the same time R that favors cooperation (for the other cases see Appendix I). If $\Delta T > \Delta R$, and especially if ΔT is larger than ΔR with an order of magnitude ($\Delta T \gg \Delta R$),

we would intuitively expect that the proportion of cooperators in mixed equilibrium is decreasing. This is, however, not the case for all values of α . The explanation is that if a mixed equilibrium exists, the increase in T has only an impact on the upper bound, but not on the lower bound of the range of mixed equilibrium.¹ On the other hand, a tiny increase in R already has the consequence that a mixed equilibrium will exist also for α values lower than the original lower bound of α_L . This is displayed on Figure .8. We see a paradox in the range between α'_L and α_T . Between α'_L and α_L the full defection equilibrium has been replaced by a mixed equilibrium and between α_L and α_T the proportion of cooperators in mixed equilibrium has increased.²

INSERT FIGURE .7 HERE

INSERT FIGURE .8 HERE

3.2.2. The paradox of cooperation benefits in the Prisoner's Dilemma with positive assortment

Consider the situation when $\alpha_L < \alpha_H$ that is $\frac{P-S}{R-S} < \frac{T-R}{T-P}$. This means that a mixed equilibrium exists in the Prisoner's Dilemma game with positive assortment (see Figure .2). When the temptation reward T is increased (to T') and R or S are increased (to R' and S') or P is decreased (to P'), then a paradox occurs in the following range of α :

$$\alpha'_L = \frac{P' - S'}{R' - S'} < \alpha \leq \frac{P - S}{R - S} = \alpha_L$$

where a mixed equilibrium will be ESS while originally, full defection was the only stable equilibrium (see Figure .7). In addition, the proportion of

¹Changing P and R is a special case, since both parameters have an effect on both boundaries of α . And yet, as can be seen in Appendix I, this case may also yield a paradox. See Figure .7.

²Let's consider two cases, when $\frac{\Delta T}{\Delta R} \rightarrow \infty$:

- ΔR is fixed and $\Delta T \rightarrow \infty$:
The range of α in which a paradox occurs approaches $[R', R]$ which has a fixed length, but Δz^* approaches zero, so the paradox disappears in limit value.
- $\Delta R \rightarrow 0$ and ΔT is fixed:
The length of the range of α in which a paradox occurs approaches zero, so the paradox disappears in limit value.

cooperators in the mixed equilibrium increases in the range:

$$\alpha_L = \frac{P - S}{R - S} < \alpha < \alpha_T$$

where α_T can be obtained from:

$$z^* = \frac{P - \alpha_T R - (1 - \alpha_T)S}{(1 - \alpha_T)(R + P - S - T)} = \frac{P' - \alpha_T R' - (1 - \alpha_T)S'}{(1 - \alpha_T)(R' + P' - S' - T')}$$

that gives:

$$\alpha_T = \frac{\frac{P-S}{R+P-S-T} - \frac{P'-S'}{R'+P'-S'-T'}}{\frac{R-S}{R+P-S-T} - \frac{R'-S'}{R'+P'-S'-T'}} \quad (2)$$

Consider now the situation when $\alpha_L > \alpha_H$ that is $\frac{P-S}{R-S} > \frac{T-R}{T-P}$. This means that there is no mixed equilibrium (see Figure .3). When the temptation reward T and the cooperation reward R are both increased and $\Delta T > \Delta R$, and especially if $\Delta T \gg \Delta R$, then conditions are seemingly more advantageous for defection. Paradoxically, in a certain range of α , conditions become more favorable for cooperation (see Figures .9 and .10).

INSERT FIGURE .9 HERE

Figure .9 indicates the case, when $\alpha'_L > \alpha'_H$. For

$$\alpha'_L = \frac{P - S}{R' - S} < \alpha \leq \frac{P - S}{R - S} = \alpha_L$$

only full cooperation is possible (if the initial z is greater than the critical z^* value), while originally full defection was also a stable equilibrium.

For

$$\alpha_T < \alpha < \alpha'_L = \frac{P - S}{R' - S}$$

the critical value of z^* is decreased, which is clearly favorable for cooperation. If the initial ratio of cooperators is random (marked with an x on Figure .9), a lower z^* means a higher chance of reaching full cooperation.

INSERT FIGURE .10 HERE

Figure .10 indicates the case, when $\alpha'_L < \alpha'_H$, so the new upper and lower bounds are swapped back.

For

$$\alpha_H < \alpha < \alpha'_L$$

full defection is the only stable equilibrium instead of full cooperation and full defection depending on the initial z . This is favorable for defection.³
For

$$\alpha'_H < \alpha < \alpha_L$$

full cooperation is the only stable equilibrium instead of full cooperation and full defection depending on the initial z . This is favorable for cooperation, thus paradoxical.⁴
For

$$\alpha'_L < \alpha < \alpha'_H$$

the mixed equilibrium z^* becomes ESS instead of full cooperation and full defection. As α approaches α'_H , the change in the parameters gets more favorable for cooperation, but there is no unambiguous interval where the effect of change is paradoxical.

3.3. Hawks and Doves with positive assortment

3.3.1. Boundary conditions (Hawks and Doves)

A similar analysis can be carried out for the Hawks and Doves game with positive assortment. We will avoid overlapping discussions. It is easy to see, for instance, that the effects of T , R , P and S on z^* are the same as in the Prisoner's Dilemma with positive assortment (see Section 3.2.1).

