Evolutionary stability for matrix games under time constraints

József Garay [*]   Villő Csiszár [†]   Tamás F. Móri [†]

December 8, 2016

Abstract

Game theory focuses on payoffs and typically ignores time constraints that play an important role in evolutionary processes where the repetition of games can depend on the strategies, too. We introduce a matrix game under time constraints, where each pairwise interaction has two consequences: both players receive a payoff and they cannot play the next game for a specified time duration. Thus our model is defined by two matrices: a payoff matrix and an average time duration matrix. Maynard Smith's concept of evolutionary stability is extended to this class of games.

We illustrate the effect of time constraints by the well-known prisoner's dilemma game, where additional time constraints can ensure the existence of unique evolutionary stable strategies (ESS), both pure and mixed, or the coexistence of two pure ESS.

Our general results may be useful in several fields of biology where evolutionary game theory is applied, principally in ecological games, where time constraints play an inevitable role.

Keywords: evolutionary stability, matrix game, prisoner's dilemma, sharing problem, time constraint

1 Introduction

Every interaction takes time. In classical economical and evolutionary game theory, the time durations of different interactions are not widely considered. However, in ecology, activity-dependent time constraints are important. For

---

[*]MTA-ELTE Theoretical Biology and Evolutionary Ecology Research Group and Department of Plant Systematics, Ecology and Theoretical Biology, Eötvös Loránd University, Pázmány P. s. 1/C, H-1117 Budapest, Hungary, e-mail: `garayj@caesar.elte.hu`

[†]Department of Probability Theory and Statistics, Eötvös Loránd University, Pázmány P. s. 1/C, H-1117 Budapest, Hungary, e-mail: `villo@ludens.elte.hu` and `mori@math.elte.hu`

instance, Holling-type functional response [14] takes into account that the number of active predators is less than their total number, since after a successful attack predators have to handle and digest their prey before they continue hunting. Moreover, in optimal foraging theory [7, 8], in ecological games on kleptoparasitism [3, 4, 5, 6, 26], and in the dispersal-foraging game [9, 10], time constraints have an essential effect on optimal behavior. Thus our main question arises: What is the effect of time constraints on the concept of evolutionary stability in games within one species?

Our question is motivated by the following lines of research. Our primary motivation originates in ecological games with time constraints describing the complex phenomenon of kleptoparasitism (e.g. [3, 4, 5, 6, 26]). The overwhelming majority of models on kleptoparasitism consider polymorphic populations [12]. The aim of this paper is to adapt Maynard Smith's standard concept of evolutionary stability to matrix games with time constraints in a monomorphic population.

Our secondary motivation comes from the classical prisoner's dilemma (PD) game, where cooperation can be achieved by taking account of some extra specific mechanism (e.g. [19, 21, 25, 27, 28]). Notice however that the original payoff matrix of the PD game is given by time (term of imprisonment, while the prisoner can not go out to rob). It is natural to ask whether the evolutionary stability of cooperation can be achieved by suitable time constraints. According to our knowledge, this is the first attempt to investigate the effect of time constraint in the PD.

To answer our main question, we introduce matrix games under time constraints, in which the players must wait after each interaction before they engage in the next one, and these waiting times depend on the pure strategies followed by the players. Then we conceive the definiton of ESS for this class of games. First, we derive formulas for the players' average payoff via heuristic calculation under two assumptions, then we introduce an exact mathematical model, where those requirements are met and the heuristic calculations get justified with rigorous proofs. For that we assume that the waiting times are exponentially distributed, thus we can use the standard method of continuous time Markov processes to describe the stationary state of the population (cf. [2, 30]). However, we emphasize the possibility that other, non-Markovian models could also statisfy our assumptions, and the heuristic calculations would remain valid for them.

We were also motivated by the "dynamical linking" model by Pacheco et al. [22, 23], where the number of repetitions of the interactions between two individuals depends on the payoff from the given interaction. That pair forming process modifies one of the basic assumptions of classical evolutionary games, namely, the randomness of interactions between players, since the connections between different phenotypes have different repetition numbers. In contrast, our model keeps the randomness of the pair forming process at each interaction, and after the interaction players have to wait before they get ready for the next interaction. We emphasize that both models have the same consequence: the

average interaction rates between different phenotypes are not proportional to the relative frequencies of phenotypes, unlike in classical evolutionary games.

Finally, we apply our general results in the following two cases. In the introduced prisoner's sharing game, the time constraints are given by the matrix of the prisoner's dilemma and the payoff matrix defines how the fraternal sharing is distorted by a symmetric zero-sum component with a strength of s that favors mutual cooperation if $s > 0$. When increasing s, first the defector, then a mixed strategy, and finally the cooperator is the unique evolutionarily stable strategy. In the second case, the prisoners' dilemma occurs for the payoff matrix. As the average time duration of defector strategy increases, first the defector is the unique evolutionarily stable strategy, after that the game becomes bistable, and finally the cooperator is the unique evolutionarily stable strategy.

2 A heuristic calculation of evolutionary stability

We consider pairwise interactions having different time durations. We have n pure strategies, and the phenotype is a probability distribution $p = (p_1, \ldots, p_n)^\top$ on these pure strategies. (Vectors are meant as columns; $^\top$ stands for transpose.) A matrix game under time constraints is defined by the following parameters. If the focal individual uses the i-th pure strategy and its opponent the j-th one, the focal individual's payoff is a_{ij}, and the focal individual can not play the next game during an average time duration $\tau_{ij} > 0$. Thus, each individual is either non-active or active; and only active individuals are ready to play the next game round. Hence our game is characterized by two matrices, the intake matrix $A = (a_{ij})_{n \times n}$, and the time constraint matrix $T = (\tau_{ij})_{n \times n}$.

In our heuristic calculation of evolutionary stability, we strictly follow Maynard Smith's monomorphic setup [16], as much as possible. The population is assumed to be sufficiently large and the generations do not overlap. All individuals can only differ in the strategy p and all individuals are the same from all other points of view of natural selection. Let us consider a resident population in which every individual has a resident phenotype p^*. Assume that mutation is rare enough and denote by ε the relative frequency of mutants. The rarity of mutation has two consequences: Firstly, the relative frequency of mutants is small, secondly, the time between two consecutive mutations is sufficiently long so that less fit phenotypes get selected out by natural selection. Thus only one mutant and one resident phenotype coexist at the same time. Then the relative frequency of residents is $\varepsilon^* = 1 - \varepsilon$. The interaction is well mixed: each active individual finds another active individual uniformly at random. Assume that the lifetime D of one generation is large enough and individuals play the above game during the whole D.

After an individual finishes an interaction, it looks for an opponent for the next interaction, which also takes time. The searching time depends on the

searching process. For instance, if active individuals A and B are looking for opponents, and each of them covers the average distance between them during τ_0, then the encounter only takes time $\tau_S = \tau_0/2$, since until the encounter both cover half the distance between them. The same is true if the random searching times are independent and exponentially distributed with equal means. In this case the interaction can follow as a result of either participant's finding the other one, hence the waiting time in fact is the minimum of two exponentially distributed searching times with mean τ_0, which is exponential with mean $\tau_0/2$. By symmetry, at every encounter both players must have the same probability to select and to be selected.

Of course, it can happen that a searching individual finds an inactive one; in this case the searching period starts over. We will term the time span between two searches (that is, τ_S plus the time of interaction, when the searching individual finds an active opponent) a *turn of activity*.

Our heuristic calculation is based on the following two assumptions.

Assumption 1. The population is in a stationary state, i.e., each individual having the same phenotype possesses the same activity distribution.

Assumption 2. The total intake of each phenotype is equal to the average intake in its stationary state (cf. [15]).

