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The evolution of *n*-player cooperation—threshold games and ESS bifurcations

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Abstract

An evolutionary game of individuals cooperating to obtain a collective benefit is here modelled as an *n*-player Prisoner's Dilemma game. With reference to biological situations, such as group foraging, we introduce a threshold condition in the number of cooperators required to obtain the collective benefit. In the simplest version, a three-player game, complex behaviour appears as the replicator dynamics exhibits a catastrophic event separating a parameter region allowing for coexistence of cooperators and defectors and a region of pure defection. Cooperation emerges through an ESS bifurcation, and cooperators only thrive beyond a critical point in cost-benefit space. Moreover, a repelling fixed point of the dynamics acts as a barrier to the introduction of cooperation in defecting populations. The results illustrate the qualitative difference between two-player games and multiple player games and thus the limitations to the generality of conclusions from two-player games. We present a procedure to find the evolutionarily stable strategies in any *n*-player game with cost and benefit depending on the number of cooperators. This was previously done by Motro [1991. Co-operation and defection: playing the field and the ESS. J. Theor. Biol. 151, 145–154] in the special cases of convex and concave benefit functions and constant cost.

Keywords: *n*-Player game; Prisoner's Dilemma; Cooperation; Bifurcation; Hysteresis

1. Introduction

Game theoretical analysis has been widely applied in evolutionary theory. The canonical metaphor for the dilemma arising when cooperative and competitive relations between individuals collide is the Prisoner's Dilemma (von Neumann and Morgenstern, 1944; Maynard-Smith, 1982; Hofbauer and Sigmund, 1998; Gintis, 2000). The Prisoner's Dilemma game can either be represented as a two-player game or more generally as an *n*-player game, sometimes termed the 'public goods game' (Boyd and Richerson, 1988). The *n*-player game describes a situation in which several individuals can cooperate to achieve a common benefit, which in turn is shared among both the cooperators and the (free riding) defectors in the group. An often used 'tragic' sociological metaphor—the tragedy of the commons—describes the overexploitation of a grassland resource shared by village farmers (Hardin, 1968). Indeed this metaphor represents the rational outcome of an *n*-player game. The verbalized public goods game illustrates a situation where the social agents contribute some amount of resource (money) to a common pool, which is then increased with some factor (interest rate). Subsequently the total quantity is distributed among all players regardless of their individual contribution

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(Hauert et al., 2002). In its pure form the outcome is identical to the tragedy of the commons. However, cooperation can be promoted by evoking further mechanisms such as e.g. punishment (Boyd and Richerson, 1992; Gardner and West, 2004), or optional participation either in groups (Hauert et al., 2002) or in iterated two-player games (Batali and Kitcher, 1996).

A crucial notion to analytically describe the properties and ultimate outcome of a conflict or a game situation is the evolutionarily stable strategy (ESS). Roughly, a strategy is evolutionarily stable if no alternative strategy can invade it (see (Maynard-Smith, 1982; Hofbauer and Sigmund, 1998; Axelrod and Hamilton, 1981; Riechert and Hammerstein, 1983)). In evolutionary theory, however, the ESS analysis is mainly applied in two-player games only (but see e.g. (Boyd and Richerson, 1988; Hauert et al., 2002)).

As in the public goods game the per capita benefit is often implicitly assumed to increase in a linear fashion with the number of cooperators, i.e. the effect of cooperation is additive. In an n-player game, Motro (1991) relaxed this assumption and investigated two further classes of strictly increasing benefit functions describing the benefit obtained by group members as a function of the number of cooperators. For linear (additive) and convex (superadditive) benefit functions only the two trivial ESSs of full defection or full cooperation appear, depending on whether the additional benefit obtained by a single member switching to cooperative behaviour exceeds the individual cost of cooperation (Motro, 1991). However, for concave (subadditive) benefit functions there may exist a polymorphic ESS consisting of both strategies (or alternatively a homogenous population of mixed strategies). Hence, under such condition some degree of cooperation in the population can be expected (Motro, 1991).

In various natural situations the assumption of the benefit function having a monotonic derivative, let alone being linear, sometimes fails to capture the nature of the interaction. Animals that are dependent on very aggregated resources that require joint effort to handle and process, may face a reality best represented by a threshold scenario. In such case the benefit represents a single discrete all-or-nothing event, thus the benefit function becomes a step function. In other words, the benefit function may be characterized by a discrete transition between a plateau of low or zero benefit and a plateau of high benefit that is reached only if sufficiently many group members cooperate. A conspicuous natural situation complying with this model is the group hunting of certain predators, as for example the African wild dog (*Lycaon pictus*) (Boesch, 1994; Frame et al., 1979; Courchamp 2000a, b; Courchamp and Macdonald, 2001). The collective effort of individuals in the groups ensures that large prey can be caught that no single individual could ever capture (Frame et al., 1979). Moreover, the hunting success seemingly depends on the propensity to cooperate among group members. A minimum number of hunters seems required in order to capture large prey items as the fatigue of the prey cannot be provoked without a joint effort of a number of individuals (Courchamp and Macdonald, 2001). As the prey is either captured or not, a game representation should account for the binary outcome.

