Preventing the tragedy of the commons through punishment of over-consumers and encouragement of under-consumers

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Abstract

The conditions that can lead to the exploitative depletion of a shared resource, i.e., the tragedy of the commons, can be reformulated as a game of prisoner’s dilemma: while preserving the common resource is in the best interest of the group, over-consumption is in the interest of each particular individual at any given point in time. One way to try and prevent the tragedy of the commons is through infliction of punishment for over-consumption and/or encouraging under-consumption, thus selecting against over-consumers. Here, the effectiveness of various punishment functions in an evolving consumer-resource system is evaluated within a framework of a parametrically heterogeneous system of ordinary differential equations (ODEs). Conditions leading to the possibility of sustainable coexistence with the common resource for a subset of cases are identified analytically using adaptive dynamics; the effects of punishment on heterogeneous populations with different initial composition are evaluated using the Reduction theorem for replicator equations. Obtained results suggest that one cannot prevent the tragedy of the commons through rewarding of under-consumers alone - there must also be an implementation of some degree of punishment that increases in a non-linear fashion with respect to over-consumption and which may vary depending on the initial distribution of clones in the population.

Keywords: tragedy of the commons, mathematical model, Reduction theorem, adaptive dynamics
Introduction

Ecological and social systems are complex and adaptive, composed of diverse agents that are interconnected and interdependent [12, 15, 16]. Heterogeneity within these systems often drives the evolution and adaptability of the system components enabling them to withstand and recover from environmental perturbations. However, it is also heterogeneity that makes the appearance and short-term prosperity of over-consumers possible, which in turn can eventually lead to exhaustion of the common resources (tragedy of the commons [4]) and consequent collapse of the entire population, also known as evolutionary suicide [6]).

Elinor Ostrom has focused on the question of avoiding the tragedy of the commons from the point of view of collective decision making in small fisheries [14]. She observed that the mutually satisfactory and functioning institution of collective action could be developed in small communities where the possible resource over-consumption by each individual was immediately noticeable and punished, such as in water-monitoring systems instituted in Spanish huertas, where each user was able to closely watch the other, and where punishment for stealing scarce water was instituted not only in monetary fines but also in public humiliation. This illustrates a first path to prevent the tragedy of the commons: infliction of punishment/tax for over-consumption, effectively selecting against over-consumers. For instance, Ostrom cites as an example of a successful adaptive governance system rural villages in Japan, where about 3 million hectares of forests and mountain meadows were successfully managed even until now in no small part because “accounts were kept about who contributed to what to make sure no household evaded its responsibilities unnoticed. Only illness, family tragedy, or the absence of able-bodied adults ... were recognized as excuses for getting out of collective labor... But if there was no acceptable excuse, punishment was in order”. Another situation, when the tragedy was successfully avoided, is when the community introduces some kind of “social currency”, where an individual is rewarded for cooperation with social status [11, 18]. This is an example of a second approach to preventing the tragedy of the commons: bestowing reward/subsidy to under-consumers.

The dynamics of trade-offs between personal and population good have been studied through classical game theory [13, 17, 5]. However, many of the potentially relevant results have been obtained for largely homogeneous populations of players. In this paper we approach the question of preventing the tragedy of the commons through instituting punishment/reward systems in heterogeneous populations using two
recently developed methods for studying evolving heterogeneous populations in equation-based models, namely adaptive dynamics [1] and the Reduction theorem for replicator equations [7, 8].

This paper is organized as follows: first we give a derivation of a previously studied model, modified to incorporate the effects of a punishment/reward system on overall population survival. Next, we describe different approaches for studying the effects of punishment and reward on population composition, namely, adaptive dynamics and the Reduction theorem for replicator equations. Then we apply the two techniques to a variety of punishment/reward structures, obtaining both analytical and numerical results for sample populations that differ in their initial composition with respect to over- and under-consumers. We end the paper with a reformulation of the obtained results in the context of the prisoner’s dilemma, as well as with a comparison of the two modeling methods.

Model Description

In order to answer the questions posed in the introduction, we first turn to a modified version of a mathematical model of ‘niche construction’ proposed by Krakauer et al.[10], where a population of consumers \( x(t) \) interact with a collectively constructed ‘niche’, represented as a common dynamical carrying capacity \( z(t) \). Rather than restricting the model to a specific physical resource, we take the ‘niche’ to be a generalized abstract ‘resource’, such as available nutrients, energy and other characteristics of the environment that may affect both the individuals’ survival and fecundity (in case of financial systems, the ‘resource’ could be an inter-convertible unit such as money) that each individual can invest or subtract from the ‘common good’. Different individuals can contribute to the common dynamical carrying capacity, or they can subtract from it at different rates. Since sufficient reduction of the common ‘carrying capacity’ can indeed lead to population collapse, this model allows to model effectively in a conceptual framework the question of the effects of over-consumption on the survival of the population.

Within the frameworks of the model, each individual is characterized by his or her own intrinsic value of resource consumption, denoted by parameter \( c \); a set of consumers that are characterized by the same value of \( c \) is referred to as \( c \)-clone. The total population of all consumers is \( N(t) = \sum_k x_c \) if \( c \) takes on discrete values and \( N(t) = \int_A x_c dc \) if \( c \) is continuous, where \( A \) denotes the range of possible values of parameter \( c \).

The individuals \( x_c(t) \) grow according to a logistic growth function, where the carrying capacity is not
constant but is a dynamic variable. Each individual invests in resource restoration at a rate proportional to \((1 - c)\); an individual is considered to be an over-consumer if \(c > 1\). Moreover, each individual is punished or rewarded according to a general continuous function \(f(c) \in C^1(\mathbb{R}^+)\) that directly affects the fitness of each consumer-producer such that each clone is immediately punished for over-consumption if \(c > 1\) or rewarded for under-consumption when \(c < 1\).

The dynamics of the resource is determined by a natural restoration rate \(\gamma\) and decay/loss rate \(\delta z(t)\). Restoration process is accounted for by the term \(e(1 - c)\frac{N}{z(t) + N(t)}\), where \(z(t)\) is restored both proportionally to each individual’s investment, accounted for by parameter \(c\), and to the total amount of ‘resource’ consumed by the entire population, represented by \(N(t)/z(t)\).