In order to calculate the fitness of mutant and resident phenotypes, we will consider a focal mutant, resp. a focal resident individual, who plays against the whole population. Since the interaction is well mixed, a focal individual (independently of its phenotype) has the following encounter distribution based on the stationary state of the whole population $(r, \varepsilon - r, r^*, \varepsilon^* - r^*)$, where r and r^* are the relative frequencies of active (interaction is possible) mutants and residents, resp., while $\varepsilon - r$ and $\varepsilon^* - r^*$ are the relative frequencies of inactive (interaction is not possible) mutants and residents, resp. We emphasize that these proportions are defined by the stationary distribution, thus ε, ε^*, r, r^* do not vary with time: the main point is that the state of the population is aperiodic. Furthermore, the encounter distribution depends on the phenotypes of resident and mutant.

Now, the time average of an arbitrary activity turn of a focal mutant individual is

$$E_p = \tau_S + r\, p^\top T p + r^* p^\top T p^*.$$

Indeed, τ_S is the time to find the next opponent to play the game against, r and r^* are the probabilities that the focal mutant meets an active mutant or an active resident individual in a stationary population, respectively. Finally, $p^\top T p$ resp. $p^\top T p^*$ is the average time duration when the focal mutant plays the game with a mutant or a resident opponent. Similarly, the time average of one turn of activity of a focal resident is

$$E_{p^*} = \tau_S + r\, p^{*\top} T p + r^* p^{*\top} T p^*.$$

The time constraint on interactions determines the average number of interactions of individuals during the lifetime D of one generation, thus the number of

4

games played by the mutant and that by the resident phenotype are defined as

$$G_p := \frac{D}{E_p} \quad \text{and} \quad G_{p^*} := \frac{D}{E_{p^*}},$$

respectively.

Since the interactions are well mixed during D (i.e., each individual interacts with mutant and resident with probability r and r^*, respectively), each mutant individual has the following total average payoff,

$$G_p(r\, p^\top A p + r^* p^\top A p^*).$$

Indeed, here $r\, p^\top A p + r^* p^\top A p^*$ is the average intake of the focal mutant individual from one turn of interaction. Similarly, the total average payoff of a resident individual is

$$G_{p^*}(r\, p^{*\top} A p + r^* p^{*\top} A p^*).$$

Based on classical Darwinism, supposing that the mutant is rare enough, the mutant phenotype is outperformed by the resident phenotype if the fitness of the resident phenotype is higher than that of the mutant one, that is,

$$\frac{r\, p^{*\top} A p + r^* p^{*\top} A p^*}{\tau_S + r\, p^{*\top} T p + r^* p^{*\top} T p^*} > \frac{r\, p^\top A p + r^* p^\top A p^*}{\tau_S + r\, p^\top T p + r^* p^\top T p^*}. \tag{1}$$

When the population is sufficiently large and the mutation is rare enough, p^* is an ESS if in (1) strict inequality holds for all possible mutant strategies $p \neq p^*$.

We emphasize that the above formalism includes the original ESS definition of Maynard Smith [16]. Indeed, if each interaction takes the same amount of time, i.e., $\tau_{ij} = \tau$ for all i, j, then $E_p = E_{p^*}$ holds for all mutant phenotypes p, so we get back to the traditional definition of an ESS.

The assumption that the population is in a stationary state is a crucial one, since if the active and non-active states of the population follow periodically, then our heuristic calculation does not work, because the "speed" over the period affects the average payoff and the average time duration of one interaction for the phenotypes. However, fast convergence to equilibrium in a well mixed population can reasonably be assumed in most cases (see [15]).

The obstacle to an analytical condition for (1) is that the stationary distribution of the population depends on the time constraint matrix T, and the strategies of mutant and resident phenotypes. We will make the assumption that the mutant's frequency is arbitrarily small. Formally, if $\varepsilon \to 0$, then $r \to 0$, thus, from (1) we get

$$\frac{p^{*\top} A p^*}{\tau_S + r^*(0)\, p^{*\top} T p^*} \geq \frac{p^\top A p^*}{\tau_S + r^*(0)\, p^\top T p^*}, \tag{2}$$

where $r^*(0)$ denotes the limit of r^* as the relative frequency ε of mutants tends to zero, thus $r^*(0)$ is the proportion of active residents in the pure resident

population in the stationary state. Obviously, though (1) implies (2), the reverse does not hold in general (cf. Theorem 2 later). However, if (2) holds with strict inequality, then condition (1) is satisfied provided the frequency of mutants is sufficiently small.

Next, we will compute $r^*(0)$ in particular cases. Since we concentrate on the case where $\varepsilon \to 0$, we can suppose that the whole population consists of resident individuals. Remember that the population is supposed to be in stationary state. In this case, the average duration of one turn of activity of an arbitrary resident individual is

$$\tau_S + r^*(0)\, p^{*\top} T p^*.$$

During this period, τ_S is the time when the individual is active. Consequently, the proportion of time when an individual is active, is equal to

$$\frac{\tau_S}{\tau_S + r^*(0)\, p^{*\top} T p^*}\,,$$

and by stationarity, this is just the probability that an individual is active at a given moment. Hence, it must be equal to the proportion of active individuals in the population, as well, leading to the following equation.

$$r^*(0) = \frac{\tau_S}{\tau_S + r^*(0)\, p^{*\top} T p^*}\,. \tag{3}$$

The only positive solution of (3) is

$$r^*(0) = \frac{2}{1 + \sqrt{1 + \frac{4}{\tau_S}\, p^{*\top} T p^*}}\,. \tag{4}$$

Thus our heuristic calculation ends at the following Nash equilibrium condition, for all possible mutant strategies $p \neq p^*$

$$\frac{\frac{p^{*\top} A p^*}{2}}{\tau_S + \frac{1 + \sqrt{1 + \frac{4}{\tau_S}\, p^{*\top} T p^*}}{} \, p^{*\top} T p^*} \geq \frac{\frac{p^{\top} A p^*}{2}}{\tau_S + \frac{1 + \sqrt{1 + \frac{4}{\tau_S}\, p^{*\top} T p^*}}{} \, p^{\top} T p^*}\,.$$

In section 4 and in subsection 3.3.3 we give examples where the above Nash equilibrium is strict.

Clearly, the above intuitive reasoning is strictly based on Assumptions 1 and 2. In Section 3, in the framework of a continuous time Markov model, we will see that the above reasoning works, if the searching and waiting times are supposed to be independent and exponentially distributed, with means contained in the time constraint matrix T. The main point is that this kind of Markov process always has a stationary distribution and, in the long run, it leads to the same results that our intuitive calculations give. Furthermore, in the framework of our Markov process we calculate the stability condition for a matrix game under time constraints.

6

3 A Markov model

In this section, we introduce a more general mathematical model where the assumptions we needed for the heuristic calculations are met. Detailed proofs of this section's results can be found in Appendix A.1.

Consider a polymorphic population with m phenotypes, consisting of N_1, N_2 ..., N_m individuals, resp. Let $N = N_1 + \cdots + N_m$, the total size of the population.

Each individual can be either active or inactive. Active individuals are searching for opponents to interact with. Searching takes time τ_0 on average. In this period the searching individual can also be selected by another active one for interaction. Should it not be the case, at the end of the searching period the searching individual selects an opponent uniformly at random. If the selected opponent turns out to be inactive, the searching period starts over. Interaction is assumed to be instantaneous, but it is followed by a time of inactivity before participants become active again. In an interaction both participants can choose one of n possible pure strategies. Their choice is independent and random (a mixed strategy), and the probability disribution depends on the phenotype: a type i individual chooses strategy u with probability p_{iu}, $1 \leq i \leq m$, $1 \leq u \leq n$. When an individual following strategy u interacts with one following strategy v, its intake is a_{uv}, and it will be inactive for time τ_{uv} in average. Active and inactive periods follow each other alternately.