Territory defence is another example of a benefit function which should be represented by a threshold scenario since the result of the joint defence is of a binary nature in the sense that the territory will either be lost or maintained. Game theoretical considerations has arisen from the observation that in female groups of lions (*Panthera leo*) certain individuals seem to consistently refrain from contributing to the common territory defence (Heinsohn and Packer, 1995; Svenstrup and Christiansen, 2000).

In this paper we wish to investigate the simplest possible game allowing for a step-wise or threshold relation between the proportion of cooperators in a group and the benefit obtained. In a three-player game we introduce a threshold level of two cooperators that has to be exceeded in order to obtain the benefit. We describe this game in Section 2, and show that even this simple case yields complex evolutionary behaviour as the system exhibits hysteresis around critical parameter values separating a regime with stable coexistence of defectors and cooperators and a regime of pure defection. In Section 3 we generalize Motro's work and describe a procedure to find all ESSs for any benefit function. We then proceed to find conditions for when the dynamics is similar to that of our three-player threshold game. In Section 4 we discuss the implications and biological relevance of our findings.

2. Single group and mean field models

Initially, assume we have a group of three players. Each player has the choice of cooperating (C) or defecting (D). If at least two players cooperate, all three players will receive a benefit of r. Otherwise, all players will receive no benefit. Additionally, cooperating bears some cost c, which is inflicted whether or not the benefit is achieved. The payoff to ego is summarized by the table:

	CC	CD	DD
C	$r-c$	$r-c$	$-c$
D	r	0	0

We see that the pure strategy of always defecting is a Nash equilibrium while the pure strategy of cooperating never is. Let the mixed strategy x be to cooperate with probability x, and defect with probability $1-x$. Assume that two of the players play strategy x. If player A plays strategy y, its expected payoff is given by the function:

$$W(y;x) = rx^2 + y(2rx(1-x) - c) = rx^2 + y \cdot g(x). \quad (1)$$

According to classical game theory, there is a *mixed* Nash equilibrium when this payoff is independent of y. In our case this is when $g(x) = 0$. This is the case only for the two x values

$$x_- = \frac{1}{2} - \frac{1}{2}\sqrt{1 - 2\frac{c}{r}}, \quad x_+ = \frac{1}{2} + \frac{1}{2}\sqrt{1 - 2\frac{c}{r}}. \quad (2)$$

Thus, there are only mixed Nash equilibria when $r \geqslant 2c$.

The same game can also be regarded as an evolutionary game. Here, the setting is a large population where triples of players are randomly selected and play the game. A strategy x is said to be evolutionarily stable if it is resistant to all invading strategies. That is, if any alternative strategy y is played by a sufficiently small fraction of the population, x always does better than y. The notion of ESS was introduced in Maynard-Smith (1974) for two-player games. We use the natural extension to n-player games defined in Broom et al. (1997), namely the condition that

$$W(x; \varepsilon y + (1-\varepsilon)x) > W(y; \varepsilon y + (1-\varepsilon)x) \quad (3)$$

for all $y \in [0,1]$, $y \neq x$ and ε smaller than some $\varepsilon(y)$. By (1) and Taylor expansion we have

$$\begin{aligned} &W(x; \varepsilon y + (1-\varepsilon)x) - W(y; \varepsilon y + (1-\varepsilon)x) \\ &\quad = (x-y)g(x + \varepsilon(y-x)) \\ &\quad = (x-y)g(x) - \varepsilon(x-y)^2 g'(x) + O(\varepsilon^2). \end{aligned} \quad (4)$$

Hence, for a mixed strategy x to be an ESS it must satisfy $g(x) = 0$ (Nash equilibrium) and additionally $g'(x) < 0$. Consequently, x_+ in (2) is an ESS while x_- is not. The Nash equilibrium where players always defect is also an ESS, since always defecting in this case is the unique best reply to itself. Note that while having a mixed ESS and a pure strategy ESS coexisting for the same parameter values is impossible for a two-player game, it is not in a three-player game (Broom et al., 1997).