One can see from Figure .4 that a mixed equilibrium is ESS in the Hawks and Doves game with positive assortment for $\alpha \leq \alpha_H = \frac{T-R}{T-P}$. The effects of single payoff parameters on this boundary are the same as in the Prisoner's Dilemma.

³If $\alpha'_L < \alpha_H$, the equilibrium between the two is mixed instead of the original full defection, which is favorable for cooperation, thus paradoxical.

⁴If $\alpha_L < \alpha'_H$, the equilibrium between the two is mixed instead of the original full cooperation, which is favorable for defection, so there is no paradox.

3.3.2. The paradox of cooperation benefits in the Hawks and Doves game with positive assortment

Let's increase T and R (to T' and R'), so that $\Delta T > \Delta R$. A paradox occurs in the following range of α :

$$\alpha'_H = \frac{T' - R'}{T' - P} < \alpha < \frac{T - R}{T - P} = \alpha_H$$

where mixed equilibrium gives place to full cooperation. In addition, the proportion of cooperators in the mixed equilibrium increases in the range:

$$\alpha_T < \alpha < \alpha'_H = \frac{T' - R'}{T' - P}$$

where α_T is defined in equation (2). See Figure .11.
INSERT FIGURE .11 HERE

3.4. Stag Hunt with positive assortment

3.4.1. Boundary conditions (Stag Hunt)

The effects of T , R , P and S on z^* are the same as in the Prisoner's Dilemma except for their signs. The effects of T , R , P and S on α_L are the same as in the Prisoner's Dilemma.

3.4.2. The paradox of cooperation benefits in the Stag Hunt game with positive assortment

Let's increase T and R (to T' and R'), so that $\Delta T > \Delta R$. A paradox occurs in the following range of α :

$$\alpha'_L = \frac{P - S}{R' - S} < \alpha \leq \frac{P - S}{R - S} = \alpha_L$$

where only full cooperation will be stable while originally both full cooperation and full defection were stable depending on the initial z . In addition, the critical value z^* above which full cooperation can develop decreases in the range:

$$\alpha_T < \alpha < \alpha'_L = \frac{P - S}{R' - S}$$

where α_T is defined in equation (2). See Figure .12.
INSERT FIGURE .12 HERE

Finally, note that although we have modified T and R in our examples, other changes in the payoff parameters also induce similar paradoxes. In short, for a paradox to occur it is necessary that at least two payoff values change at the same time. The pairs of payoffs that at least need to change and the direction of change are indicated in Table .2. More than two changes also result in paradoxes, but these cannot be interpreted in such a straightforward way as our examples. As we determined α_T in equation (2) in a general way, this could help us to derive other paradoxes. Furthermore, we have listed paradoxical results in Appendix I for the non-trivial cases of parameter changes in Table .2.

4. Evolution of positive assortment

It has been demonstrated that when individuals are able to select their interaction partners, this increases cooperation in the population (partner selection: Yamagishi et al, 1994; Yamagishi and Hayashi, 1996; or exit: Schuessler, 1989; Vanberg and Congleton, 1992). Furthermore, when cooperation cannot evolve in networks with high connectivity, an additional mechanism of topological co-evolution ensures the survival of cooperation (Santos et al, 2006).

Some studies have also highlighted that humans have a cognitive capacity to guess accurately who are cheaters or defectors (Yamagishi et al, 2003). This trait might have evolved as a result of remembering cheater characteristics (Cosmides, 1989; Cosmides and Tooby, 1992) or just as a result of remembering characteristics (either cheaters or cooperators) that are less frequently found in the population (Barclay, 2008).

A possible extension of our model could be to let the positive assortment parameter α evolve endogenously. This is equivalent to introducing an evolvable trait that enables individuals to recognize and select their interaction partners with a certain degree of accuracy. As Wilson and Dugatkin (1997) notes, it is likely that the cognitive prerequisites for assortative interactions are often satisfied. If defectors are able to recognize the type of others, it is reasonable to assume that they do not choose an interaction partner of their own type (cf. Bergstrom, 2003). They would rather choose cooperators; because this provides them with higher payoffs. In this model extension α denotes the positive assortment of cooperators and β denotes the negative assortment of defectors. We assume that a certain individual is randomly selected and based on the α (β) parameter of

this individual, an interaction partner is chosen. The interaction partner is forced to play, thus his or her α (β) parameter does not influence whether the interaction takes place or not.

The average fitness of cooperators and of defectors can be expressed as:

$$w_C = z \frac{[\alpha + (1 - \alpha)z]2R + (1 - \alpha)(1 - z)S}{z} + (1 - z) \frac{[\beta + (1 - \beta)z]S}{z}$$

$$w_D = z \frac{(1 - \alpha)(1 - z)T}{1 - z} + (1 - z) \frac{[\beta + (1 - \beta)z]T + (1 - \beta)(1 - z)2P}{1 - z}$$