Thus, the environment is characterized by the mean searching time τ_0 and two $n \times n$ matrices: the intake matrix $A = (a_{uv})$, and the inactivity time matrix $T = (\tau_{uv})$. Note that these matrices need not be symmetric. Further parameters of the model are the phenotype sizes N_1, ..., N_m and the mixed strategies p_1, ..., p_m.

We are interested in the average intake of each phenotype per individual and per unit time in the long run, as a function of the strategy distributions. For a continuous time Markov model we suppose all waiting times independent and exponentially distributed with prescribed mean. Each individual can be in the state of activity, denoted by zero, or in state (u, v), which means that it is inactive after an interaction of type (u, v). The state of the whole population is therefore described by an N-vector in segmented form

$$s = \left(s_{11}, \ldots, s_{1,N_1} \,|\, s_{21}, \ldots, s_{2,N_2} \,|\, \ldots \,|\, s_{m1}, \ldots, s_{m,N_m} \right),$$

where each coordinate belongs to the set

$$\{0\} \cup \{(u, v) : 1 \leq u \leq n,\, 1 \leq v \leq n\}.$$

The set $\mathcal{S}$ of such vectors is the state space of our continuous time homogeneous Markov chain. Though this state space is huge, $|\mathcal{S}| = (n^2 + 1)^N$, it is still finite. To describe the transition rates we only indicate the coordinates that change. There are two kinds of transitions: firstly, when two active individuals meet and interact; secondly, when an inactive individual becomes active again.

- $s_{ij} : 0 \mapsto (u, v)$ and $s_{k\ell} : 0 \mapsto (v, u)$, where either $i < k$, or $i = k$ and $j < \ell$, with rate

$$\frac{2}{\tau_0} \cdot \frac{p_{iu} p_{kv}}{N - 1}$$

  (here the multiplier 2 is present because both individuals can be the chooser).

- $s_{ij} : (u, v) \mapsto 0$, with rate $\dfrac{1}{\tau_{uv}}$.

This Markov chain is clearly irreducible, hence ergodic (positive recurrent). It has a unique stationary distribution, which can be obtained by solving a system of linear equations. Let us label the states from 1 to $|\mathcal{S}|$ arbitrarily (e.g., if zero coordinates are replaced with pairs $(0,0)$, then $\mathcal{S}$ can be considered a subset of $\{0, 1, 2, \dots\}^{2N}$, and lexicographic labelling can be applied). Construct the infinitesimal generator matrix Λ by writing the transition rates at the off-diagonal positions, while the leading diagonal terms are such that all row sums are 0. Then the row vector $q^\top$ of the stationary distribution satisfies $q^\top \Lambda = 0$. Properties of continuous time Markov chains can be found e.g. in [18].

3.1 Average intake

Theorem 1. *Let W_i denote the limit of the average intake of phenotype i per individual and per time unit, as first the time of observation, then also the size N of the whole population tends to infinity, in such a way that the proportions N_i/N converge to ε_i, $0 < \varepsilon_i < 1$, $i = 1, \dots, m$. Then*

$$W_i = \frac{2\varrho_i}{\tau_0} \sum_{j=1}^m p_i^\top A p_j \, \varepsilon_j \varrho_j \,, \quad 1 \le i \le m, \tag{5}$$

where $\varrho_1, \dots, \varrho_m$ are the only nonnegative solution of the system of equations

$$\varrho_i = \frac{1}{1 + \frac{2}{\tau_0} \sum_{j=1}^m p_i^\top T p_j \, \varepsilon_j \varrho_j} \,, \quad 1 \le i \le m. \tag{6}$$

Remark 1. Equivalently,

$$W_i = \frac{p_i^\top A z}{1 + p_i^\top T z} \,, \quad 1 \le i \le m, \tag{7}$$

where the vector $z \in \mathbb{R}^n$ satisfies

$$z = \frac{2}{\tau_0} \sum_{j=1}^m \frac{\varepsilon_j \, p_j}{1 + p_j^\top T z} \,. \tag{8}$$

3.2 Particular cases

Let us examine how our formulas are simplified in certain particular cases.

3.2.1 Rare mutations

Suppose $\varepsilon_1 \to 1$. This is the case when rare mutations attempt to invade a large resident population. Phenotype 1 is resident, phenotypes 2, ..., m are different types of mutants. Then in the limit we obtain that

$$\varrho_i = \frac{1}{1 + \frac{2}{\tau_0}\, p_i^\top T p_1\, \varrho_1}, \quad 1 \le i \le m.$$

Particularly, by setting $i = 1$ we get a quadratic equation for ϱ_1, from where

$$\varrho_1 = \frac{2}{1 + \sqrt{1 + \frac{8}{\tau_0}\, p_1^\top T p_1}}.$$

The average intake of phenotype i is

$$W_i = \frac{\frac{2}{\tau_0}\, p_i^\top A p_1\, \varrho_1}{1 + \frac{2}{\tau_0}\, p_i^\top T p_1\, \varrho_1} = \frac{p_i^\top A p_1}{\frac{\tau_0}{4}\left(1 + \sqrt{1 + \frac{8}{\tau_0}\, p_1^\top T p_1}\right) + p_i^\top T p_1}$$

Since W_1 does not depend on the competing strategies p_i, $i \ge 2$, and for $i \ge 2$, W_i only depends on p_1 and p_i, it follows that if p_1 is an ESS, then it still prevents invasion in the presence of arbitrary many invading phenotypes provided they are rare enough. (Note that ESS is defined as the strategy protecting against *one* rare invading mutant phenotype.) This may serve as a starting point for extending evolutionary stability from a monomorhic to a polymorphic setup.

3.2.2 Negligible searching time

Suppose that $\tau_0 \to 0$. If there is no searching time at all, then there cannot be more than one active individuals. Either every individual is inactive, or, when one becomes active, it has to wait for another one to be active. As soon as it occurs, they interact, and a new period of no active individuals begins. This means that all $\varrho_i = 0$, and our formulas (5), (6), and (8) take the form of $0/0$. Notice that ϱ_i tends to 0 in the order of $\sqrt{\tau_0}$. Let $\varrho_i = \sigma_i \sqrt{\tau_0}$, then

$$\sigma_i = \frac{1}{\sqrt{\tau_0} + 2\sum_{j=1}^{m} p_i^\top T p_j\, \varepsilon_j \sigma_j},$$

hence, in the limit we have

$$\sigma_i = \frac{1}{2\sum_{j=1}^{m} p_i^\top T p_j\, \varepsilon_j \sigma_j}$$

and

$$W_i = 2\sigma_i \sum_{j=1}^{m} p_i^\top A p_j\, \varepsilon_j \sigma_j = \frac{\sum_{j=1}^{m} p_i^\top A p_j\, \varepsilon_j \sigma_j}{\sum_{j=1}^{m} p_i^\top T p_j\, \varepsilon_j \sigma_j}.$$

3.2.3   The length of the inactive period is proportional to the intake

Suppose $A = \kappa T$. In this case from (5) and (6) we get

$$W_i = \frac{2\varrho_i\kappa}{\tau_0}\sum_{j=1}^{m} p_i^\top T p_j\, \varepsilon_j \varrho_j = \varrho_i\kappa\left(\frac{1}{\varrho_i} - 1\right) = \kappa(1 - \varrho_i);$$

that is, the less time is spent active (waiting for interaction), the larger the average intake is. Thus, a mixed strategy p_i outperforms all the others if and only if $\varrho_i < \varrho_j$ for all $j \neq i$.