This yields the following system of equations:

\[
x'_c(t) = r x_c(t) \left( c - \frac{N(t)}{kz(t)} \right) + x_c(t)f(c), \quad (1)
\]

\[
z'(t) = \gamma + \frac{e \sum_A x_c(t)(1 - c)}{z(t) + N(t)} - \delta z(t), \quad (2)
\]

The meaning of all the variables and parameters summarized in Table 1.

| Variable | Meaning | Range |
|---------|---------|-------|
| \(z(t)\) | abstract generalized ‘resource’ | \(z \geq 0\) |
| \(c\) | rate of resource consumption | \(c \in [c_0, c_f]\) |
| \(x_c(t)\) | population of individuals competing for the resource | \(x_c \geq 0\) |
| \(N(t)\) | total population size \(N(t) = \int_A x_c(t)dc\) | \(N(t) \geq 0\) |
| \(r\) | individual proliferation rate | \(r \geq 0\) |
| \(k\) | ‘resource’ conversion factor | \(k \geq 0\) |
| \(e\) | efficiency of construction of common ‘niche’ | \(e \geq 0\) |
| \(\gamma\) | intrinsic rate of ‘resource’ restoration independent of \(x_c\) | \(\gamma \geq 0\) |
| \(\delta\) | per capita rate of natural ‘resource’ decay | \(\delta \geq 0\) |
| \(c_0\) | lower boundary value of parameter \(c\) | \(c_0 \geq 0\) |
| \(c_f\) | upper boundary value of parameter \(c\) | \(c_f \geq 0\) |

Table 1: Summary of variables and parameters used in System 1.
The case, where \( f(c) = 0 \) was previously completely studied in [9], both for the case of a parametrically homogeneous and parametrically heterogeneous system with respect to parameter \( c \). Several transitional regimes were identified with increasing parameter \( c \), ranging from sustainable coexistence with the common resource with ever decreasing domain of attraction to sustained oscillatory regimes to collapse due to exhaustion of the common resource. The results are summarized in Figure 1. In Domain 1, when the parameter of resource consumption is small, the common carrying capacity remains large, successfully supporting the entire population, since no individual is taking more resource than they restore. In Domain 2, a parabolic sector appears near the origin, decreasing the domain of attraction of the non-trivial equilibrium point \( A \). The population can still sustainably coexist with the resource even with moderate levels of over-consumption but the range of initial conditions, where it is possible, decreases. As the value of \( c \) is further increased, the range of possible parameter values that allow sustainable coexistence with the common resource decreases and is now bounded by the unstable limit cycle, which appears around point \( A \) through a catastrophic Hopf bifurcation in Domain 3, and via generalized Hopf bifurcation in Domain 6. Finally, in Domain 4 and 5, population extinction is inevitable due to extremely high over-consumption rates unsupportable by the resource.

In this paper we will investigate the question of whether timely infliction of punishment for over-consumption or rewarding under-consumption can prevent such a collapse and consequently prevent the tragedy of the commons. We will also investigate the degree of effectiveness of punishment depending on initial composition of the population with respect to parameter \( c \). Finally, we will try to investigate the question of whether punishing those who over-consume or rewarding those who under-consume will yield better results. These questions will be addressed using two recently developed methods for modeling parametrically heterogeneous populations, namely, adaptive dynamics [1] and Reduction theorem for replicator equations [7, 8].
Figure 1: Bifurcation diagram of System 1 when \( f(c) = 0 \) in the \((\gamma, c)\) and \((N, z)\) phase spaces for fixed positive parameters \( e \) and \( \delta \). The non-trivial equilibrium point \( A \) is globally stable in Domain 1; it shares basins of attraction with equilibrium \( O \) in Domains 2 and 3. The separatrix of \( O \) and the unstable limit cycle that contains point \( A \), serve, correspondingly, as the boundaries of the basins of attraction. Only equilibrium \( O \) is globally stable in Domains 4, which also contains also unstable non-trivial \( A \), and 5, which contains the elliptic sector. Domain 6 exists only for \( \delta > 5 + \sqrt{24} \), where the stable limit cycle that is in turn contained inside an unstable limit cycle, shares basins of attraction with equilibrium \( O \). Boundaries between Domains \( K, S, H, Nul, C \) correspond respectively to appearance of an attractive sector in a neighborhood of \( O \), appearance of unstable limit cycle containing \( A \), change of stability of equilibrium \( A \) via Hopf bifurcations, disappearance of positive \( A \) and saddle-node bifurcation of limit cycles.
Adaptive dynamics

Adaptive dynamics is a series of techniques that have been recently developed to address questions of system invasibility by rare ‘mutant’ clones. The main focus of this method is in evaluating a “mutant’s” ability to proliferate in an environment set by the ‘resident’ population [1]. We use this method to evaluate different punishment/reward functions and their efficiency in preventing the tragedy of the commons. It is worth noting that a more general theory of systems with inheritance, which allows studying the problem of ‘external stability’ of a population of ‘residents’ to invasion by a ‘mutant’ population, has been developed in [2]; it was later published in English in [3].

Consider the equation for the dynamics of a rare mutant $x_m$ in an environment set by the resident $x_{res}$. The total population size is $x_m + x_{res} \approx x_{res}$, since $x_m$ is assumed to be present at such low frequency that its contribution to the size of the entire population is negligible.

Let $x^*_{res}$ satisfy $\frac{dx_{res}}{dt} = 0$, which implies that $x^*_{res} = \frac{kz}{r}(f(c_{res}) + rc_{res})$. Now introduce a mutant, such that

$$\frac{dx_m}{dt} = rx_m(c_m - \frac{x_m + x_{res}}{kz(t)}) + x_m f(c_m).$$

(3)

When the two subpopulations interact, the outcome of their interaction is determined by the sign of the dominant eigenvalue of System

$$\frac{dx_{res}}{dt} = rx_{res}(c_{res} - \frac{x_m + x_{res}}{kz(t)}) + x_{res} f(c_{res}),$$

$$\frac{dx_m}{dt} = rx_m(c_m - \frac{x_m + x_{res}}{kz(t)}) + x_m f(c_m)$$

$$\frac{dz}{dt} = \gamma + \epsilon \frac{x_{res}(1 - c_{res}) + x_m(1 - c_m)}{z + x_m + x_{res}} - \delta z

(4)