Unsurprisingly, evolution selects for $\alpha = 1$ ($\frac{\partial w_C}{\partial \alpha} > 0$). The ESS value of β depends on T and P ($\frac{\partial w_D}{\partial \beta} = (1 - z)(T - 2P)$). If $T > 2P$, evolution selects for $\beta = 1$ (defectors prefer exploiting cooperators by selecting them). If $T < 2P$, evolution selects for $\beta = 0$ (defectors prefer interacting with themselves by selecting randomly). In the latter case, however, $w_C > w_D$ for every z , so $z^* = 1$ is the evolutionary stable equilibrium. In the former case ($T > 2P$, $\beta = 1$), there are more subcases:

- if $S = 0$
 - if $2R > T$, then $z^* = 1$
 - if $2R < T$, then $z^* = 0$
 - if $2R = T$, then z^* does not exist
- if $S > 0$
 - if $2R \geq T$, then $z^* = 1$
 - if $2R < T$, then $z^* = \frac{S}{T+S-2R}$

If $S > 0$ and $T > 2R$, then $z^* = \frac{S}{T+S-2R}$. If we increase T and R simultaneously, and $\Delta R < \Delta T < 2\Delta R$, then the ratio of cooperators increases, which is a paradox.

5. Discussion

This study has demonstrated that raising the rewards of cooperation might play against the success of cooperative behavior in populations where

cooperators are more likely to meet other cooperators than by chance. We found this new and counter-intuitive result for all social dilemmas: in the Prisoner's Dilemma, in the Hawks and Doves game as well as in the Stag Hunt game.

It is important to note, however, that there is no paradox if only one payoff parameter is modified. Increasing purely the rewards for mutual cooperation (R), for instance, always provides improved conditions for cooperation. To obtain a paradoxical result, it is necessary that at least two payoff parameters are changed. We have shown, for instance, the case when both the temptation reward (T) and the reward for mutual cooperation (R) have been increased in the Prisoner's Dilemma with positive assortment such that $\Delta T \gg \Delta R$. This is a situation that is favorable for defectors. We have demonstrated, however, that in this case, there is always a non-zero range of positive assortment; when the equilibrium proportion of cooperators increases.

Furthermore, the paradox only occurs at a certain range of positive assortment. This means that at certain probabilities, which describe how much more likely two cooperators meet each other, rewards of cooperation backfire and increase the proportion of defectors in the population. Similarly, it applies only to a limited range of positive assortment that payoffs that favor defection backfire and increase the proportion of cooperators. Typically, when cooperators too often or too rarely meet each other, then increasing the rewards of cooperation will not diminish their chances of survival. In this paper, we have shown the exact conditions when the increase of rewards of cooperation and when the increase of rewards of defection contributes to a paradoxical change in the equilibrium proportion of cooperators and defectors in the Prisoner's Dilemma, in the Hawks and Doves game, and in the Stag Hunt game.

We have also clarified why the paradox occurs. A mixed proportion of cooperators and defectors is evolutionary stable in a certain range of positive assortment in all social dilemmas. The boundary conditions of mixed equilibrium unequivocally determine the equilibrium proportion of cooperators within the boundaries. The boundary conditions, however, are not affected by all payoff values. The lower bound is independent of the temptation reward (T) and the upper bound is independent of the sucker's reward (S). This implies that a change of T or S and another parameter will leave place for paradoxical results. Furthermore, paradoxes can also occur when both boundaries change (P and R are modified).

The paradox we found in this paper is very counter-intuitive in the light of previous theoretical results on the evolution of cooperation. Hamilton's rule (1964) asserts that altruists will spread in a population if $ab - c > 0$. This means that if the benefits of cooperation increase, it always benefits altruists (cooperators) and results in their dissemination (see Appendix II). In this paper, we found justification for this result and found no paradoxes in a special case of payoff structure that has restrictions on payoffs using a single benefit and cost parameter (see e.g. Doebeli and Hauert, 2005: Table 1). We highlighted that the counter-intuitive cases have been overlooked previously due to the simplified representation of social dilemma games. On the contrary, we determined the conditions of paradoxical situations in which increased cooperation benefits result in a lower share of cooperators using the four payoff parameters (T , R , P , S) of the more general description of social dilemmas (see e.g. Axelrod, 1984). Our result might seem narrow, because paradoxes only occur for a certain parameter range, but they provide a general warning for research on the evolution of cooperation that parameter restrictions in social dilemmas can result in a loss of important insights.

The fact that in most empirical social dilemma situations, we find cooperators and defectors co-existing, underline the relevance of these results. In empirical cases, matching is not random, but is biased towards meeting the same types (see e.g. Ohtsuki et al, 2006). This might be voluntary (homophily) or unconscious, as it is the case in spatially structured populations. This paper has highlighted paradoxical effects of cooperation benefits concerning these empirically highly relevant situations. As empirical situations are always more complex than simple models, it is difficult to justify that these paradoxical effects frequently occur in nature. Although there might be other explanations, there are some documented cases that at least partially in line with our theoretical findings. Human societies vary in their level of assortativity, but interactions rarely occur randomly. In some societies people rely less on market exchange than in others (i.e., there is a lower degree of market integration), which is presumably linked to assortativity. Experiments find more cooperation in societies with higher degree of market integration (Henrich et al, 2001; 2004). In Ultimatum Game experiments conducted in societies with a moderate degree of market integration, larger stakes caused no or only minor changes in behavior (Fehr and Tougareva, 1995; Slonim and Roth, 1998; Cameron, 1999; Fehr and Schmidt, 2005).