3.2.4   Constant mean length of inactivity

Suppose the length of inactivity does not depend on the type of interaction. By changing the time unit one can always achieve $\tau_{ij} = 1$ for all pairs (i, j). Now, from (6) we can compute ϱ_i explicitly. Since $p_i^\top T p_j = 1$, we have

$$\varrho_i = \frac{1}{1 + \frac{2}{\tau_0}\sum_{j=1}^{m} \varepsilon_j \varrho_j}\,;$$

thus $\varrho_1 = \varrho_2 = \cdots = \varrho_m = \varrho$, where

$$\varrho = \frac{1}{1 + \frac{2}{\tau_0}\varrho}\,.$$

Solving the quadratic equation we get

$$\varrho = \frac{\tau_0}{4}\left(-1 + \sqrt{1 + \frac{8}{\tau_0}}\,\right) = \frac{2}{1 + \sqrt{1 + \frac{8}{\tau_0}}}\,,$$

and finally

$$W_i = \frac{2\varrho^2}{\tau_0}\sum_{j=1}^{m} \varepsilon_j\, p_i^\top A p_j\,.$$

That is, the proportion of active individuals is the same for each phenotype, and the average intake is proportional to the expected intake in one interaction, where the opponent is chosen from the whole population uniformly at random.

3.3   Evolutionarily stable strategies

As we have seen in 3.2.1, it is sufficient to consider only one mutant phenotype. Let us modify our notations a little. Instead of using numerical subscripts, we will mark quantities corresponding to the residents by a superscript *, while the same quantity without asterisk refers to mutants. Thus, we will write p^*, p, ε^*, ε, ϱ^*, ϱ, W^*, and W.

3.3.1 Conditions for ESS

Recall that a strategy p^* is called an ESS, if for an arbitrary mutant strategy $p \neq p^*$ we have $W^* > W$; that is, the inequality

$$\varrho^* \left(p^{*\top} A p^* \varepsilon^* \varrho^* + p^{*\top} A p \, \varepsilon \varrho \right) > \varrho \left(p^\top A p^* \varepsilon^* \varrho^* + p^\top A p \, \varepsilon \varrho \right) \tag{9}$$

holds for every ε small enough. Note that ϱ^* and ϱ depend on ε, and this dependence will be denoted when necessary. Namely, they can be obtained as the only nonnegative solution of the system

$$\varrho^* \left[1 + \tfrac{2}{\tau_0} \left(p^{*\top} T p^* \varepsilon^* \varrho^* + p^{*\top} T p \, \varepsilon \varrho \right) \right] = 1,$$
$$\varrho \left[1 + \tfrac{2}{\tau_0} \left(p^\top T p^* \varepsilon^* \varrho^* + p^\top T p \, \varepsilon \varrho \right) \right] = 1. \tag{10}$$

Theorem 2. *Strategy p^* is an ESS if for every strategy $p \neq p^*$*

$$\varrho_0^* \, p^{*\top} A p^* \geq \varrho_0 \, p^\top A p^*, \tag{11}$$

and, if

$$\varrho_0^* \, p^{*\top} A p^* = \varrho_0 \, p^\top A p^*, \tag{12}$$

then

$$\varrho_0^* \left(\vartheta^* \, p^{*\top} A p^* + p^{*\top} A p \right) > \varrho_0 \left(\vartheta \, p^\top A p^* + p^\top A p \right), \tag{13}$$

where

$$\varrho_0^* = \frac{2}{1 + \sqrt{1 + \tfrac{8}{\tau_0} \, p^{*\top} T p^*}}, \qquad \varrho_0 = \frac{1}{1 + \tfrac{2}{\tau_0} \, p^\top T p^* \varrho_0^*}, \tag{14}$$

$$\vartheta^* = \frac{1 - \varrho_0^*}{2 - \varrho_0^*} \left(\frac{\varrho_0^*}{\varrho_0} - \frac{p^{*\top} T p}{p^{*\top} T p^*} \right), \tag{15}$$

$$\vartheta = (1 - \varrho_0) \left(\frac{\varrho_0^*}{\varrho_0} - \frac{p^\top T p}{p^\top T p^*} - \vartheta^* \right). \tag{16}$$

If (11) holds for every $p \neq p^*$ we speak of a *Nash equilibrium*, while formula (13) is referred to as *the stability condition*.

Remark 2. Suppose equality $\vartheta = \vartheta^*$ happens to hold true in addition to (12). This can be rewritten in the following symmetric form,

$$\frac{1 - \varrho_0^*}{2 - \varrho_0^*} \left(\frac{\varrho_0^*}{\varrho_0} - \frac{p^{*\top} T p}{p^{*\top} T p^*} \right) = \frac{1 - \varrho_0}{2 - \varrho_0} \left(\frac{\varrho_0^*}{\varrho_0} - \frac{p^\top T p}{p^\top T p^*} \right).$$

Then condition (13) reduces to

$$\varrho_0^* \, p^{*\top} A p > \varrho_0 \, p^\top A p,$$

which resembles what is sometimes called Maynard Smith's second (stability) condition [17].

3.3.2 Negligible searching time

Here we will study how the conditions of an ESS change if the mean searching time τ_0 becomes negligible. Let $\tau_0 \to 0$. In the limit we obtain the following sufficient conditions for a strategy p^* to be ESS.

Theorem 3. *Strategy p^* is an ESS if for every strategy $p \neq p^*$*

$$\frac{p^{*\top} A p^*}{p^{*\top} T p^*} \geq \frac{p^\top A p^*}{p^\top T p^*}, \tag{17}$$

and, if

$$p^\top T p^* \cdot p^{*\top} A p^* = p^{*\top} T p^* \cdot p^\top A p^*, \tag{18}$$

then

$$p^\top T p \cdot p^{*\top} A p^* + p^\top T p^* \cdot p^{*\top} A p > p^{*\top} T p \cdot p^\top A p^* + p^{*\top} T p^* \cdot p^\top A p. \tag{19}$$

3.3.3 NE and ESS

A plausible question is whether an ESS under time constraint always exists. The answer is, of course, negative, since an ESS does not always exist in standard games either, which constitute a particular case. The following examples utilize that the matrix game with time constraints in consideration can be connected with games without time constraints.

Example 1. Elementary calculation shows that a classical *totally mixed* NE of a matrix game A (i.e., all coordinates of p^* are positive) satisfies $p^{*\top} A p^* = p^\top A p^*$ for all $p \neq p^*$, hence it satisfies

$$\frac{p^{*\top} A p^*}{1 + \frac{2}{\tau_0} p^{*\top} T p^* \varrho_0^*} \geq \frac{p^\top A p^*}{1 + \frac{2}{\tau_0} p^\top T p^* \varrho_0^*}$$

(which is necessary for p^* to be an ESS), if and only if $p^{*\top} T p^* = p^\top T p^*$ for all $p \neq p^*$, which means that p^* is a mixed NE for matrix T, as well.

Example 2. Elementary calculation shows that, if both inequalities $p^\top A p^* \leq p^{*\top} A p^*$ and $\frac{p^{*\top} A p^*}{p^{*\top} T p^*} \geq \frac{p^\top A p^*}{p^\top T p^*}$ hold, and at least one of them is strict, then a strict inequality holds in (2). In other words, (2) is satisfied with strict inequality, if p^* is a NE for the matrix game defined by matrix A, and p^* is also a NE for the game where the payoff function of a p-strategist against a q-strategist is $p^\top A q / p^\top T q$ (cf. [9]), and, furthermore, at least one of these NE-s is a strict one.

Example 3. If A is a positive matrix, both inequalities $p^\top A p^* \leq p^{*\top} A p^*$ and $p^\top T p^* \geq p^{*\top} T p^*$ hold, and at least one of them is strict, then so is inequality (2). Consider a positive matrix A for which p^* is a strict ESS. Let $T = -A + C$, where all entries of matrix C are equal to $1 + \max a_{ij}$. Clearly, matrix T is also positive, and $p^\top A p^* < p^{*\top} A p^*$ for all $p \neq p^*$ implies that $p^\top T p^* > p^{*\top} T p^*$. (Of

course, this can only hold for pure strategies p^*.) So in this special class of matrix games under time constraint there exists ESS. Observe that an individual, by choosing strategy p^*, simultaneously maximizes its average intake and minimizes the average time duration of one round.