The stability of the single positive non-trivial equilibrium point $(x^*_r, x^*_m, z^*)$ under the assumption that the mutant is rare, i.e., when $x^*_m \approx 0$, is determined by the dominant eigenvalue of System [4], which is given by $\lambda = r(c_m - c_{res}) - f(c_{res}) + f(c_m)$: the mutant will be able to invade if $\lambda > 0$ and it will not succeed if $\lambda < 0$. Invasion fitness of the mutant, i.e., the expected growth rate of a mutant in an environment set by the resident, is given by

$$\lim_{T \to \infty} \frac{1}{T} \int_0^T \left[ r(c_m - \frac{x_{res}(t)}{kz(t)}) + f(c_m) \right] dt = r(c_m - \frac{1}{k} \frac{x_{res}}{z}) + f(c_m) = r(c_m, E_{res}),$$

(5)
where \( \left( \frac{x_{res}}{z} \right) = \lim_{T \to \infty} \frac{1}{T} \int_0^T x_{res}(t) \frac{dt}{z(t)} \). The selection gradient, which is defined as the slope of invasogrammen fitness, determines if the invasion will be successful (positive sign of the selection gradient predicts successful invasion) and is then given by

\[
D(c_m) = \frac{\partial}{\partial c_m} r(c_m, E_{res})|_{c_m=c_{res}} = r + f'(c_m).
\] (6)

These conditions allow answering a question of “long-term” invasibility, i.e., whether a mutant with a slightly difference value of \( c_m \) will be able to permanently invade the population of individuals, characterized by parameter \( c_{res} \). The points where selection gradient is zero are known as evolutionarily singular strategies (ESS) and are denoted here as \( c_{res}^* \). Stability of \( c_{res}^* \) for different types of punishment/reward functions is discussed below; summary of some of the possible types of \( c_{res}^* \) is given in Table 3.

| Adaptive dynamics | Reduction theorem |
|-------------------|-------------------|
| **Goal** | Model evolution of parametrically heterogeneous populations |
| **Assumptions** | Clonal reproduction |
| | Separation of evolutionary and ecological time scales |
| **Environment** | Can be variable and affected by changes in population composition (also known as seascape, or a dancing landscape) |
| **Population** | Two types: invader and resident |
| | Small initial frequency of the invader |
| | Can introduce new “mutants” |
| | Requires “Lotka-Volterra” type growth rates \( (x' = xF(t)) \) |
| **Purpose/ question** | Invasion: can a mutant invade the resident population? |
| | Evolution of a parametrically heterogeneous system over time due to natural selection |
| **Visual representation** | Pairwise invasibility plot (PIP) |
| | Bifurcation diagram of the corresponding parametrically homogeneous system |

Table 3: A comparison of adaptive dynamics and the Reduction theorem

**Different types of punishment/reward functions**

**Case 1. Moderate punishment**

Consider the case, when the punishment function is of the form \( f(c) = \frac{a - c}{1 + c} \). This functional form allows to incorporate moderate levels of punishment/reward, the severity of which is determined by the value
of the parameter $a$.

The pairwise invasibility plot (PIP), which allows to visualize under what relative values of $c_m$ and $c_{res}$ the dominant eigenvalue $\lambda$ changes its sign, can be seen on Figure 2b,c, for $a = 1$ and $a = 4$. Blue regions correspond to the case when $\lambda(c_{res}, c_m) < 0$, and consequently the mutant cannot invade; red regions correspond to the case when $\lambda(c_{res}, c_m) > 0$, and the mutant can invade. The point of intersection of the two curves corresponds to a convergence stable (CSS) but evolutionarily unstable strategy, which can be invaded by “mutants” with large enough values of $c_m$.

The selection gradient for this punishment function, $D(c_m) = r - \frac{2a}{1+2c_m}$, so the mutant with $c_m \approx c_r$ can invade when $a < \frac{r}{2}(1 + c_m)^2$ (see Figure 2a).

![Figure 2: Selection gradient and pairwise invasibility plots (PIPs) for function of the type $f(c) = a\frac{1-c}{1+c}$. Blue regions correspond to parameter values where the mutant cannot invade; red regions correspond to parameter values where it can invade. (a) selection gradient, defined in Equation (6) (b) PIP for $a = 1$; the singular strategy $c_{res}^*$ is evolutionarily unstable and convergence stable (c) PIP for $a = 4$; the singular strategy $c_{res}^*$ is evolutionarily unstable and convergence stable. This punishment/reward function is not effective against aggressive over-consumers.](image)

These results suggest that modest punishment can therefore protect only from modest over-consumers. However, more aggressive over-consumers cannot be kept of out the population, as the punishment is not severe enough.

**Case 2. Severe punishment/generous reward**

Now consider a case, when the punishment function is of the form $f(c) = a(1 - c)^3$, which allows to impose much more severe punishment on over-consumers and more generous reward on under-consumers compared to the previous case.
The PIP for this functional form can be seen on Figure 3 for $a = 0.1$ and $a = 0.6$. Once again, blue regions correspond to the case when $\lambda(c_{res}, c_m) < 0$, and consequently the mutant cannot invade; red regions correspond to the case when $\lambda(c_{res}, c_m) > 0$, and the mutant can invade.

For this type of punishment/reward function, there is a region where invader can invade but unlike the previous case, there exists an upper boundary for the possible values of successful $c_m$. Unlike in the previous case, singular strategy is stable, which predictably implies that punishment needs to be severe enough in order to be able to prevent invasion by over consumers. Moreover, for large enough values of $a$, there can exist two singular strategies, one evolutionarily stable and one evolutionarily unstable. In this case, the more “altruistic” ESS, which corresponds to smaller values of $c_{res}^*$, is unstable, probably because in this case the reward for under-consumption is insufficiently large, and the punishment is not sufficiently severe. The second ESS, which corresponds to larger values of $c_{res}^*$ is evolutionarily stable, and so the mutant over-consumer cannot invade.

For this punishment function, the selection gradient is $D(c_m) = r - 3a(1 - c_m)^2$, so $D(c_m) > 0$ if either $c_m > 1 - \sqrt{\frac{a}{3a}}$ or $c_m < 1 + \sqrt{\frac{a}{3a}}$. One can see that there exists a region, where the mutant cannot invade even when the enforcement of punishment, accounted for with parameter $a$, is quite small. This can be interpreted as the rewards of over-consumption being too small below the red invasibility zone, and the costs of punishment being too great above the red invasibility zone.