In the classical Prisoner's Dilemma experiments of Rapoport and Chammah (1965), consistent with later findings (cf. Ledyard, 1995), modifying single payoff parameters produced the expected changes in cooperation rates. In some cases, where there are more than one payoff difference between the two games compared, however, unexpected differences occur in cooperation rates. For instance, the comparison of Games II ($T = 10, R = 1, P = -9, S = -10$) and IV ($T = 2, R = 1, P = -1, S = -2$) reveal that modifying P in favor of defection and two other parameters (T, S) in favor of cooperation equally within the same experiment does not cause higher, but lower cooperation rates (Game II: 77%, Game IV: 66%). A similar paradox with three payoff differences occur for the comparison of Games I ($T = 10, R = 9, P = -1, S = -10$) and IV (Game I: 73%; Rapoport and Chammah, 1965: 37).

Our results imply that interventions that invest less in cooperation benefits lead to a larger proportion of cooperators if interactions take place at a certain level of positive assortment, but also imply that environmental systems that reward cooperators to a lesser extent can sustain more cooperation, if cooperators meet each other more often than pure chance would dictate.

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Appendix I

In this appendix, we will look at cases in Table .2 (Prisoner's Dilemma with positive assortment and $\alpha_L < \alpha_H$) marked with asterisk. For all pairs of parameters there are two mirrored cases, so we only need to analyze one of them. In all the cases below we refer to α_T , which is defined in equation (2).

Increasing T and R

- if $(1 <) \frac{T-P}{R-P} < \frac{\Delta T}{\Delta R}$

then $\Delta\alpha_L < 0$ and $\Delta\alpha_H > 0$: paradox for $\alpha < \alpha_T$, where beneficial for C (vs $\Delta T > \Delta R$). See Figure .8 for this case. $\frac{T-P}{R-P} < \frac{\Delta T}{\Delta R}$ can be deduced from $\alpha'_H > \alpha_H$ that is $\frac{T+\Delta T-R-\Delta R}{T+\Delta T-P} > \frac{T-R}{T-P}$. Other results in the Appendix are obtained in a similar way.

- if $1 < \frac{\Delta T}{\Delta R} < \frac{T-P}{R-P}$
then $\Delta\alpha_L < 0$ and $\Delta\alpha_H < 0$: paradox for every α , because it is beneficial for C (vs $\Delta T > \Delta R$)
- if $\frac{\Delta T}{\Delta R} < 1$
then $\Delta\alpha_L < 0$ and $\Delta\alpha_H < 0$: normal for every α

Increasing T and decreasing P

- if $1 < \frac{T-R}{R-P}$:
 - if $\frac{T-R}{R-P} < \frac{\Delta T}{|\Delta P|}$
then $\Delta\alpha_L < 0$ and $\Delta\alpha_H > 0$: paradox for $\alpha < \alpha_T$, where beneficial for C (vs $\Delta T > |\Delta P|$)
 - if $1 < \frac{\Delta T}{|\Delta P|} < \frac{T-R}{R-P}$
then $\Delta\alpha_L < 0$ and $\Delta\alpha_H < 0$: paradox for every α , because it is beneficial for C (vs $\Delta T > |\Delta P|$)
 - if $\frac{\Delta T}{|\Delta P|} < 1$
then $\Delta\alpha_L < 0$ and $\Delta\alpha_H < 0$: normal for every α
- if $\frac{T-R}{R-P} < 1$:
 - if $1 < \frac{\Delta T}{|\Delta P|}$
then $\Delta\alpha_L < 0$ and $\Delta\alpha_H > 0$: paradox for $\alpha < \alpha_T$, where beneficial for C (vs $\Delta T > |\Delta P|$)
 - if $\frac{T-R}{R-P} < \frac{\Delta T}{|\Delta P|} < 1$
then $\Delta\alpha_L < 0$ and $\Delta\alpha_H > 0$: paradox for $\alpha > \alpha_T$, where beneficial for D (vs $\Delta T < |\Delta P|$)
 - if $\frac{\Delta T}{|\Delta P|} < \frac{T-R}{R-P}$
then $\Delta\alpha_L < 0$ and $\Delta\alpha_H < 0$: normal for every α

Increasing T and S

- if $\Delta T > \Delta S$
 $\Delta\alpha_L < 0$ and $\Delta\alpha_H > 0$: paradox for $\alpha < \alpha_T$, where beneficial for C
 (vs $\Delta T > \Delta S$)
- if $\Delta T < \Delta S$
 $\Delta\alpha_L < 0$ and $\Delta\alpha_H > 0$: paradox for $\alpha > \alpha_T$, where beneficial for D
 (vs $\Delta T < \Delta S$)

Increasing R and P

- if $\frac{\Delta P}{\Delta R} < \frac{P-S}{R-S} (< 1)$
 then $\Delta\alpha_L < 0$ and $\Delta\alpha_H < 0$: normal for every α
- if $\frac{P-S}{R-S} < \frac{\Delta P}{\Delta R} < 1$
 then $\Delta\alpha_L > 0$ and $\Delta\alpha_H < 0$: paradox for $\alpha < \alpha_T$, where beneficial for D (vs $\Delta P < \Delta R$)
- if $1 < \frac{\Delta P}{\Delta R} < \frac{T-P}{T-R}$
 then $\Delta\alpha_L > 0$ and $\Delta\alpha_H < 0$: paradox for $\alpha > \alpha_T$, where beneficial for C (vs $\Delta P > \Delta R$)
- if $(1 <) \frac{T-P}{T-R} < \frac{\Delta P}{\Delta R}$
 then $\Delta\alpha_L > 0$ and $\Delta\alpha_H > 0$: normal for every α