The replicator equation for the system determines the dynamics of the game when players reproduce proportionally to their achieved payoff. The equation is given by (Hofbauer and Sigmund, 1998):

$$\dot{x} = x(f(x) - \bar{f}). \quad (5)$$

Here, $f(x)$ is the fitness of cooperators and $\bar{f}$ is the mean fitness of the total population. In our case the exact form is given by

$$\dot{x} = x(1-x)g(x). \quad (6)$$

The fixed points of this dynamical system are the same as the Nash equilibria of the group game, along with the point $x = 1$, since pure populations always will be fixed points of the replicator system. It is easily checked that the stable fixed points are those corresponding to ESSs for the group game. We can thus represent the dynamics of the game by the bifurcation diagram in Fig. 1. The diagram shows that we have a saddle-node bifurcation at $\alpha = \frac{c}{r} = \frac{1}{2}$. Here, one stable and one unstable fixed point are created as α decreases. Consequently, in the case that $\alpha < \frac{1}{2}$ the system will settle in state x_+ if the initial fraction of cooperators is higher than x_-. Otherwise, the system will settle in a state consisting entirely of defectors. The last outcome is always the case when $\alpha > \frac{1}{2}$. Note that this leads to a hysteresis effect. If the system initially is in the cooperating state x_+ and α is increased beyond $\frac{1}{2}$, the system will settle in the state of pure defection. However, a subsequent decrease of α will not suffice to reestablish the cooperative state due to the fact that $x = 0$ also is an ESS. This effect is discussed in Section 4. The dynamics of threshold games with more than three players are similar, see Example 6.

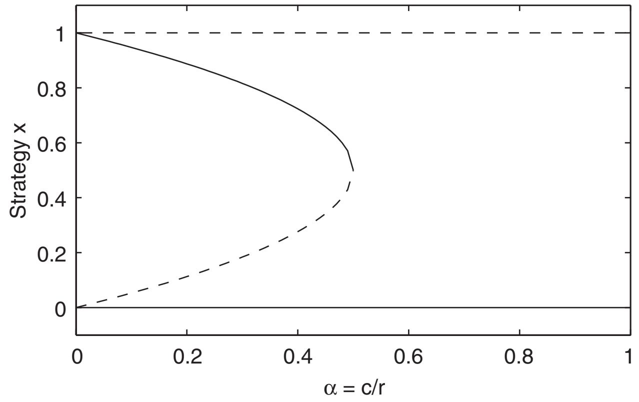


Fig. 1. The bifurcation diagram for the replicator system (6). Fixed points are plotted versus the parameter $\alpha = \frac{c}{r}$. Solid-drawn lines represent stable fixed points. These are ESSs for the system. Dashed lines represent unstable fixed points.

3. General conditions for threshold type dynamics

Considering the general case, we wish to find a general procedure to understand the dynamics of an n-player evolutionary game as well as obtain conditions under which the game will have dynamics equal to the dynamics of our three player threshold model. Assume we have a group of N players (capital N is hereafter used to indicate a fixed group size). Denote by r_k the benefit to each group member if k players opt to cooperate and $N-k$ players defect. Furthermore, assume that cooperation bears an additional cost of c_k when k of the players cooperate, that is, the cost is specified by the vector $\mathbf{c} = (c_1, \ldots, c_N)$. Define $\mathbf{r} = (r_0, \ldots, r_N)$ as the vector containing the benefits. It may be natural that r_k

is non-decreasing and c_k is non-increasing in k, but we do not require this. This game is formally defined as

Definition 1. Let the game $\Gamma(N, \mathbf{r}, \mathbf{c})$, with $\mathbf{c} \in [0, \infty)^N$ and $\mathbf{r} \in [0, \infty)^{N+1}$, have N players, each with the strategy set $S = \{C, D\}$. The payoff is defined as following: If k players play C, these will obtain $r_k - c_k$ and the remaining $N - k$ players will obtain r_k.

The game with constant cost considered by Motro (1991) is referred to as $\Gamma_c(N, \mathbf{r}) = \Gamma(N, \mathbf{r}, (c, c, \ldots, c))$. Before proceeding we introduce a useful terminology.

Definition 2. The forward difference operator Δ is defined on the sequence $\mathbf{r}$ by

$$\Delta r_k = r_{k+1} - r_k$$

for $0 \leqslant k \leqslant N - 1$. Its higher iterates are defined recursively by

$$\Delta^m r_k = \Delta^{m-1} r_{k+1} - \Delta^{m-1} r_k$$

for $0 \leqslant k \leqslant N - m$.

Note that $\Delta r_k - c_{k+1}$ is the additional payoff ego will obtain by switching from D to C if exactly k other players cooperate. Denote by $W_{\mathbf{r},\mathbf{c}}(y; x)$ the expected payoff to ego playing strategy y while the remaining $N - 1$ players are playing strategy x. Equivalently, the remaining $N - 1$ players might be drawn at random from a large population of which a fraction x always plays C and the rest plays D. In both cases the number of players in the group playing C will be binomially distributed. Consequently, $W_{\mathbf{r},\mathbf{c}}(y; x)$ is given by

$$W_{\mathbf{r},\mathbf{c}}(y; x) = \sum_{k=0}^{N-1} \binom{N-1}{k} x^k (1 - x)^{N-1-k} r_k + y \cdot g_{\mathbf{r},\mathbf{c}}(x), \tag{7}$$

where

$$g_{\mathbf{r},\mathbf{c}}(x) = \sum_{k=0}^{N-1} \binom{N-1}{k} x^k (1 - x)^{N-1-k} (\Delta r_k - c_{k+1}). \tag{8}$$

The function $g_{\mathbf{r},\mathbf{c}}(x)$ is a polynomial defined on the interval [0,1]. It is called the *gain function* because $g_{\mathbf{r},\mathbf{c}}(x)$ is interpreted as the expected increase in payoff ego will gain if playing C rather than D. As argued in the previous section, a strictly mixed strategy x can only be a Nash equilibrium if $g_{\mathbf{r},\mathbf{c}}(x) = 0$.