![Figure 3: Selection gradient and pairwise invasibility plots for function of the type $f(c) = a(1 - c)^3$. Blue regions correspond to parameter values where the mutant cannot invade; red regions correspond to parameter values where it can invade. (a) selection gradient, defined in Equation (6) (b) PIP for $a = 0.1$; the singular strategy $c_{res}^*$ is evolutionarily and convergence stable (c) PIP for $a = 0.6$; there seem to appear two singular strategies for large enough values of $a$; one of the strategies is evolutionarily unstable, as neither the reward is large enough for the under-consumers, nor the punishment severe enough for over-consumers; the second strategy is $c_{res}^*$ is evolutionarily and convergence stable. This punishment/reward function is effective against aggressive over-consumers.](image-url)
Case 3. Separating punishment and reward

Finally, consider the following punishment/reward function: \( f(c) = \rho(1 - c^\eta) \). This functional form allows to separate the impact of punishment for over-consumption, which is increased or decreased depending on the value of parameter \( \eta \), and reward for under-consumption, which is influenced primarily by the value of parameter \( \rho \). In this case, the dominant eigenvalue is given by \( \lambda = r(c_m - c_{res}) - \rho(c_m^\eta - c_{res}^\eta) \).

As one can clearly see, if for instance \( r = \rho \), then \( \lambda > 0 \) when \( \eta < 1 \), and so the mutant should be able to invade, since the punishment for over-consumption is always less than its reproductive benefits; if \( \eta > 1 \), the inequality is reversed, and punishment overwhelms reproductive benefits. If \( \eta = 1 \), then everything is determined solely by the relative values of growth rate \( r \) and the reward parameter \( \rho \). If \( c_m \approx c_{res} \), then the mutant can (or cannot) invade if \( D(c_m) = r - \rho \eta c_m^{(\eta-1)} \) is positive (negative).

As one can see on Figure 4 and 5, this type of function behaves like case 1 for \( \eta < 1 \) and like case 2 for \( \eta > 1 \). These results reiterate the claim that was made in the previous two cases: punishment needs to be severe enough in order to successfully prevent invasion by over-consumers.

Figure 4: Pairwise invasibility plots for function type \( f(c) = \rho(1 - c^\eta) \), \( \eta = 0.9 \). The effectiveness of this function is the same as was for case 1: punishment is not severe enough to keep over-consumers out of the population.
Modeling parametrically heterogeneous populations using the Reduction theorem

Adaptive dynamics allows to obtain analytical results about system susceptibility to invasion in the case when the invading “mutant” (in this case an over-consumer with a higher value of $c_m$) is rare. However, what if the initial mutant is not rare (invasion by a group)? What if there is more than one type of mutant (the system did not have time to recalibrate before the new mutant came along)? We attempt to address these questions through application of the Reduction theorem for replicator equations.

Without incorporating heterogeneity one cannot study the effects of natural selection on the system, and until recently any attempts to write such models resulted in systems of immense dimensionality. However, the proposed approach allows us to overcome this problem.

Assume that each individual in the population studied is characterized by its own value of some intrinsic parameter, such as birth, death, resource consumption rates, etc. (a set of individuals characterized by a particular value of the parameter studied is referred to here as a clone). The distribution of clones will change over time due to system dynamics, since different clones impose different selective pressures on each other. Consequently, the mean of the parameter studied also changes over time. The mean can be computed at each time point using the moment generating function of the initial distribution of clones in the population. The changes in the mean of the parameter allows easy tracking of changes in population
composition in response to changes in micro-environment (such as varying nutrient availability) or with respect to different initial distributions of clones.

Now let us introduce an auxiliary variable $q(t)$, which satisfies $q(t)' = \frac{N(t)}{kz(t)}$, so that one may rewrite the system in the following form:

\[
\begin{align*}
\frac{x_c'(t)}{x_c(t)} &= r(c - q(t)') + f(c), \\
z'(t) &= p - dz(t) + e \frac{N(t)(1 - E'[c])}{N(t) + z(t)}.
\end{align*}
\]

Then

\[x_c(t) = x_c(0)e^{-q(t)+t(rc+f(c))}, \tag{7}\]

Total population size is then given by

\[N(t) = \int_{c \in \mathcal{A}} x_c(t)dc = N(0)e^{-q(t)} \int_{c} e^{t(rc+f(c))} P_c(0)dc, \tag{8}\]

where $P_c(0) = \frac{x_c(0)}{N(0)}$, and the current-time pdf is given by

\[P_c(t) = \frac{x_c(t)}{N(t)} = \frac{e^{t(rc+f(c))}P_c(0)}{\int_c e^{t(rc+f(c))} P_c(0)dc}, \tag{9}\]

Now, the expected value of $c$ can be calculated from the definition:

\[E'[c] = \int_c cP_c(t) = \frac{\int_c ce^{t(rc+f(c))} P_c(0)dc}{\int_c e^{t(rc+f(c))} P_c(0)dc}. \tag{10}\]

The final system of equations becomes:

\[
\begin{align*}
z'(t) &= p - dz + e \frac{N(t)(1 - E'[c])}{N(t) + z(t)}, \tag{11} \\
q'(t) &= \frac{N(t)}{kz(t)}. \tag{12}
\end{align*}
\]
where \(N(t)\) and \(E^t[c]\) are defined above.

The case, when \(f(c) = 0\) was investigated in [9]. The authors observed that although it takes longer for a heterogeneous population to go extinct, tragedy of the commons eventually happens if the maximum value of \(c\) is large enough. Moreover, one could observe transitional regimes as the population was evolving towards being composed of increasingly efficient over-consumers. This situation can be used to forecast upcoming crisis and start implementing punishment functions.

In the proposed form, if the system is parametrically homogeneous system, i.e. when \(E^t[c]\) is constant, \(f(c)\) can be factored into equation \(\frac{dx'}{x} = r(c + f(c) - \frac{bxk}{c})\), and consequently, the spectrum of possible dynamical behaviors for this modified system should be qualitatively the same compared to the initial model, analyzed in [9] and summarized in Section 2. However, while in [9] nothing prevented increase of \(E^t[c]\) up to the maximum possible value, here we want to investigate punishment/reward functions that will prevent the increase of \(E^t[c]\) that would otherwise drive the dynamics outside of the regions of sustainable coexistence with the common resource.