Increasing R and decreasing S

- if $1 < \frac{P-S}{R-P}$:
 - if $\frac{P-S}{R-P} < \frac{|\Delta S|}{\Delta R}$
 then $\Delta\alpha_L > 0$ and $\Delta\alpha_H < 0$: paradox for $\alpha > \alpha_T$, where beneficial for C (vs $|\Delta S| > \Delta R$)
 - if $1 < \frac{|\Delta S|}{\Delta R} < \frac{P-S}{R-P}$
 then $\Delta\alpha_L < 0$ and $\Delta\alpha_H < 0$: paradox for every α , because it is beneficial for C (vs $|\Delta S| > \Delta R$)
 - if $\frac{|\Delta S|}{\Delta R} < 1$
 then $\Delta\alpha_L < 0$ and $\Delta\alpha_H < 0$: normal for every α

- if $\frac{P-S}{R-P} < 1$:
 - if $1 < \frac{|\Delta S|}{\Delta R}$
 then $\Delta\alpha_L > 0$ and $\Delta\alpha_H < 0$: paradox for $\alpha > \alpha_T$, because it is beneficial for C (vs $|\Delta S| > \Delta R$)
 - if $\frac{P-S}{R-P} < \frac{|\Delta S|}{\Delta R} < 1$
 then $\Delta\alpha_L > 0$ and $\Delta\alpha_H < 0$: paradox for $\alpha < \alpha_T$, where beneficial for D (vs $|\Delta S| < \Delta R$)
 - if $\frac{|\Delta S|}{\Delta R} < \frac{P-S}{R-P}$
 then $\Delta\alpha_L < 0$ and $\Delta\alpha_H < 0$: normal for every α

Increasing P and S

- if $(1 <) \frac{R-S}{R-P} < \frac{\Delta S}{\Delta P}$
 then $\Delta\alpha_L < 0$ and $\Delta\alpha_H > 0$: paradox for $\alpha > \alpha_T$, where beneficial for D (vs $\Delta S > \Delta P$)
- if $1 < \frac{\Delta S}{\Delta P} < \frac{R-S}{R-P}$
 then $\Delta\alpha_L > 0$ and $\Delta\alpha_H > 0$: paradox for every α , because it is beneficial for D (vs $\Delta S > \Delta P$)
- if $\frac{\Delta S}{\Delta P} < 1$
 then $\Delta\alpha_L > 0$ and $\Delta\alpha_H > 0$: normal for every α

Appendix II

Consider the special case where $T = b$, $R = b - c$, $P = 0$, and $S = -c$, hence $T - R = P - S = c$. In this special case, we have fewer parameters (b , c) and these parameters can simply be interpreted as benefits and costs. In this case, $z = 0$ is evolutionary stable if $\alpha b - c < 0$, $z = 1$ is evolutionary stable if $\alpha b - c > 0$, and there is no mixed equilibrium. Hence, we have obtained a re-derivation of Hamilton's rule for this special case with positive assortment (a similar re-derivation is given in Hamilton, 1971; 1975; Bergstrom, 2003). Furthermore, there are no paradoxical cases as the increase of c is always beneficial for defection and the increase of b is always

beneficial for cooperation. The simultaneous increase of c and b (if $\Delta c > \Delta b$) also benefits defection.⁵

In short, the fundamental reason why Hamilton's rule leaves no space for paradoxes lies in the simplification of the social dilemma with a single cost (c) and benefit (b) parameter with the restriction of $T - R = P - S = c$. The simplified Prisoner's Dilemma game nicely applies to symmetric decisions of altruistic help, where altruists suffer costs, but the benefits of their altruistic act are only enjoyed by their interaction partner (e.g. Doebeli and Hauert, 2005; Ohtsuki et al, 2006). This is however, only a special case of the Prisoner's Dilemma game. If the payoffs of the Prisoner's Dilemma are expressed as independent parameters with their ordinal ranking fixed (see e.g. Axelrod, 1984), then we obtain the paradoxical results in which the increase in cooperation benefits can result in fewer cooperators.

⁵A paradoxical case ($\Delta c > \Delta b$ and increasing $\alpha b - c$) might occur when $b < c$, but it implies that $R < P$, which cannot hold in a social dilemma game.

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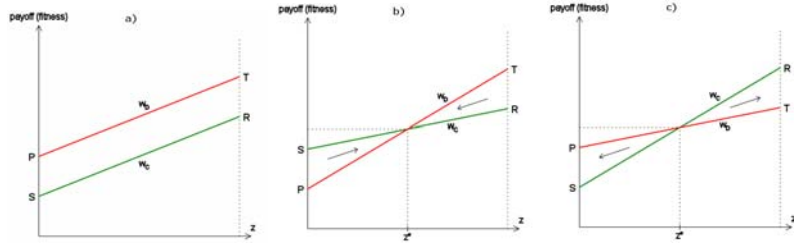


Figure .1: ESS in Social Dilemmas with Complete Mixing. a) There is no mixed equilibrium in the Prisoner's Dilemma. The only ESS is defection. b) The only ESS in the Hawks and Doves game is a mixed equilibrium. c) The mixed equilibrium is not an ESS in the Stag Hunt game. $z^* = \frac{P - \alpha R - (1 - \alpha)S}{(1 - \alpha)(R + P - S - T)}$. For the meaning of α see section 2.1.