For the constant-cost game $\Gamma_c(N, \mathbf{r})$ Motro (1991) found the possible ESS for the special case of all $\Delta^2 r_i$ having the same sign. In this case, the gain function is strictly monotonic, as implied by Eq. (A.2). We will refer to the gain function of $\Gamma_c(N, \mathbf{r})$ as $\tilde{g}_{\mathbf{r},c}(x)$.

Example 3. Consider the game where the cooperators share a fixed cost c, that is, $\mathbf{c} = c\boldsymbol{\sigma}$ with $c \in [0, \infty)$ and $\boldsymbol{\sigma} = \left(1, \frac{1}{2}, \frac{1}{3}, \ldots, \frac{1}{N}\right)$. The function $g_{\mathbf{r},\mathbf{c}}(x)$ is then given by

$$g_{\mathbf{r},c\boldsymbol{\sigma}}(x) = \tilde{g}_{\mathbf{r},c}(x) + c(1 - \gamma(x)),$$

where $\tilde{g}_{\mathbf{r},c}(x)$ corresponds to the game $\Gamma_c(N, \mathbf{r})$ and

$$\gamma(x) = \frac{1 - (1 - x)^N}{Nx} \quad \text{and} \quad \gamma(0) = 1.$$

In $\Gamma_c(N, \mathbf{r})$ with $r_k = r_0 + kc$, $k = 1, 2, \ldots, N$, we have $\tilde{g}_{\mathbf{r},c}(x) \equiv 0$ (i.e., all strategies are Nash equilibria). With cost sharing and

$$r_k = r_0 + c \sum_{i=1}^{k} \frac{1}{i},$$

we again have $g_{\mathbf{r},\mathbf{c}}(x) \equiv 0$. A particular Nash equilibrium may thus exist with a quite moderate increase in reward in the cost-sharing game, as compared to the constant-cost game.

We will now describe a general procedure to locate the Nash equilibria and ESS of the game defined by $\mathbf{r}$ and $\mathbf{c}$. These properties of the game are decided by the function $g_{\mathbf{r},\mathbf{c}}(x)$ alone. In the proposition below, Cases (1)–(3) are the common cases while (4) contains special cases which occur if the derivative $g'_{\mathbf{r},\mathbf{c}}(x)$ is zero or, for the endpoints, $g_{\mathbf{r},\mathbf{c}}(x)$ is zero.

Proposition 4. *Consider the function $g_{\mathbf{r},\mathbf{c}}(x)$ defined in* (8). *All symmetric Nash equilibria* (*NE*) *and all ESS to the game $\Gamma(N, \mathbf{r}, \mathbf{c})$ in Definition* 1 *are given by the following cases:*

1. *If $g_{\mathbf{r},\mathbf{c}}(0) < 0$, then $x = 0$ is an ESS.*
2. *If $g_{\mathbf{r},\mathbf{c}}(1) > 0$, then $x = 1$ is an ESS.*
3. *If $g_{\mathbf{r},\mathbf{c}}(x) = 0$, then x is a NE. If additionally $g'_{\mathbf{r},\mathbf{c}}(x) < 0$, then x is also an ESS.*
4. *x is an ESS in the special cases*:
   - (a) $0 < x < 1$, $g_{\mathbf{r},\mathbf{c}}(x) = 0$, $g'_{\mathbf{r},\mathbf{c}}(x) = 0$ *and there is an* $m \in \mathbb{N}$ *such that* $g^{(k)}_{\mathbf{r},\mathbf{c}}(x) = 0$ *for* $k \leqslant 2m$ *and* $g^{(2m+1)}_{\mathbf{r},\mathbf{c}}(x) < 0$.
   - (b) $x = 0$, $g_{\mathbf{r},\mathbf{c}}(0) = 0$ *and there is an* $m \in \mathbb{N}$ *such that* $g^{(k)}_{\mathbf{r},\mathbf{c}}(0) = 0$ *for* $k < m$ *and* $g^{(m)}_{\mathbf{r},\mathbf{c}}(0) < 0$.
   - (c) $x = 1$, $g_{\mathbf{r},\mathbf{c}}(1) = 0$ *and there is an* $m \in \mathbb{N}$ *such that* $g^{(k)}_{\mathbf{r},\mathbf{c}}(1) = 0$ *for* $k < m$ *and* $(-1)^{m+1} g^{(m)}_{\mathbf{r},\mathbf{c}}(1) < 0$.