**Results**

We evaluated the effectiveness of several punishment/reward functions on the dynamics of growth of a heterogeneous population of consumers supported by a common dynamical carrying capacity, which can be increased or decreased by the individuals themselves. We evaluated the effects of the same type of punishment on populations with two different types of initial distributions of clones, namely truncated exponential with parameter \(\mu = 10\), and Beta distribution with parameters \(\alpha = 2, \beta = 2\) and \(\alpha = 2, \beta = 5\) (see Figure 6). Parameter values were chosen in such a way as to give different shapes of the initial distribution of clones within the population We hypothesized that the effectiveness of punishment will depend not only intrinsic parameter values of the system but also on the initial composition of the population. Specifically, we hypothesized that higher levels of punishment/reward will be necessary for initial distributions, where population composition is spread out further away from small values of \(c\), such as Beta distributions with parameters \(\alpha = 2, \beta = 5\) and even more so Beta distribution with parameters \(\alpha = 2, \beta = 2\) (see Figure 6b) compared to truncated exponential distribution, where fewer over consumers are initially present in the population (see Figure 6b).
First, we evaluated the effectiveness of the moderate punishment function of type $f(c) = a \frac{1 - c}{1 + c}$; the severity of punishment is captured through varying parameter $a$. The initial distribution was taken to be truncated exponential with parameter $\mu = 10$. We took parameter $a = 0; 0.5; 1; 2$ and plotted the changes in $x_c(t)$ for various $c$ over time (Figure 7), as well as the changes in the total population size and the amount of resource (Figure 8). We observed that when the punishment imposed is moderate, over-consumption could be avoided only when the value of $a$ was very high, i.e. when punishment is imposed very severely.
Figure 7: (a) Truncated exponential, moderate punishment (case 1), set 1, \( a = 0 \). (b) Truncated exponential, case 1, set 1, \( a = 0.5 \). (c) Truncated exponential, case 1, set 1, \( a = 1 \). (d) Truncated exponential, case 1, set 1, \( a = 2 \).

Figure 8: Truncated exponential distribution, set 1, case 1, dynamics of the total population size and total resource with respect to different values of \( a \) (different levels of severity of imposed punishment). One can see that successful management of over consumers was possible only when punishment implementation was very high.

Similar results were observed for the cases of Beta distribution with parameters \( \alpha = 2, \beta = 2 \) and \( \alpha = 2, \beta = 5 \) (additional figures are provided in Appendix). The value of \( a \) that was necessary for successful management of over-consumers varied depending on different initial distributions, indicating that in order to be able to prevent the tragedy of the commons, one needs to evaluate not only the
type of punishment and the severity of its enforcement but also match it to the composition of the population, since one level of punishment can be effective for one distribution of clones within a population of consumers and not another. Noticeably, this kind of insight would be impossible to obtain using the analytical methods of adaptive dynamics.

Next, we conducted the same set of numerical experiments for the severe punishment\generous reward function $f(c) = a(1 - c)^3$. We observed that the value of $a$ that would correspond to successful restraint of over-consumers was much lower than in the previous case for all initial distributions considered here (see Figures 9 and 10; additional examples are provided in Appendix). The system was able to support individuals with higher values of parameter $c$ present in the initial population than in the previous case. In some cases we were also able to observe brief periods of oscillatory transitional dynamical behavior before the system collapsed (see Figures 9 and 10).

Figure 9: Severe punishment/generous reward (case 2). Beta distribution with parameters $[\alpha, \beta] = [2, 2]$. (a) $a = 0$, (b) $a = 0.1$, (c) $a = 0.17$, (d) $a = 0.2$. One can see the population going through transitional regimes before collapse, when the punishment is implemented severely but not quite severely enough (when $a = 0.7$). This most probably corresponds to the expected value of parameter $c$ going through region 3 in the phase parameter portrait of the non-distributed system.
Figure 10: Case 2, set 1. Beta distribution with parameters $[2,2]$. Changes in total population size and of the common resource over time.

Finally, we evaluated punishment function of the type $f(c) = \rho(1 - c^\eta)$, where the intensity of punishment and reward are accounted for by parameters $\eta$ and $\rho$ respectively. We observed that in order to evaluate the expected effectiveness of the punishment/reward system one needs to not only adjust parameters $\rho$ and $\eta$ (see Figure 11) to each particular case considered but also be able to evaluate the expected range of parameter $c$ (see Figure 12), since one level of punishment may be appropriate for one set of initial conditions but not another. For instance, as one can see on Figure 12, the time to collapse under fixed values of parameter $\rho$ and $\eta$ is different for different initial distributions depending on the maximum value of $c$ present in the initial population. Moreover, in accordance with our hypothesis, indeed the time to collapse varies depending on the initial distribution of the clones within the population, and the higher the frequency of over-consumers is in the initial population, the worse the prognosis. For the examples considered, population in which the clones are distributed according to truncated exponential distribution is less likely to collapse due to over-consumption than Beta distribution with parameters $\alpha = 2$, $\beta = 5$ which in turn is slightly less prone to collapse than Beta distribution with parameters $\alpha = 2$, $\beta = 2$ (Figure 6).
Figure 11: $f(c) = \rho(1 - c^\eta)$, initial Beta distribution with parameters $\alpha = 2, \beta = 2$, $c \in [0, 3]$, $\eta = 1.2$.

Figure 12: The importance of evaluating the range of possible values of $c_f$, illustrated for different initial distribution. Punishment function is of the type $f(c) = \rho(1 - c^\eta)$, where $\rho = 0.6$, $\eta = 1.2$. Initial distributions are taken to be truncated exponential with parameter $\mu = 10$, and Beta with parameters $\alpha = 2, \beta = 2$ and $\alpha = 2, \beta = 5$; $\rho = 0.6$, $\eta = 1.2$. The top row corresponds to $c \in [0, 3]$; the bottom row corresponds to $c \in [0, 4]$. 
On the existence and properties of stationary distributions

The adaptive dynamics approach assumes that there exists a stable state of a population composed from a single clone $x_{res}$. In the absence of punishment, any initial distribution evolves in such a way, that asymptotically only the clone having maximal possible value of the parameter $c$ will persist. In contrast, introducing a punishment function allows for the possibility of a stationary distribution of clones that is concentrated in more than one point. Specifically, we show below that a population in a stationary state may consist of up to 2 clones with punishment function of the 1st and 3rd type and of up to 3 clones with punishment function of the 2nd type.