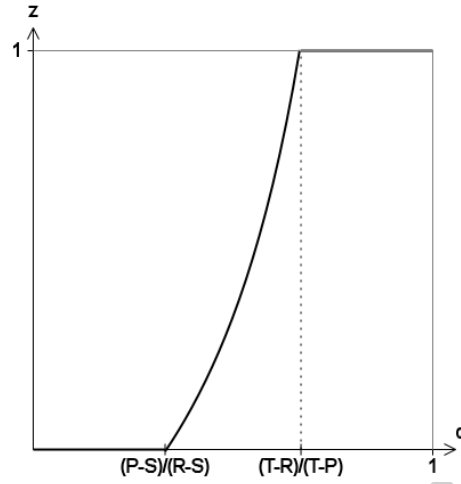


Figure .2: Evolutionary stable values of z as a function of α in Prisoner's Dilemma with positive assortment if $\frac{P-S}{R-S} < \frac{T-R}{T-P}$.

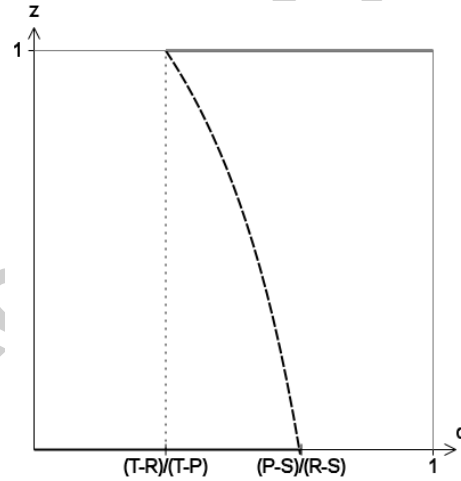


Figure .3: $z(\alpha)$ in Prisoner's Dilemma with positive assortment if $\frac{P-S}{R-S} > \frac{T-R}{T-P}$. The solid lines indicate the stable equilibria of full cooperation and full defection. The dashed line indicates the unstable mixed equilibrium z^* .

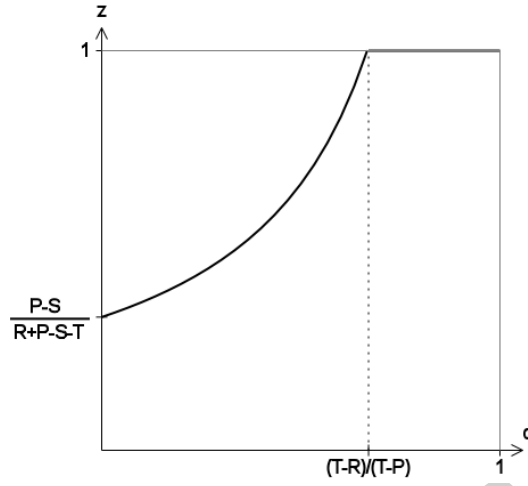


Figure .4: Evolutionary stable values of z as a function of α in the Hawks and Doves game with positive assortment.

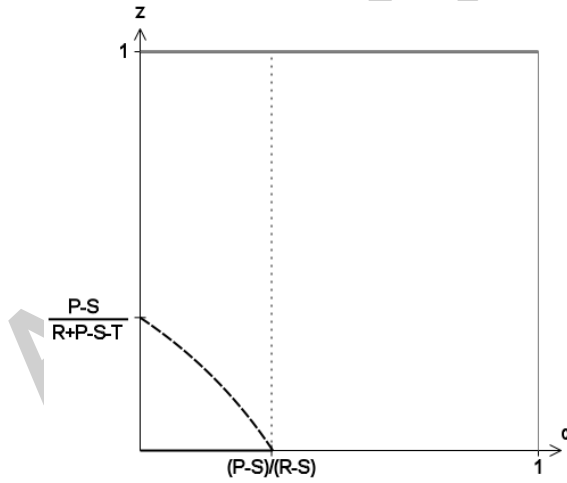


Figure .5: $z(\alpha)$ in Stag Hunt with positive assortment. The solid lines indicate the stable equilibria of full cooperation and full defection. The dashed line indicates the unstable mixed equilibrium z^* .

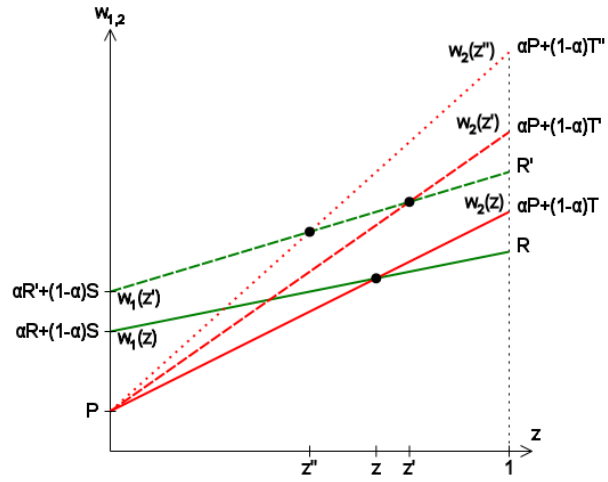


Figure .6: Mixed equilibria (ESS) in the Prisoner's Dilemma with positive assortment when R and T are increased. The solid lines indicate the original fitness functions. Dashed and dotted lines indicate the new fitness functions. $w_1(z)$ in green and $w_2(z)$ in red. z'' is the normal, z' is the paradoxical case.