The analysis is easily done graphically by plotting the function $g_{\mathbf{r},\mathbf{c}}(x)$. Note that $g_{\mathbf{r},\mathbf{c}}(x) = 0$ is satisfied at no more than $N - 1$ values of x, since $g_{\mathbf{r},\mathbf{c}}(x)$ is a polynomial of degree $N - 1$. Also note that $g_{\mathbf{r},\mathbf{c}}(0) = \Delta r_0 - c_1$ and $g_{\mathbf{r},\mathbf{c}}(1) = \Delta r_{N-1} - c_N$. The proof of Proposition 4 is found in the appendix, as are the proofs for the propositions stated below.

Example 5. Consider the five player game $\Gamma_c(5, \mathbf{r})$ with $r_0 = 0, r_1 = 0.15, r_2 = 0.3, r_3 = 0.7, r_4 = 0.8, r_5 = 1$. The

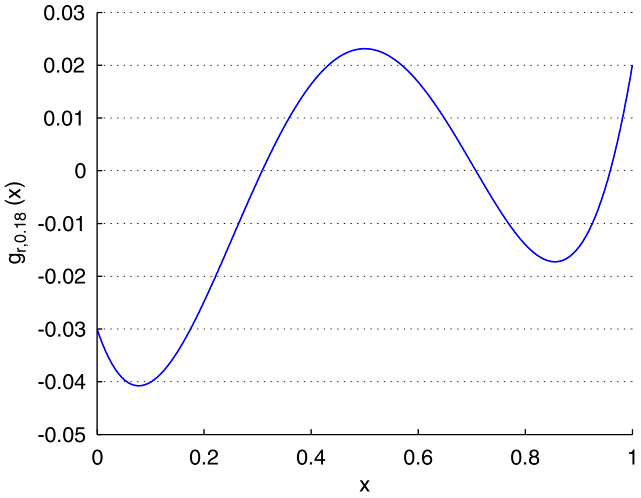


Fig. 2. The function $g_{\mathbf{r},c}(x)$ for $c = 0.18$ and **r** from Example 5. We see that one mixed ESS is present, and located at $x = 0.708$. Also, $x = 0$ and $x = 1$ are ESSs.

function $g_{\mathbf{r},c}(x)$ is plotted for $c = 0.18$ in Fig. 2. We have the following ESS for various values of c:

Range of c	ESS
$c < 0.139$	$x = 1$
$0.139 < c < 0.15$	one mixed ESS, $x = 1$
$0.15 < c < 0.163$	$x = 0$, $x = 1$
$0.163 < c < 0.2$	$x = 0$, one mixed ESS, $x = 1$
$0.2 < c < 0.203$	$x = 0$, one mixed ESS
$0.203 < c$	$x = 0$

Hence this five-player case generates the following ESS-bifurcations: at $c = 0.139, 0.163$ and 0.203 saddle-node bifurcations emerge, and at $c = 0.15$ and 0.2 transcritical bifurcations separate the regions of distinct evolutionary dynamics.

Example 6. Consider a threshold game $\Theta_{r,c}(N, M)$ with N players, where a threshold of M cooperators brings a reward of r per player and the cost of cooperating is constant and equal to c. The benefit is thus $r_k = 0$ for $k < M$ and $r_k = r$ for $k \geqslant M$. In this case,

$$\tilde{g}_{\mathbf{r},c}(x) = r\binom{N-1}{M-1}x^{M-1}(1-x)^{N-M} - c. \tag{9}$$

For $1 < M < N$, this function has a single maximum in $[0, 1]$, located at $\tilde{x} = \frac{M-1}{N-1}$. Define

$$\gamma_{N,M} = \binom{N-1}{M-1}\left(\frac{M-1}{N-1}\right)^{M-1}\left(\frac{N-M}{N-1}\right)^{N-M}. \tag{10}$$

The bifurcation diagram for the system will look qualitatively similar to that in Fig. 1. For $\frac{c}{r} < \gamma_{N,M}$ the system has a mixed ESS x_+ and an unstable mixed NE $x_- < x_+$. For $\frac{c}{r} > \gamma_{N,M}$ the pure strategy of defecting is the only ESS.

Finally, we state some general conditions under which the dynamic of a game $\Gamma_c(N, \mathbf{r})$ is equal to that of our three player threshold game presented in Section 2.

Proposition 7. *Consider the game* $\Gamma_c(N, \mathbf{r})$. *If*

(1) $\Delta^3 r_i \leqslant 0$ *for* $0 \leqslant i \leqslant N-3$
(2) $\Delta^2 r_0 > 0$ *and* $\Delta^2 r_{N-2} < 0$

then there exists a $c^* > \max\{\Delta r_0, \Delta r_{N-1}\}$ *such that*

(1) *For* $c < \Delta r_{N-1}$ *and for* $c > c^*$, *there are no strictly mixed ESS.*
(2) *For* $\Delta r_{N-1} < c < c^*$ *there exists a single strictly mixed ESS* $x = x_+$.
(3) *For* $\Delta r_0 < c < c^*$ *a there exist a NE* $x = x_-$ *with* $x_- < x_+$.
(4) *Additionally,* $x = 1$ *is an ESS for* $c < \Delta r_{N-1}$ *and* $x = 0$ *is an ESS for* $c > \Delta r_0$.