Example 4. One can ask wether the well-known fact that there is no classical mixed ESS in a zero-sum matrix game (see [13]) remains valid for the matrix game under time constraint. Zero sum matrix games are associated with skew symmetric matrices A, that is, for which $a_{ij} = -a_{ji}$ for every i, j. By symmetry, the value of the game is 0, and both players have the same mixed NE strategy. Note that $p^\top A q = -q^\top A p$, and hence $p^\top A p = 0$ for all vectors p and q.

Take an arbitrary time duration matrix T. Condition (9) for a resident strategy p^* to be ESS reduces to

$$\frac{p^\top A p^* \varepsilon^* \varrho^*}{\frac{1}{2}\tau_0 + p^\top T p \varepsilon \varrho + p^\top T p^* \varepsilon^* \varrho^*} < \frac{p^{*\top} A p \varepsilon \varrho}{\frac{1}{2}\tau_0 + p^{*\top} T p \varepsilon \varrho + p^{*\top} T p^* \varepsilon^* \varrho^*}$$

(ε is small enough). Since there is no mixed ESS in the original game, for every mixed resident strategy p^* there exists a mutant strategy p such that $p^\top A p^* \geq 0 \geq p^{*\top} A p$. Consequently,

$$\frac{p^\top A p^* \varepsilon^* \varrho^*}{\frac{1}{2}\tau_0 + p^\top T p \varepsilon \varrho + p^\top T p^* \varepsilon^* \varrho^*} \geq 0 \geq \frac{p^{*\top} A p \varepsilon \varrho}{\frac{1}{2}\tau_0 + p^{*\top} T p \varepsilon \varrho + p^{*\top} T p^* \varepsilon^* \varrho^*} \ .$$

Thus, introduction of time constraints would not make p^* an ESS, either.

4 Prisoner's dilemma revisited

Now, we are going to answer the question whether time constraints can guarantee the evolutionary stability of the cooperator. We consider two matrix games under time constraint: firstly, the time constraint matrix, and secondly, the intake matrix is of PD type. In both games, prisoners aim at maximizing their average loot during their life. Though our examples are quite arbitrary, they illustrate the possibility of a unique ESS, pure or mixed, and the coexistence of two pure ESS.

For computational details see section A.2 of the Appendix.

4.1 Prisoner's sharing game

Start from the original story of the PD with the following matrix of time to be served in prison

$$\begin{array}{ccc} & \text{Cooperate} & \text{Defect} \\ \text{Cooperate} & \text{2 years} & \text{4 years} \\ \text{Defect} & \text{1 year} & \text{3 years} \end{array} \ , \quad \text{thus } T = \begin{bmatrix} 2 & 4 \\ 1 & 3 \end{bmatrix}.$$

It is well-known that the defector strategy minimizes the average waiting time. However, the original story does not consider what the prisoners had done before they got arrested. There are plausible scenarios where the loot is not exactly halved. E.g., assume the two robbers agree to deposit a part of the loot with a fence who does not trust in a person who collaborates with the police. In such a case the cooperator gets more. On the other hand, since the defector has less time to serve in prison, he can access the hidden loot earlier and take more. Intuitively, if the cooperator gets the smaller part of the loot, then the defector strategy maximizes the intake and minimizes the waiting time simultaneously, so the defector must be evolutionarily stable. However, if the cooperator gets the bigger part of the loot, then the defector strategy minimizes the waiting time, but the cooperator strategy maximizes the intake, so there is a trade-off between intake and waiting time. Based on that we consider the following intake matrix.

$$
\begin{array}{ccc}
 & \text{Cooperate} & \text{Defect} \\
\text{Cooperate} & \frac{1}{2} & \frac{1+s}{2} \\
\text{Defect} & \frac{1-s}{2} & \frac{1}{2}
\end{array}
\quad , \quad \text{thus } A = \frac{1}{2}\begin{bmatrix} 1 & 1+s \\ 1-s & 1 \end{bmatrix}.
$$

A natural question is whether there exists a sharing parameter s such that purely "rational" robbers might cooperate? For the sake of simplicity, let $\tau_0 = 2$ (the arrangement of the robbery is quite a long process, compared to the punishment). Then, if $s \leq s_1 = 0.188$, the possibly increased share of loot still cannot compensate for longer time served in prison, so the defector strategy is the only ESS. On the other hand, if $s \geq s_2 = 0.25$, the situation is reversed, and the cooperator strategy proves to be an ESS. For every $s_1 < s < s_2$ there exists a unique ESS, which is a mixed strategy, see Appendix A.2.1.

4.2 Prisoner's dilemma under time constraint

Consider the canonical PD payoff matrix as the intake matrix

$$
\begin{array}{ccc}
 & \text{Cooperate} & \text{Defect} \\
\text{Cooperate} & R = 3 & S = 1 \\
\text{Defect} & T = 4 & P = 2
\end{array}
\quad , \quad \text{thus } A = \begin{bmatrix} 3 & 1 \\ 4 & 2 \end{bmatrix}.
$$

It is a prisoners' dilemma game in the strong sense, because $T > R > P > S$. In addition, $2R > T + S$, which is the condition for stability of cooperation in the iterated PD. In the framework of classical matrix games, without loss of generality, we assume that $S > 0$, which only means that the robbery is remunerative. Without loss of generality we can assume that $\tau_0 = 2$. Now, we have to set the time constraints. Intuitively, if the defector has sufficiently long inactivity time, then his average intake will be smaller than the cooperator's. In addition, if the average waiting time of defectors increases then so does the interaction rate between cooperators, and this increases the cooperator's average intake. Thus, for the sake of simplicity let us consider the following

time duration matrix,

$$
\begin{array}{lcc}
 & \text{Cooperate} & \text{Defect} \\
\text{Cooperate} & \tau_{11} = 1 & \tau_{12} = 1 \\
\text{Defect} & \tau_{21} = t & \tau_{22} = t
\end{array}
\quad , \quad \text{so } T = \begin{bmatrix} 1 & 1 \\ t & t \end{bmatrix}.
$$

In this game we get, on the one hand, that if $t \leq t_1 = 1.872$, then the defector strategy is the only ESS. On the other hand, if $t \geq t_2 = 4.982$, the cooperator strategy is the only ESS. Finally, for t strictly between t_1 and t_2 there are two ESS: both the cooperator and the defector are pure ESS (bistable case). In this game no mixed strategy can be an ESS (see Appendix A.2.2).

5 Summary

The evolutionary stability of cooperative strategies is well studied; for instance, when the interactions occur either on a social network [25, 24, 1] or locally on a two dimensional surface [20, 21]. Our results point out that time costraints can also guarantee the evolutionary stability of cooperation. Similar conclusions are reported by Pacheco et al. [22, 23], who studied the consequences of dynamical linking, where the number of repetitions of the interactions between two individuals depends on the payoff from the given interaction. We note that both in the dynamical linking model and in our example in subsection 4.2, the same factor implies the evolutionary stability of cooperation: namely that the interaction rate between cooperators is high enough.

Finally, as we have already mentioned in the introduction, time constraints have an essential effect on the solution in optimal foraging theory. We think that our concept presented here will be useful in the study of ecological games. For instance, the Hawk-Dove game can be used to model territorial fights and kleptoparasitism. In both these ecological selection situations, time constraints are important. In kleptoparasitism, the time duration of a fight for a food item is not equal to that of searching for a food item. In the Hawk-Dove game, on the other hand, the presence of recovery time decreases the number of active hawk strategists. In general, in all selection situations when matrix games are used and there are time constraints, the ESS will change, as we have shown in the PD game.