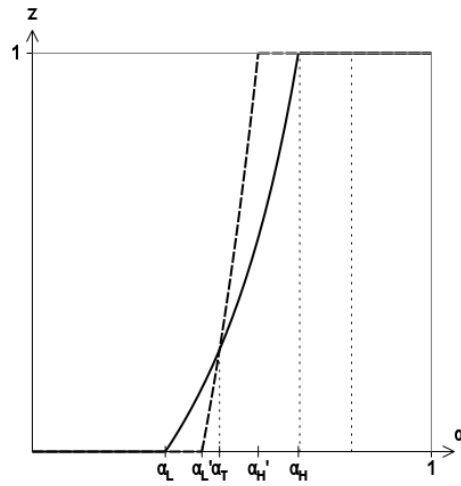


Figure 7: The paradox of cooperation benefits in the Prisoner's Dilemma with positive assortment and $\alpha_L < \alpha_H$. The solid line is the original $z(\alpha)$ function. The dashed line shows the case when P and R are increased. Parameter values for this figure are: $T = 7$, $R = 3$, $P = 1$, $S = 0$, $\Delta R = 1$, and $\Delta P = 0.7$ ($\Delta R > \Delta P$).

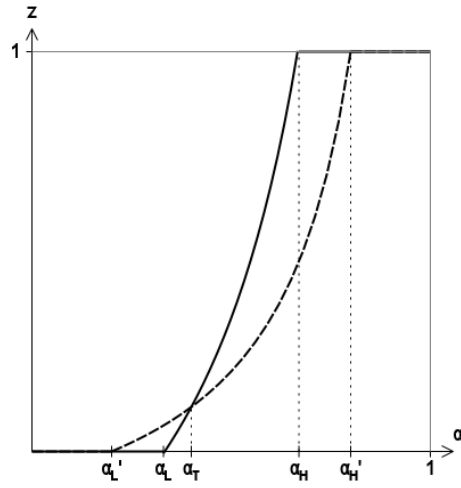


Figure .8: The paradox of cooperation benefits in the Prisoner's Dilemma with positive assortment and $\alpha_L < \alpha_H$. The solid line is the original $z(\alpha)$ function. The dashed line shows the case when R and T are increased. Parameter values for this figure are: $T = 7$, $R = 3$, $P = 1$, $S = 0$, $\Delta T = 14$, and $\Delta R = 2$ ($\Delta T \gg \Delta R$).

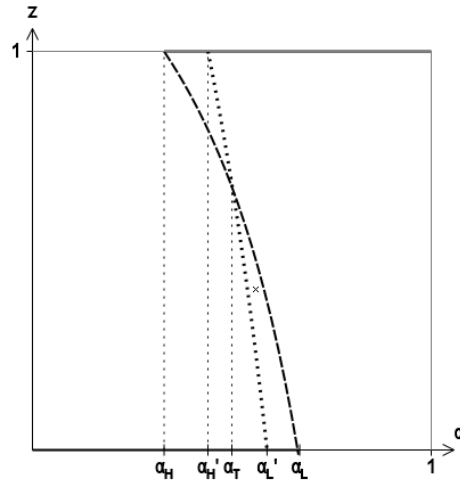


Figure .9: The paradox of cooperation benefits in the Prisoner's Dilemma with positive assortment and $\alpha_L > \alpha_H$ and $\alpha'_L > \alpha'_H$. The solid lines indicate the original stable equilibria of full cooperation and full defection. The dashed line indicates the unstable mixed equilibrium z^* . The dotted line shows the case when R and T are increased (the mixed equilibrium is still unstable). Parameter values for this figure are: $T = 1.75$, $R = 1.5$, $P = 1$, $S = 0$, $\Delta T = 0.5$, and $\Delta R = 0.2$ ($\Delta T > \Delta R$). The x indicates a random initial ratio which evolves to full defection with the original parameters, and to full cooperation with the modified ones.

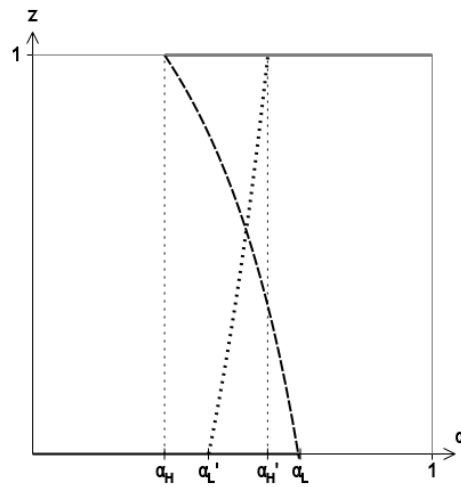


Figure .10: The paradox of cooperation benefits in the Prisoner's Dilemma with positive assortment and $\alpha_L > \alpha_H$ and $\alpha'_L < \alpha'_H$. The solid lines indicate the original stable equilibria of full cooperation and full defection. The dashed line indicates the unstable mixed equilibrium z^* . The dotted line shows the case when R and T are increased (the mixed equilibrium becomes stable). Parameter values for this figure are: $T = 1.75$, $R = 1.5$, $P = 1$, $S = 0$, $\Delta T = 2.34$, and $\Delta R = 0.77$ ($\Delta T > \Delta R$).