Thus, when the conditions in the proposition are satisfied we have the same situation as in our three-player threshold game. When the cost c is high the only ESS is $x = 0$ and when the cost is low the only ESS is $x = 1$. The last case is not present in $\Theta_{r,c}(3, 2)$ of Section 2 since there $\Delta r_{N-1} = 0$. In addition $x = 0$ is an ESS coexisting with x_+ in the interval $\Delta r_0 < c < c^*$.

Note that the while Proposition 7 gives a sufficient condition, it is not necessary. For a three-player game ($N = 3$), however, the second condition in Proposition 7 is both necessary and sufficient. From the proof of Proposition 7 it follows that the first condition in the proposition has an alternative formulation.

Proposition 8. *The first condition in Proposition 7 can be replaced with*:

(1) *The polynomial*

$$\sum_{k=0}^{N-2}\binom{N-2}{k}x^k(1-x)^{N-2-k}\Delta^2 r_k$$

has at most one zero in (0,1).

Let this zero be $\tilde{x}$. *Then the critical value* c^* *is given by* $\tilde{g}_{\mathbf{r},0}(\tilde{x})$.

4. Discussion

Besides the interest in relaxing the assumptions of linear or strictly sub- or super-linear relations in the theory of group games, there are biological observations suggesting to go beyond such premises. The described extensions to threshold games allow a natural relation between the per capita costs and benefit and the number of cooperators, and indeed this scenario turned out to exhibit a complex evolutionary dynamics (Figs. 1 and 2). The multiplayer threshold game we have studied yields dynamics not possible for two player games, in particular the appearance of a catastrophic event at a critical parameter value c^* separating very different ESS profiles.

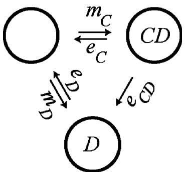
The three-player game is the simplest possible threshold game and yet sufficient to yield complex dynamics. Above the critical cost c^* is a parameter region where only defection is stable, and below this point two alternative attracting states appear. One of these is an ESS comprising both cooperators and defectors and the other is a trivial ESS with pure defection. The cooperative state may disappear as a drastic event when the cost increases above the critical cost (for $\alpha > \frac{1}{2}$ in Fig. 1). Moreover, the system exhibits hysteresis behaviour. By this we mean that a system in the mixed state will experience a sudden transition and settle in the defecting state for gradually decreasing reward values or gradually increasing costs making the system traverse a critical line in the cost–benefit space. However, a subsequent complete recovery of parameter values allowing for cooperation will not recover the cooperative state. The population is trapped in the attractive basin of the defecting state.

Such dynamics suggest the prediction that populations thriving near a critical point in parameter space can show drastic transformations among polymorphic states with cooperation or collapse into the trap of the fully defecting state. Subtle changes in environmental conditions may therefore induce a regime shift as the cooperative state suddenly collapse and disappear. A mere recovery of the original environmental conditions will then be insufficient to reinstall cooperation and mechanisms external to the game are required. Group foragers often depend on individually inaccessible and aggregated resources, such as large prey items. Such feeding strategies require a population density that make group behaviour feasible. The populations may accordingly be prone to complex evolutionary dynamics, as for instance rapid extinctions, when exposed to minor environmental changes that affect the cost–benefit parameters and/or population density. Unless, of course, alternative and individually accessible resources are available.

Initial evolution of cooperation from the defecting state needs alternative mechanisms as, for instance, kin selection or repeated interactions among individuals. However, when the cost–benefit ratio is low the attracting region of defection is small (Fig. 1), and this in turn facilitates the exit from the defection trap by stochastic fluctuations. Indeed, cooperation can gain foothold when, due to local fluctuations, the fraction of cooperators rises above a certain level (that is, above the repelling state x_- in the three-player game).

This scenario offers an alternative mechanism for the initial evolution of cooperation from the defecting state, in that stochastic fluctuations may originate in a metapopulation structure of the species. Cooperative group behaviour increases the productivity of the local population, because resources are increased beyond those that are exploitable by the individual. A subpopulation with cooperative behaviour will thus have a higher probability of inoculating an empty environmental patch, as compared to a defective population in a similar environment.