Authors are indebted to an anonymous referee whose careful work and valuable comments significantly helped with improving the quality of this paper.

A   Appendix

In this section, we present the proofs of Theorems 1–3, and detailed computations for the numerical examples of Section 4.

A.1   Proofs of Theorems 1–3

First we need two auxiliary lemmas, interesting in their own right.

The following simple result, stated in a more general form, implies that for each phenotype the limit of the average intake per individual and per time unit as the time of observation tends to infinity exists almost surely.

Lemma 1. *Consider a continuous time irreducible Markov chain with finite state space $\mathcal{S}$. Let λ_{ij} denote the rate of transition $i \to j$ ($i \neq j$), and let $(q_i, \ i \in \mathcal{S})$ be the (unique) stationary distribution. Let $N_{ij}(t)$ denote the number of $i \to j$ transitions up to time t, and finally, let $f : \mathcal{S} \times \mathcal{S} \to \mathbb{R}$ be an arbitrary function. Then*

$$V(t) = \frac{1}{t} \sum_{i \neq j} N_{ij}(t) f(i,j) \to V = \sum_{i \neq j} q_i \lambda_{ij} f(i,j)$$

almost surely as $t \to \infty$, independently of the initial state.

Proof. It is clearly sufficient to show that $\lim_{t \to \infty} t^{-1} N_{ij}(t) = q_i \lambda_{ij}$. This is intuitively clear, because the probability that an $i \to j$ transition occurs in a time interval of infinitesimally small length δt is just $q_i \lambda_{ij} \delta t$. More precisely, let $R_i(t)$ denote the number of visits at state i. By the ergodicity of the process the time spent in state i up to t is asymptotically equal to $q_i t$ as $t \to \infty$, i.e., the ratio of the two quantities converges to 1 with probability 1. On the other hand, the duration of a stay in state i is exponential with mean $\left(\sum_{k \neq i} \lambda_{ik} \right)^{-1}$, hence, by the strong law of large numbers, the time spent in state i is asymptotically equal to $R_i(t) \left(\sum_{k \neq i} \lambda_{ik} \right)^{-1}$. Consequently, $R_i(t) \sim q_i \sum_{k \neq i} \lambda_{ik} \, t$ (here, as usual, $\sim$ stands for "asymptotically equal"). The probability that the chain, staying in state i, will step to j the next time, is $\lambda_{ij} \left(\sum_{k \neq i} \lambda_{ik} \right)^{-1}$, hence

$$N_{ij}(t) \sim R_i(t) \frac{\lambda_{ij}}{\sum_{k \neq i} \lambda_{ik}} \sim q_i \lambda_{ij} t$$

with probability 1, as $t \to \infty$. □

When applying this lemma we can always suppose that our Markov process is stationary, for the limit is independent of the initial distribution.

Lemma 2. *The following system of nonlinear equations in m variables,*

$$x_i = \frac{1}{1 + \sum_{j=1}^m c_{ij} x_j} \,, \quad 1 \le i \le m,$$

where the c_{ij} are positive numbers, has a unique solution in the unit hypercube $[0,1]^m$.

Proof. The function

$$f(x) = \left(\frac{1}{1 + \sum_{j=1}^m c_{ij} x_j} \,, \ 1 \le i \le m \right)$$

continuously maps the hypercube into itself. By Brouwer's fixed point theorem [11, Ch.5] there exists an $x \in [0,1]^m$ such that $x = f(x)$. We have to show that this fixed point is unique. Suppose x and y are different fixed points. Every coordinate function of f is strictly decreasing in all its variables, hence if $x \le y$ held coordinatewise, then $x = f(x) > f(y) = y$ would also follow, a contradiction. We therefore have $M = \max_{1 \le i \le m}(x_i / y_i) > 1$. Consequently,

$$\frac{y_i}{x_i} = \frac{1 + \sum_{j=1}^m c_{ij} x_j}{1 + \sum_{j=1}^m c_{ij} y_j} \le \frac{1 + \sum_{j=1}^m c_{ij} y_j M}{1 + \sum_{j=1}^m c_{ij} y_j} < M,$$

thus

$$\max_{1 \le i \le m} \frac{y_i}{x_i} < \max_{1 \le i \le m} \frac{x_i}{y_i}.$$

By symmetry, the opposite inequality must be true as well, thus there cannot be more than one fixed points. $\square$

Proof of Theorem 1. By Lemma 1, for the computations we may suppose that our Markov process started from the stationary distribution, hence it is a stationary process.

The transition rate matrix Λ does not change if we permute the states of our Markov chain in such a way that only individuals of the same phenotype can be permuted. Consequently, the stationary distribution is also invariant to such permutations. Let us denote the state of the jth individual of the ith phenotype at time 0 by X_{ij}. It follows that $X_{i1} X_{i2}, \ldots, X_{i,N_i}$ are exchangeable random variables. Introduce $\pi_i = \mathbb{P}(X_{ij} = 0)$, and let Y_i denote the proportion of active individuals in phenotype i at time 0. Then the total intake of type i individuals in the infinitesimally small time interval $[0, \delta t)$ is equal to

$$\frac{N_i Y_i (N_i Y_i - 1)}{N - 1} \, p_i^\top A p_i \cdot \frac{2}{\tau_0} \, \delta t + \sum_{j \ne i} \frac{N_i N_j Y_i Y_j}{N - 1} \, p_i^\top A p_j \cdot \frac{2}{\tau_0} \, \delta t,$$

where the first term stands for the intake from interaction between two individuals of phenotype i, while the second sum contains the intake from interactions

of type i individuals with those of a different type. By Lemma 1 the time average of the per individual intake over a long interval converges almost surely to

$$\frac{1}{N-1}\left[N_i\,\mathbb{E}\left(Y_i\left(Y_i - \tfrac{1}{N_i}\right)\right)p_i^\top A p_i + \sum_{j \neq i} N_j\,\mathbb{E}\left(Y_i Y_j\right)p_i^\top A p_j\right]\frac{2}{\tau_0}. \qquad (20)$$

Writing T in place of A we get the average proportion of time an individual of phenotype i spends inactive. Thus,

$$1 - \pi_i = \frac{1}{N-1}\left[N_i\,\mathbb{E}\left(Y_i\left(Y_i - \tfrac{1}{N_i}\right)\right)p_i^\top T p_i\right.$$
$$\left. + \sum_{j \neq i} N_j\,\mathbb{E}\left(Y_i Y_j\right)p_i^\top T p_j\right]\frac{2}{\tau_0}. \qquad (21)$$

Now, let $N \to \infty$. We will show that

$$\lim_{N \to \infty}\mathbb{E}\left(Y_i\left(Y_i - \tfrac{1}{N_i}\right)\right) = \varrho_i^2, \quad \lim_{N \to \infty}\mathbb{E}\left(Y_i Y_j\right) = \varrho_i \varrho_j,$$

where the limiting proportions $\varrho_1, \ldots, \varrho_m$ satisfy (6).

Let η_{ij} denote the indicator of the event $\{X_{ij} = 0\}$, then $Y_i = (\eta_{i1} + \cdots + \eta_{i,N_i})/N_i$, and $\eta_{i1}, \eta_{i2}, \ldots, \eta_{i,N_i}$ are exchangeable for every fixed i. Moreover, they are negatively correlated, because the more active individuals are present, the easier can a fixed one find an active opponent, hence, the less is the stationary probability that it is active. Consequently,

$$\mathbb{V}\mathrm{ar}(Y_i) \leq \frac{1}{N_i}\mathbb{V}\mathrm{ar}(\eta_{i1}) = \frac{\pi_i(1 - \pi_i)}{N_i}\,.$$

It follows that the proportion of active individuals of phenotype i is more and more concentrated around its expectation, that is, $Y_i = \pi_i + o_p(1)$, as $N \to \infty$, where $o_p(1)$ denotes a remainder tending to 0 in probability. Note that π_i also varies with N, though this dependence is suppressed in the notation. By boundedness we have

$$\mathbb{E}\left(Y_i\left(Y_i - \tfrac{1}{N_i}\right)\right) - \pi_i^2 \to 0, \quad \mathbb{E}\left(Y_i Y_j\right) - \pi_i \pi_j \to 0,$$

as $N \to \infty$.