Assume that there exists a stationary distribution $P_c(t) = \frac{x_c(t)}{N(t)}$ of clones $x_c$ that stabilizes over time, which would occur when

$$\frac{dP_c(t)}{dt} = \frac{x'_c}{N} - \frac{x_c}{N^2}N' = P_c(t)[rc + f(c) - E^t[rc] - E^t[f(c)]] = 0,$$

which holds only when

$$rc + f(c) = E^t[rc] + E^t[f(c)].$$

The left hand side of Equation (14) does not depend on time, while the right hand side is independent of $c$, which implies that Equation (14) holds only when

$$rc + f(c) = K,$$

where $K$ is a constant.

Recall that $\{c_i\}$ is the support of a probability distribution $P$ if $P(c) > 0$ for all $c_i$ and $P(c) = 0$ otherwise. In our case, if there exists a constant $K$ such that

$$f(c_i) = K - rc_i,$$

then to each $K$ corresponds a stationary distribution $P(c_i)$, whose support $\{c_i\}$ coincides with the solution to this equation. Therefore, Equation (16) can be used to identify the values of $c$ that correspond to distributed evolutionary steady states. (Note that a) any distribution concentrated in a single point $c$ is clearly stationary, and b) if $f(c) \equiv ac$, where $a$ is a constant, then every stationary distribution is
concentrated in a single point.)

It follows from Equation (16) that for a given punishment function $f(c)$, the set of solutions to Equation (16) at fixed $K$ can be represented geometrically as a set $S(K)$ of abscissas of points of intersection of the curve $y = f(c)$ and the line $y = K - rc$. The constant $K$ is free, so by changing $K$ in such a way that the set $S(K)$ is not empty, we obtain all possible supports of the stationary distributions (see Figure 13).

![Figure 13: stead states are concentrated at the points of intersection of punishment function $y = f(c)$ and a line $y = K - rc$. Depending on the type of punishment function and on the angle of the line $y = K - rc$, one may have up to three clone types at the stationary state.](image)

An important conclusion can be made from these figures alone. As one can see in Figure 13, for instance, the two points of intersection of $f(c)$ and $y = K - rc$ that correspond to points of concentration of clones at a stationary state, can be less than or greater than 1, depending on the parameter $r$, which is the slope of the line $y = K - rc$. The case when one of the points of intersection is less than one (“altruistic” under-consuming clones) and one is greater than one (over-consumers) can be interpreted as a population of under-consumers “supporting” the population of over-consumers at a stationary state. Asymptotic behavior of the population, i.e., population survival or extinction, will be determined by the dynamics of System (17), which is derived below, and corresponding parameter values.

Once again, let $\{c_i\}$ be a support of stationary probability distribution. Then

$$\frac{dx_{c_i}}{dt} = r(K - \frac{N}{K})$$

The right hand side does not depend on $i$, which implies that

$$\ln(x_{c_i}(t)) - \ln(x_{c_j}(t)) = \text{const, for all } i, j$$

and

$$\frac{x_{c_i}(t)}{x_{c_j}(t)} = \frac{x_{c_i}(0)}{x_{c_j}(0)}$$

for all $t$. (Note that $i, j$ notation is used in this section to distinguish the fact that
we are no longer dealing with rare clones in a resident population, and hence previously used \( m, res \) notation is no longer appropriate.)

The dynamics of System (4) in this case can be described by

\[
\begin{align*}
\frac{dN}{dt} &= rN(K - \frac{N}{kz}) \\
\frac{dz}{dt} &= \gamma - \delta z + \frac{eN}{z+N}(1-E),
\end{align*}
\]

where \( E = E^t[c] = const \) and consequently does not depend on \( t \).

Now let \( A_i = \frac{x_{c_i}(0)}{\sum_j x_{c_j}(0)} \) be the initial frequency of clones \( x_{c_i} \); then \( E = \sum_i A_i c_i \). Therefore, by changing the initial values of \( x(c_i) \) we can vary the value of \( E \) from \( min(c_i) \) up to \( max(c_i) \). Stable equilibria \((N^*, z^*)\) of System (17) can now be found from \( N^* = kKz^* \) and \( \gamma - \delta z^* + \frac{eN^*}{z^*+N^*}(1-E) = \gamma - \delta z^* + B = 0 \), where \( B = \frac{(1-E)ckK}{1+ckK} = const \). Therefore, \( z^* = \frac{\gamma + B}{\delta} \), given that \( \gamma + B > 0 \).

System (17) is very similar to the initial parametrically homogeneous model with no punishment; the difference is that now the values of \( K \) and \( E \) are not identical: the value \( K \) is in one-to-one correspondence with the support \( \{c_i\} \), and the value of \( E \) is defined by the support \( \{c_i\} \) and initial values \( \{x_{c_i}(0)\} \). These results suggest that if the system has a stationary distribution, then the dynamics of the resource would be determined not by absolute sizes of the populations of ‘invaders’ and ‘residents’, but by their ratio.

Remark. In this work we are considering punishment functions, where the support of the stationary distribution can consist of up to three points, i.e., the system can be composed of up to three clones (see Figure 13b). However, one can conceive of a punishment function that can support an arbitrary number of clones in the population at the stationary distribution, which correspond to points of intersection of the curve \( y = f(c) \) and the line \( y = K - rc \). Such system is of course unlikely to survive for any significant period of time unless the number of individuals in the clones with \( c^* \gg 1 \) is small enough. Such a case can be interpreted as a large number of under-consumers supporting a very small number of over-consumers.

**Example 1.**

Consider the punishment function of the form \( f(c) = \frac{a(1-c)}{1+ce} \); the points of tangency of the curve \( y = \frac{a(1-c)}{1+ce} \) and the line \( y = K - rc \) are \( c_{i,2}^* = \pm \sqrt{2a/r} - 1 \). In order for \( c^* = \sqrt{2a/r} - 1 > 0 \), condition \( 2a > r \) must be satisfied. At \( c^* \), \( f(c^*) = \sqrt{2ar} - a \), so the line \( y = K - rc \) is tangent with \( y = f(c) = \frac{a(1-c)}{1+ce} \) at
\( K = K^* = \sqrt{2ar} - A + r(\sqrt{2a/r} - 1) \) (see dotted line in Figure 13).

Hence, the line \( y = K - rc \) intersects the curve \( y = f(c) \) in two points (see dashed red line in Figure 13) for all \( K^* < K < a \).