Consider an exceedingly simple model of this situation made in the tradition of Slatkin (Slatkin, 1974; Christiansen and Fenchel, 1977). Three kinds of patches may exist: empty patches, patches with defectors only, and patches with defectors and cooperators. The frequency of these are P_0, P_D, and P_{CD}, $P_0 + P_D + P_{CD} = 1$. Cooperators can only invade empty patches, and this occurs at the rate $m_C P_{CD}$. After invasion defectors invade so rapidly that we can assume it to occur immediately. Defectors can invade empty patches both from defecting patches and from cooperating patches, and we model the rate as $m_D Q_D$, where $Q_D = w_D P_D + w_{CD} P_{CD}$ and $w_D < 1$. Extinction of all individuals in defecting and cooperating patches occurs at the rates e_D and e_C, respectively, and in addition we allow extinction of cooperators from cooperating patches at the rate e_{CD}. The model may be summarized as



described by the equations:

$$\dot{P}_0 = -(m_C P_{CD} + m_D Q_D) P_0 + e_C P_{CD} + e_D P_D, \tag{11}$$

$$\dot{P}_D = m_D Q_D P_0 + e_{CD} P_{CD} - e_D P_D, \tag{12}$$

$$\dot{P}_{CD} = m_C P_{CD} P_0 - (e_C + e_{CD}) P_{CD}. \tag{13}$$

A trivial equilibrium with no cooperators always exists:

$$\tilde{P}_0 = \frac{e_D}{m_D w_D + e_D} \quad \text{and} \quad \tilde{P}_D = \frac{m_D w_D}{m_D w_D + e_D}, \tag{14}$$

and cooperators can invade this equilibrium when $e_C + e_{CD} < m_C \tilde{P}_0$. The invasion condition then becomes

$$1 + w_D \frac{m_D}{e_D} < \frac{m_C}{e_C + e_{CD}}. \tag{15}$$

The colonization rate of cooperators must thus be somewhat higher than their extinction rate for invasion to proceed. The extinction rate e_{CD} therefore must be small, which requires a polymorphic equilibrium in the patch and a defection trap, that is not too large. The requirement is, however, moderate, because the addend to one on the left side is expected to be small. The defecting patches are supposed to have a comparatively low population size because of fewer available resources. This causes their emigration potential (parameter w_D) to be low, and their colonization ability of empty patches (parameter m_D) will be low because of fewer resources. Finally their extinction rate (e_D) is higher. In other words, such an ecological scenario illustrates, in terms of the invasion condition (15), how increasing group facilitation makes it increasingly likely that a more extensive attractive basin of defection can be surmounted and cooperation can gain foothold.

Scenarios similar to the threshold model may apply to other levels of organization of adaptive biological systems. Aggregates of cells sometimes produce generic biochemical compounds, which are required in order to trigger a beneficial event. A specific local concentration has to be reached in order to increase cell proliferation and hence fitness. The onset of aberrant neovascularization in tumour growth has been modelled as an evolutionary game process in which groups of cells compete for attracting the budding of existing blood vessels (Tomlinson, 1997; Bach et al., 2001). More precisely, certain threshold levels of vascular growth factor (VGF), a blood vessel stimulating compound, are required in order to attract the extension of newly formed blood vessels (Carmeliet and Jain, 2000). A model of neovascularization occurring as a discrete event in the among-cell competitive process with threshold conditions showed similarly complex patterns in the evolutionary proliferation dynamics (Bach et al., 2001).

Previous models have shown that mechanisms such as kin selection and reciprocation may become important in small and/or spatially stable groups and could hence facilitate cooperation (Hamilton, 1963; Trivers, 1971). Small groups tend to accumulate high degrees of local relatedness, which increase the potential for kin selection and thereby cooperation (especially in polygynous species such as e.g. Lions). Repeated interaction with neighbouring individuals may also favour cooperation due to reciprocation as for example in cells situated in solid tissue, which interact repeatedly with neighbouring cells (Bach et al., 2003). The mechanisms promoting cooperation have been most thoroughly investigated in evolutionary games with only two players as in the well known repeated games (Axelrod and Hamilton, 1981), games with punishment and reputation (Leimar and Hammerstein, 2001), or spatially structured games (Nowak and May, 1992). Such effects would most likely also promote cooperation in multiple player games. Nevertheless, the purpose of our model was to investigate the scope for cooperation and evolutionary dynamics in the multiple player threshold game and related games without invoking additional mechanisms already known to promote cooperation. Due to the general definitions of the cost and benefit this analysis may offer more suitable scenarios of the evolutionary dynamics of group interactions compared to previous models. However, it should be noted that this type of analysis is still based on certain assumptions that preclude additional realistic features potentially affecting group behaviour, such as e.g. instantaneous information on the other players' strategies and a corresponding conditional decision making.

One should note that the type of behaviour we have found in the threshold game, i.e. bifurcations and hysteresis, is only possible in games with at least three players. In fact, in two-player games a mixed ESS cannot coexist with a pure ESS for the same parameter values (Broom et al., 1997). This suggest that modelling scenarios with a set of two player games instead of an n-player game may cause the model to miss important aspects of the dynamics. The exclusive use of two player games is however a common practice, and should perhaps be exerted with caution.

Future work include plans to extend the threshold models to include a hierarchical structure with competitive relations among groups with repeated interactions.