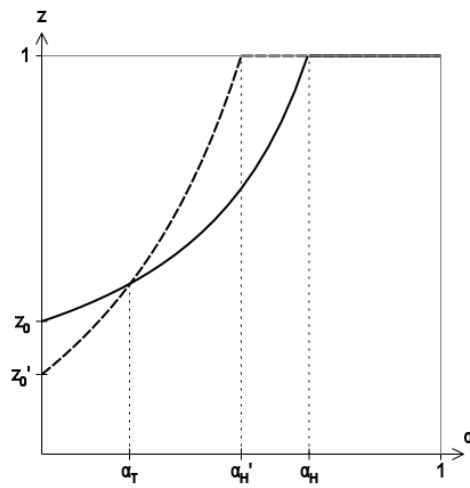


Figure .11: The paradox of cooperation benefits in the Hawks and Doves game with positive assortment. The solid line is the original $z(\alpha)$ function. The dashed line shows the case when R and T are increased. Parameter values for this figure are: $T = 3$, $R = 1$, $P = 0$, $S = 1$, $\Delta T = 5$, and $\Delta R = 3$ ($\Delta T > \Delta R$).

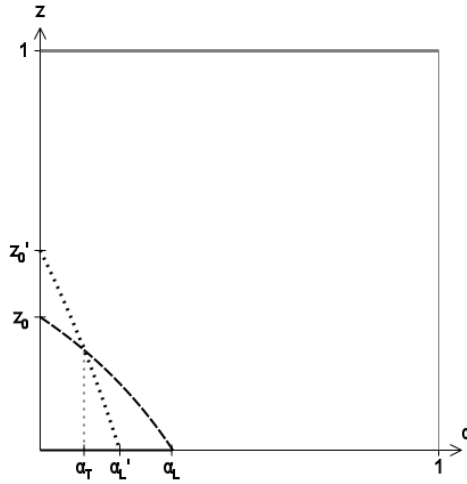


Figure .12: The paradox of cooperation benefits in the Stag Hunt game with positive assortment. The solid lines indicate the original stable equilibria of full cooperation and full defection. The dashed line indicates the unstable mixed equilibrium z^* . The dotted line shows the case when R and T are increased. Parameter values for this figure are: $T = 1$, $R = 3$, $P = 1$, $S = 0$, $\Delta T = 3$, and $\Delta R = 2$ ($\Delta T > \Delta R$).

	C	D
C	R,R	S,T
D	T,S	P,P

Table .1: Payoffs in Social Dilemma Games. $T > R > P > S$ in the Prisoner's Dilemma, $T > R > S > P$ in the Hawks and Doves game, and $R > T > P > S$ in the Stag Hunt game.

parameters	α_L	α_H	paradox
T \uparrow R \uparrow	\downarrow (C)	?	*
T \uparrow R \downarrow	\uparrow (D)	\uparrow (D)	
T \downarrow R \uparrow	\downarrow (C)	\downarrow (C)	
T \downarrow R \downarrow	\uparrow (D)	?	*
T \uparrow P \uparrow	\uparrow (D)	\uparrow (D)	
T \uparrow P \downarrow	\downarrow (C)	?	*
T \downarrow P \uparrow	\uparrow (D)	?	*
T \downarrow P \downarrow	\downarrow (C)	\downarrow (C)	
T \uparrow S \uparrow	\downarrow (C)	\uparrow (D)	**
T \uparrow S \downarrow	\uparrow (D)	\uparrow (D)	
T \downarrow S \uparrow	\downarrow (C)	\downarrow (C)	
T \downarrow S \downarrow	\uparrow (D)	\downarrow (C)	**
R \uparrow P \uparrow	?	?	*
R \uparrow P \downarrow	\downarrow (C)	\downarrow (C)	
R \downarrow P \uparrow	\uparrow (D)	\uparrow (D)	
R \downarrow P \downarrow	?	?	*
R \uparrow S \uparrow	\downarrow (C)	\downarrow (C)	
R \uparrow S \downarrow	?	\downarrow (C)	*
R \downarrow S \uparrow	?	\uparrow (D)	*
R \downarrow S \downarrow	\uparrow (D)	\uparrow (D)	
P \uparrow S \uparrow	?	\uparrow (D)	*
P \uparrow S \downarrow	\uparrow (D)	\uparrow (D)	
P \downarrow S \uparrow	\downarrow (C)	\downarrow (C)	
P \downarrow S \downarrow	?	\downarrow (C)	*

Table .2: Effects of changing two parameters. \uparrow/\downarrow increase/decrease, C/D beneficial for cooperators/defectors, ? ambiguous (depends on the exact values of these and other parameters). * denotes cases, when there might be a paradox in certain ranges of the payoff parameters (and their changes), and ** denotes cases, when there is a paradox for certain α values for all ranges of the payoff parameters.