For the purposes of illustration, take \( a = 1, r = 0.4, K = 0.7 \) (see Figure 13). The stationary distribution is concentrated in two points \( c_1 = 0.25 \) and \( c_2 = 3 \), so in its steady state, the population is composed both of under-consumers and of over-consumers. The population dynamics is then described by system

\[
\begin{align*}
\frac{dN}{dt} &= 0.4N(0.7 - \frac{N}{kz}), \\
\frac{dz}{dt} &= \gamma - \delta z + \frac{eN}{z + N}(1 - E),
\end{align*}
\]

where \( E \in [c_1 = 0.25, c_2 = 3] \). For these particular values of parameters, the system will remain in the stable state if \( \delta z^* = \gamma + \frac{eN^*}{z^* + N^*}(1 - E) = \gamma + 0.412e(1 - E) > 0 \). Otherwise, it will go to extinction.

**Example 2.**

Now consider the punishment function of the form \( f(c) = a(1 - c)^3 \). The line \( y = K - rc \) is tangent to the curve \( y = f(c) \) at \( c^*_{1,2} = 1 \pm \sqrt{r/(3a)} \).

Denote \( \sqrt{r/(3a)} = \psi \). Then \( c^*_{1,2} = 1 \pm \psi \); the condition \( \psi < 1 \) needs to be satisfied in order for both roots to be positive.

Consequently,

\[ f(c^*_{1,2}) = \mp \psi, \]

\[ K^*_{1,2} = f(c^*_{2,1}) + rc^*_{1,2} = r(1 \pm \psi) \mp \psi^3; \]

and therefore

\[ K_{\text{min}} = r(1 + \psi) - \psi^3 < K < r(1 - \psi) + \psi^3 = K_{\text{max}}. \]

There can exist up to 3 points of intersection of the curve \( f(c) = a(1 - c)^3 \) and the line \( y = K - rc \) depending on the value of \( K \).

As one can see in Figure 13, where \( a = r = 1, \psi = \sqrt{1/3}, c^*_{1,2} = 1 \pm \sqrt{1/3} \), if \( K > K_{\text{max}} = 1.3849 \),
then there are no solutions to Equation (16); if \(1 < K < K_{\text{max}}\), then there exist 2 solutions to Equation (16); if \(0.6151 = K_{\text{min}} < K < 1\), then there can exist 3 solutions. For instance, taking \(K = 0.8\) and solving equation \(f(c) = K - rc\), i.e., \((1 - c)^3 = 0.8 - c\), we obtain the following solutions: \(c_1 = 0.121\), \(c_2 = 0.791\), \(c_3 = 2.08\). So, in this case, at the steady state, two ‘altruistic’ clones with \(c_1 = 0.121\) and \(c_2 = 0.791\) are supporting over-consuming clones with \(c_3 = 2.088\).

The overall system dynamics for this example are given by

\[
\frac{dN}{dt} = rN(0.8 - \frac{N}{kz}),
\]

\[
\frac{dz}{dt} = \gamma - \delta z + \frac{eN}{z + N}(1 - E),
\]

where \(E \in [c_1 = 0.121, c_3 = 2.088]\). If \(k = 1\), then at the stationary state \(N^* = 0.8z^*\) and \(\frac{N^*}{z^* + N^*} = \frac{0.8}{1.8} = 0.444\). The system will remain at a steady state if

\[
\delta z^* = \gamma + \frac{eN^*}{z^* + N^*}(1 - E) = \gamma + 0.444e(1 - E) > 0;
\]

Otherwise, it will go to extinction.

\[
\text{Discussion}
\]

In this paper we studied the dynamics of a consumer-resource type system in order to answer the question of whether infliction of punishment for over-consumption and reward for under-consumption can successfully prevent, or at least delay, the onset of the tragedy of the commons. We evaluated the effectiveness of three types of punishment functions, as well as the effects of punishment on populations with different initial composition of individuals with respect to the levels of resource (over)consumption.

The proposed model was studied analytically in \([9, 10]\) without incorporating punishment/reward for over-/under- consumption. It describes the interactions of a population of consumers, characterized by the value of an intrinsic parameter \(c\), with a common renewable resource in such a way that each individual can either contribute to increasing the common dynamical carrying capacity \((c < 1)\) or take more than they restore \((c > 1)\). As the value of \(c\) increases, the population goes through a series of transitional regimes from sustainable coexistence with the resource to oscillatory regime to eventually
committing evolutionary suicide through decreasing the common carrying capacity to a level that can no longer support the population.

We began by identifying analytical conditions leading to the possibility of sustainable coexistence with the common resource for a subset of cases using adaptive dynamics. This method allows to address the question of whether a mutant (in our case, an individual with a higher value of $c$) can invade a homogeneous resident population of resource consumers. We evaluated the effectiveness of three types of punishment functions: moderate punishment, $f(c) = a \frac{1-c}{1+c}$; severe punishment, $f(c) = a(1-c)^3$, where the parameter $a$ denotes the severity of implementation of punishment on individuals with the corresponding value of parameter $c$, and function of the type $f(c) = \rho(1-c^\eta)$, which allows to separate the influence of reward for under-consumption, primarily accounted for with parameter $\rho$, and punishment for over-consumption, accounted for with parameter $\eta$.

We demonstrated that while moderate punishment/reward function can be effective in keeping off moderate over-consumers at sufficiently high values of $a$ (see Figures 7 and 8), the evolutionarily singular strategy in this case is unstable, and thus eventually the population will be invaded by over-consumers with large enough value of $c$. The severe punishment/generous reward approach was uniformly effective, almost irrespective of the value of $a$, and allowed invasion of moderate over consumers only in the small region of $c \approx 1$, when the punishment is not yet severe enough to outweigh the benefits of moderate over-consumption (see Figures 9 and 10), and the reward does not yet provide sufficient payoffs in terms of higher growth rates. The evolutionarily singular strategy in this case is stable, suggesting that punishment is severe enough to prevent the tragedy of the commons.

Finally, we investigated a punishment/reward function of the type $f(c) = \rho(1-c^\eta)$ that allowed separating the influence of punishment for over-consumption (parameter $\eta$) from that of rewarding under-consumption (parameter $\rho$). This functional type behaves as a moderate punishment/reward function for $\eta < 1$, rendering it effective only for moderate over-consumers, and it behaves like the severe punishment/reward function for $\eta > 1$; in the critical case $\eta = 1$ the outcome of the interactions between resident and invader populations is determined solely by relative values of growth rate parameter $r$ and parameter $\rho$. Our results suggest that just rewarding under-consumers is not enough to prevent invasion by over consumers and hence one should not expect to be able to prevent the tragedy of the commons through reward alone.