Consider an arbitrary subsequence $(N') \subset (N)$. Then one can pick a subsubsequence from it, along which the probabilities π_i converge. Let ϱ_i denote their limit, then from (21) we get that

$$1 - \varrho_i = \frac{2}{\tau_0}\left[\varepsilon_i \varrho_i^2 p_i^\top T p_i + \sum_{j \neq i}\varepsilon_j \varrho_i \varrho_j\,p_i^\top T p_j\right] = \frac{2\varrho_i}{\tau_0}\sum_{j=1}^m \varepsilon_j p_i^\top T p_j\,\varrho_j,$$

which is tantamount to (6). Let us apply Lemma 2 with $x_i = \varrho_i$ and $c_{ij} = \frac{2}{\tau_0}\,p_i^\top T p_j\,\varepsilon_j$. It follows that the limits ϱ_i are the same for all subsequences (N').

18

This implies that $\lim_{N \to \infty} \pi_i$ exists and is equal to ϱ_i. Finally, (5) is obtained by taking limit in (20) as $N \to \infty$.

For Remark 1 introduce $z = \frac{2}{\tau_0} \sum_{j=1}^{m} \varepsilon_j \varrho_j p_j$ and plug it back into (5) and (6) to obtain (7) and (8). $\qquad\square$

Proof of Theorem 2. Let $\varepsilon \to 0$. Then (9) can be written as

$$[\varrho_0^* + \varrho_0^{*\prime} \varepsilon + o(\varepsilon)]\, p^{*\top} A p^* \varepsilon^* \varrho^*(\varepsilon) + \varepsilon \varrho^*(\varepsilon) \varrho(\varepsilon)\, p^{*\top} A p$$
$$> [\varrho_0 + \varrho_0' \varepsilon + o(\varepsilon)]\, p^{\top} A p^* \varepsilon^* \varrho^*(\varepsilon) + \varepsilon \varrho(\varepsilon)^2\, p^{\top} A p,$$

where ϱ_0^* and ϱ_0 are right limits of $\varrho^*(\varepsilon)$, resp. $\varrho(\varepsilon)$ at zero; $\varrho_0^{*\prime}$ and ϱ_0' are right derivatives. Now, (9) holds for every sufficiently small positive ε, if (11), that is, equivalently,

$$\frac{p^{*\top} A p^*}{1 + \frac{2}{\tau_0} p^{*\top} T p^* \varrho_0^*} \geq \frac{p^{\top} A p^*}{1 + \frac{2}{\tau_0} p^{\top} T p^* \varrho_0^*}, \tag{22}$$

and, in addition, if

$$\varrho_0^* \, p^{*\top} A p^* = \varrho_0 \, p^{\top} A p^*, \tag{23}$$

then

$$\varrho_0^* \varrho_0^{*\prime} \, p^{*\top} A p^* + \varrho_0^* \varrho_0 \, p^{*\top} A p > \varrho_0^* \varrho_0' \, p^{\top} A p^* + \varrho_0^2 \, p^{\top} A p, \tag{24}$$

holds. Note that the quantities $\varrho_0^{*\prime}$, ϱ_0 and ϱ_0' depend on the inactivity time matrix T, but not on the intake matrix A. Let us compute them.

From 3.2.1 we already know (14).

For the derivatives let us differentiate (10). Then we get

$$\varrho_0^{*\prime} + \frac{2}{\tau_0} p^{*\top} T p^* \left(2\varrho_0^* \varrho_0^{*\prime} - (\varrho_0^*)^2\right) + \frac{2}{\tau_0} p^{*\top} T p \, \varrho_0^* \varrho_0 = 0, \tag{25}$$
$$\varrho_0' + \frac{2}{\tau_0} p^{\top} T p^* \left(\varrho_0^* \varrho_0' + \varrho_0 \varrho_0^{*\prime} - \varrho_0 \varrho_0^*\right) + \frac{2}{\tau_0} p^{\top} T p \, \varrho_0^2 = 0. \tag{26}$$

Multiplying (25) by ϱ_0^*, and substituting $(1 - \varrho_0^*)/p^{*\top} T p^*$ for $\frac{2}{\tau_0}(\varrho_0^*)^2$ we finally obtain

$$\varrho_0^{*\prime} = \frac{1 - \varrho_0^*}{2 - \varrho_0^*} \left(\varrho_0^* - \frac{p^{*\top} T p}{p^{*\top} T p^*} \, \varrho_0\right). \tag{27}$$

Similarly, multiplying (26) by ϱ_0, then substituting $1 - \varrho_0$ for $\frac{2}{\tau_0} p^{\top} T p^* \varrho_0 \varrho_0^*$ yields

$$\varrho_0' = \varrho_0(1 - \varrho_0) \left(1 - \frac{\varrho_0^{*\prime}}{\varrho_0^*} - \frac{p^{\top} T p}{p^{\top} T p^*} \, \frac{\varrho_0}{\varrho_0^*}\right). \tag{28}$$

In (13) $\vartheta^* = \varrho_0^{*\prime}/\varrho_0$, and $\vartheta = \varrho_0^* \varrho_0'/\varrho_0^2$. Hence (27) implies (15), and (28) implies (16). $\qquad\square$

Proof of Theorem 3. From 3.2.2 we already know that $\varrho \sim \sigma \sqrt{\tau_0}$, and $\varrho^* \sim \sigma^* \sqrt{\tau_0}$ as $\tau_0 \to 0$, where

$$2\sigma^* \left(p^{*\top} T p^* \varepsilon^* \sigma^* + p^{*\top} T p \, \varepsilon \sigma\right) = 1, \tag{29}$$
$$2\sigma \left(p^{\top} T p^* \varepsilon^* \sigma^* + p^{\top} T p \, \varepsilon \sigma\right) = 1. \tag{30}$$

In these terms, the limiting payoffs are

$$W^* = 2\sigma^* \left(p^{*\top} A p^* \varepsilon^* \sigma^* + p^{*\top} A p \, \varepsilon \sigma \right),$$
$$W = 2\sigma \left(p^\top A p^* \varepsilon^* \sigma^* + p^\top A p \, \varepsilon \sigma \right).$$

Here all quantities W, W^*, σ, σ^* depend on ε. Now let $\varepsilon \to 0$. Then p^* is ESS if and only if $W^* > W$ holds for every mutant strategy p and every sufficiently small ε. Thus, (9) must hold with σ and σ^* in place of ϱ and ϱ^*. Again, it follows that p^* is ESS, if

$$\sigma_0^* \, p^{*\top} A p^* \geq \sigma_0 \, p^\top A p^*, \tag{31}$$

and, if

$$\sigma_0^* \, p^{*\top} A p^* = \sigma_0 \, p^\top A p^*, \tag{32}$$

then

$$\sigma_0^* \sigma_0^{*\prime} \, p^{*\top} A p^* + \sigma_0^* \sigma_0 \, p^{*\top} A p > \sigma_0^* \sigma_0^\prime \, p^\top A p^* + \sigma_0^2 \, p^\top A p, \tag{33}$$

analogously to (11) and (23)-(24). From (29) and (30) we now have

$$2\sigma_0^{*2} \, p^{*\top} T p^* = 1, \quad 2\sigma_0^* \sigma_0 \, p^\top T p^* = 1, \tag{34}$$

hence

$$\frac{\sigma_0^*}{\sigma_0} = \frac{p^\top T p^*}{p^{*\top} T p^*}, \quad 2\sigma_0^2 \, p^\top T p^* = \frac{p^{*\top} T p^*}{p^\top T p^*}. \tag{35}$$