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Note Added in Proof. The authors would like to clarify a statement made in the discussion. When stating that ESS bifurcations in two-strategy games only are possible in games with at least three players, we refer to *internal* bifurcations of saddle node type. Transcritical bifurcations altering the stability of monomorphic fixed points of the replicator equation or continuously transforming monomorphic ESSs to polymorphic ESSs can occur in two-player games. Hence, the difference between two- and n-player games is specifically that only the latter permits the emergence of new internal ESSs, paired with new unstable fixed points. This property allows a rich variety of distinct ESS profiles, as illustrated by Example 5. Inferentially, hysteresis behaviour in cost-benefit parameter space involving polymorph states of the population is only possible with games involving at least three players, whereas with two-player games hysteresis is limited to the population shifting among the monomorphic states.

Appendix A. Proofs

Proof of Proposition 4. A strategy x is an ESS if (3) is satisfied. Using the definition of W from (7) and a Taylor expansion around x the requirement for an ESS can be written as

$$\sum_{k=0}^{N-1} \frac{\varepsilon^k}{k!}\, g^{(k)}_{\mathbf{r,c}}(x)(y-x)^{k+1} < 0 \tag{A.1}$$

for all $y \in [0,1]$, $y \neq x$ and ε smaller than some $\varepsilon(y)$. Since ε can be chosen arbitrarily small, only the first term of the sum having $g^{(k)}_{\mathbf{r,c}}(x) \neq 0$ has to be taken into account.

For the pure strategies, (A.1) shows that $x=0$ is an ESS if $g_{\mathbf{r,c}}(0) < 0$ and that $x=1$ is an ESS if $g_{\mathbf{r,c}}(1) > 0$. If $g_{\mathbf{r,c}}(0) > 0$, (7) shows that $y=1$ is the unique best response to $x=0$, so in this case $x=0$ is not a NE. Similarly, $x=1$ is not a NE if $g_{\mathbf{r,c}}(1) < 0$.

For mixed strategies x, we see from (A.1) that if $g_{\mathbf{r,c}}(x) \neq 0$ or if an even integer k is the lowest such that $g^{(k)}_{\mathbf{r,c}}(x) \neq 0$, then the inequality (A.1) cannot be satisfied for all y because the term $(y-x)^{k+1}$ can be both positive and negative. However, if an odd integer k is the lowest such that $g^{(k)}_{\mathbf{r,c}}(x) \neq 0$, then the left hand side is always negative if $g^{(k)}_{\mathbf{r,c}}(x) < 0$ and always positive otherwise. $\square$

The special cases for $x=0$ and $x=1$ follows in the same way.

A useful property of $\tilde{g}_{\mathbf{r},c}(x)$ that we will use in the next proof is:

Proposition 9.

$$\tilde{g}'_{\mathbf{r},c}(x) = (N-1)\sum_{k=0}^{N-2}\binom{N-2}{k} x^k (1-x)^{N-2-k}\Delta^2 r_k. \tag{A.2}$$

This is proved by Motro (1991).

Proof of Proposition 7. By Proposition 9 it follows that

$$\frac{\mathrm{d}^2}{\mathrm{d}x^2}\,\tilde{g}_{\mathbf{r},c}(x) = (N-2)(N-1)\sum_{k=0}^{N-3}\binom{N-3}{k} \times x^k(1-x)^{N-3-k}\Delta^3 r_k.$$

Thus if $\Delta^3 r_i \leqslant 0$ for all i then $\tilde{g}_{\mathbf{r},c}(\tilde{x})$ is concave and has at most one critical point $\tilde{x}$. When additionally $\Delta^2 r_0 = \tilde{g}'_{\mathbf{r},c}(0) > 0$ and $\Delta^2 r_{N-2} = \tilde{g}_{\mathbf{r},c}(1) < 0$, this $\tilde{x}$ will exist and be a maximum. Let $c^* = \tilde{g}_{\mathbf{r},0}(x)$. For a given value of c, the maximal value $\tilde{g}_{\mathbf{r},c}$ takes is $c^* - c$. Thus $\tilde{g}_{\mathbf{r},c} = 0$ has no solutions when $c > c^*$.

When $c \leqslant c^*$, there is a solution to $\tilde{g}_{\mathbf{r},c}(x) = 0$ to the right of $\tilde{x}$ if and only if $\tilde{g}_{\mathbf{r},c}(1) = \Delta r_{N-1} - c \leqslant 0$. Due to the concavity of $\tilde{g}_{\mathbf{r},c}$ this solution is an ESS. A solution to the left of $\tilde{x}$ will not be an ESS, and statements (1), (2) and (3) follows. Statement (3) follows directly from Proposition 4. $\square$

Proof of Proposition 8. The statement is another way to express the condition that $\tilde{g}_{\mathbf{r},c}$ has exactly one critical point. As in the proof of Proposition 7, c^* is given by $\tilde{g}_{\mathbf{r},0}(\tilde{x})$. $\square$

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