Adaptive dynamics techniques do not yet allow answering the question of system invasibility when
the mutant is not rare, such as in cases of migration and consequent invasion by a group, or when the resident population is inhomogeneous. We address these questions using the Reduction theorem for replicator equations.

Assume that each individual consumer is characterized by his or her own value of the intrinsic parameter $c$; a group of consumers with this value of $c$ is referred to here as $c$-clones. This trait directly affects fitness, and thus the distribution of clones will change over time due to system dynamics. The clones will experience selective pressures not only from the external environment, competing for the limited resource, but also from each other. Consequently, the mean of the parameter will also change over time, affecting system dynamics. The mean of the parameter can be computed at each time point from the moment generating function of the initial distribution of clones, which allows to evaluate the effectiveness of different types of punishment/reward functions on population composition by tracking how the distribution of clones changed over time with respect to parameter $c$.

We evaluated the effectiveness of the same three types of punishment/reward functions on system evolution and calculated predicted the outcomes for different initial distributions of clones within the population, which were taken to be truncated exponential with parameter $\mu = 10$, and Beta distribution with parameters $\alpha = 2, \beta = 2$ and $\alpha = 2, \beta = 5$. The initial distributions were chosen in such a way as to give significantly different shapes of the initial probability density function; in applications they should be matched to real data, when it is available. We observed that the intensity of implementation of punishment/reward has to differ for different initial distributions if one is to successfully stop over-consumption, and so in order to be able to make any reasonable predictions one needs to understand what the initial composition of the affected population is. We hypothesized that the higher the frequency of over consumers in the initial population, the more severe the punishment for over-consumption would have to be, and the more generous the reward; specifically, for our examples, we anticipated the prognosis to be the most favorable for initial truncated exponential distribution, followed by Beta distribution with parameters $\alpha = 2, \beta = 5$ and then finally $\alpha = 2, \beta = 2$. This effect additionally implies that the results obtained analytically from adaptive dynamics can only be relevant for a subset of cases, i.e. when the invader is rare.

As anticipated, we observed that severe punishment/generous reward approach was much more effective in preventing the tragedy of the commons than the moderate punishment/reward function, particularly for the cases, when over-consumers were present at higher frequencies (such as both Beta initial
distributions). Specifically, we observed that the level of implementation, $a$, could be nearly ten times lower for severe punishment/generous reward system as compared to the moderate punishment function ($a \approx 0.2$ vs $a \approx 2$) in order to obtain the same effect of selecting against the over-consumers, which can be a very important factor in cases when there are large costs associated with implementation of such intervention systems. This comes not only from the severity of punishment but also from the fact that moderate punishment allows more time for the over-consumers to replicate, and thus by the time the punishment has an appreciable effect, the population composition had changed, and the moderate punishment will no longer be effective. So, in punishment implementation one needs to take into account not only the severity of punishment but also the time window that moderate punishment may provide, allowing over-consumers to proliferate. Within the frameworks of the proposed model, moderate implementation of more severe punishment/reward system is more effective than severe implementation of moderate punishment/reward.

Proposed here is just one way to try and modify individuals’ payoffs in order to prevent resource over-consumption - through inflicting punishment and reward that affects the growth rates of clones directly. This approach can be modified depending on different situations, inflicting punishment or reward based not just on the intrinsic value of $c$ but on total resource currently available.

**Adaptive dynamics and the Reduction theorem.** In order to address our questions we have used two recently developed methods for modeling parametrically heterogeneous populations: adaptive dynamics \[1\] and the Reduction theorem for replicator equations \[7, 8\]. Adaptive dynamics allows addressing the question of rare “mutant” clone invasion using standard bifurcation theory. The method allows to formulate analytical conditions, which can be conveniently visualized using pairwise invasibility plots (PIPs). However, the method does not allow addressing questions of system invasibility by clones that are not rare, such as in cases of invasion by a group, or when the resident population is heterogeneous. These questions can be addressed using the Reduction theorem for replicator equations.

We consider the moment of “invasion” as the initial time moment; more formally, we assume that all “invaders” must be present initially in the population, falling within some known distribution; one can then see which clone type(s) will be favored over time due to natural selection and visualize evolutionary trajectories, which cannot be achieved using adaptive dynamics. The outcome depends both on the initial
distribution of the clones within the population and on the initial state of the system, i.e., other intrinsic properties of both individuals within the population and the resources, which in this case were assumed to be fixed. However, the system of ODEs that results from the transformation done using the Reduction theorem is typically non-autonomous; hence no analytical conditions can typically be obtained using standard bifurcation theory. The two methods therefore can complement each other. A more detailed comparison of the two methods is in Table 3.

Tragedy of the commons as prisoner’s dilemma

The conditions that can lead to the tragedy of the commons can be reformulated as a game of prisoner’s dilemma: in such systems preserving the common resource is in the best interest of the group as a whole but over-consumption is in the interest of each particular individual. In the cases where decisions about the resource are made by each individual independently, tragedy of the commons seems to be inevitable. However, a number of cases have been observed, when the tragedy could be avoided if the individuals within the population were able to communicate with each other [14]. The common thread that runs through many of the available examples is that 1) in small groups the effects of over-consumption are immediately noticeable, since within a small population each individual’s actions are more visible than in larger populations, and 2) punishment is enforced without delay.

In this paper we are dealing with a particular case of a game of prisoner’s dilemma, where punishment/reward functions $f(c)$ affect individual payoffs in such a way as to give the possibility to outweigh both the benefits of over-consumption and the deleterious effects of under-consumption (see Figure 14). We were able to demonstrate that preventing the tragedy of the commons through solely rewarding under-consumers is unlikely. However, the effectiveness of “intervention” is increased when both reward and punishment systems are enforced, although they do need to be modified depending on population composition, since the choices of individuals may be affected not only by their immediate ‘payoffs’ but also by the actions of those surrounding them. Therefore, if one is to try and avert the tragedy of the commons through punishing over-consumption and rewarding under-consumption, one needs to not only find an appropriate punishment/reward function but also calibrate it to the current composition of each
Figure 14: Tragedy of the commons as prisoner’s dilemma. The tragedy can be avoided if the immediate payoffs of all the players are modified through appropriate punishment/reward functions.

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