Let us differentiate (29) and (30). We get, on the one hand,

$$\left(2\sigma_0^* \sigma_0^{*\prime} - \sigma_0^{*2} \right) p^{*\top} T p^* + \sigma_0^* \sigma_0 \, p^{*\top} T p = 0,$$

which, combined with (34), implies

$$2\sigma_0 \sigma_0^{*\prime} \, p^\top T p^* = 2\sigma_0^* \sigma_0^{*\prime} \, p^{*\top} T p^* = \frac{1}{2} \left(1 - \frac{p^{*\top} T p}{p^\top T p^*} \right). \tag{36}$$

On the other hand,

$$2 \left(\sigma_0^* \sigma_0^\prime + \sigma_0 \sigma_0^{*\prime} - \sigma_0^* \sigma_0 \right) p^\top T p^* + 2\sigma_0^2 \, p^\top T p = 0,$$

consequently, by (34), (35) and (36),

$$2\sigma_0^* \sigma_0^\prime \, p^\top T p^* = \frac{1}{2} \left(1 + \frac{p^{*\top} T p}{p^\top T p^*} \right) - \frac{p^\top T p \cdot p^{*\top} T p^*}{(p^\top T p^*)^2}. \tag{37}$$

Now, (31) and (35) gives (17), and (18) is derived similarly. Multiplying (33) by $2p^\top T p^*$, and using (34)–(37) we obtain

$$\frac{1}{2} \left(1 - \frac{p^{*\top} T p}{p^\top T p^*} \right) \frac{p^\top T p^*}{p^{*\top} T p^*} \, p^{*\top} A p^* + p^{*\top} A p^*$$

$$> \frac{1}{2} \left(1 + \frac{p^{*\top} T p}{p^\top T p^*} \right) p^\top A p^* - \frac{p^\top T p \cdot p^{*\top} T p^*}{(p^\top T p^*)^2} \, p^\top A p^*$$

$$+ \frac{p^{*\top} T p^*}{p^\top T p^*} \, p^\top A p.$$

20

In the first line, substitute $p^\top A p^*$ for $\dfrac{p^\top T p^*}{p^{*\top} T p^*} p^{*\top} A p^*$, and in the second line $p^{*\top} A p^*$ for $\dfrac{p^{*\top} T p^*}{p^\top T p^*} p^\top A p^*$. After rearranging and multiplying by $p^\top T p^*$ we get (19). $\qquad\square$

A.2 Numerical examples

A.2.1 Prisoner's sharing game

In our first example let

$$\tau_0 = 2, \quad A = \begin{bmatrix} 1 & 1+s \\ 1-s & 1 \end{bmatrix}, \quad T = \begin{bmatrix} 2 & 4 \\ 1 & 3 \end{bmatrix},$$

where $-1 \leq s \leq 1$. We are looking for an evolutionarily stable strategy of the form $p^* = [y, \, 1-y]^\top$, $0 \leq y \leq 1$, as a function of parameter s.

We will prove that for every $s \in [-1, \, 1]$ there exists a unique ESS of the form $p^* = [y, \, 1-y]^\top$, namely,

- if $-1 \leq s \leq s_1 = \dfrac{7 - \sqrt{13}}{18} = 0.188\ldots$, then $y = 0$,

- if $s_1 < s < s_2 = 1/4$, then $y = 3 - s^{-1} + s^{-1/2}$,

- if $s_2 \leq s \leq 1$, then $y = 1$.

For the proof let $p = [x, \, 1-x]^\top$ be an arbitrary mutant strategy, $x \neq y$, and let $z = x - y$. Then $p^{*\top} A p^* = y^2 + 2y(1-y) + (1-y)^2 = 1$,

$$p^{*\top} A p = yx + (1+s)y(1-x) + (1-s)(1-y)x + (1-y)(1-x) = 1 - sz,$$

and by symmetry, $p^\top A p = 1$, $p^\top A p^* = 1 + sz$.

Furthermore, $p^{*\top} T p^* = 2y^2 + 5y(1-y) + 3(1-y)^2 = 3 - y$,

$$p^{*\top} T p = 2yx + 4y(1-x) + (1-y)x + 3(1-y)(1-x)$$
$$= 3 + x - 2y = 3 - y + z,$$

hence $p^\top T p = 3 - x = 3 - y - z$, $p^\top T p^* = 3 + y - 2x = 3 - y - 2z$.

For checking (11) we first compute ϱ_0^*/ϱ_0. Remembering the equation $\frac{2}{\tau_0}(\varrho_0^*)^2 = (1 - \varrho_0^*)/p^{*\top} T p^*$ we can write

$$\frac{\varrho_0^*}{\varrho_0} = \varrho_0^* \left(1 + \frac{2}{\tau_0} p^\top T p^* \varrho_0^*\right) = \varrho_0^* + \frac{p^\top T p^*}{p^{*\top} T p^*}(1 - \varrho_0^*)$$

$$= 1 + \frac{p^\top T p^* - p^{*\top} T p^*}{p^{*\top} T p^*}(1 - \varrho_0^*) = 1 + \frac{1 - \varrho_0^*}{p^{*\top} T p^*}[1, -1] T p^* z$$

$$= 1 + \frac{2}{\tau_0}(\varrho_0^*)^2 [1, -1] T p^* z, \quad (38)$$

21

which now yields
$$\frac{\varrho_0^*}{\varrho_0} = 1 + z(\varrho_0^*)^2.$$
Clearly, inequality (11) is strict if and only if
$$\frac{\varrho_0^*}{\varrho_0} = 1 + z(\varrho_0^*)^2 > \frac{p^\top A p^*}{p^{*\top} A p^*} = 1 + sz,$$
that is, $\left((\varrho_0^*)^2 - s\right) z > 0$.

If $y = 0$, then $z > 0$, hence $s < (\varrho_0^*)^2$ is needed. By (14) we have
$$\varrho_0^* = \frac{2}{1 + \sqrt{13 - y}} = \frac{2}{1 + \sqrt{13}} = \frac{\sqrt{13} - 1}{6},$$
hence the condition for $y = 0$ to be a strict NE is
$$s < \left(\frac{\sqrt{13} - 1}{6}\right)^2 = \frac{7 - \sqrt{13}}{18} = s_1.$$

Analogously, if $y = 1$ then $z < 0$, thus the condition is
$$s > (\varrho_0^*)^2 = \left(\tfrac{1}{2}\right)^2 = \tfrac{1}{4}.$$

If $0 < y < 1$, (11) cannot hold with strict inequality. Let us continue with (12) and (13). Then
$$s = (\varrho_0^*)^2 = \frac{1 - \varrho_0^*}{3 - y},$$
hence $\varrho_0^* = \sqrt{s}$, $s = \left(\dfrac{2}{1 + \sqrt{13 - y}}\right)^2$, and $3 - y = \dfrac{1}{s} - \dfrac{1}{\sqrt{s}}$. It is easy to see that this defines a one-to-one correspondence $s \leftrightarrow y$ between the intervals $[s_1, \tfrac{1}{4}]$ and $[0, 1]$. Furthermore, by (15),
$$\vartheta^* = \frac{1 - \sqrt{s}}{2 - \sqrt{s}}\left(1 + sz - \frac{3 - y - 2z}{3 - y}\right) = \frac{1 - \sqrt{s}}{2 - \sqrt{s}}\left(s + \frac{2}{3 - y}\right) z$$
$$= \frac{1 - \sqrt{s}}{2 - \sqrt{s}}\left(s + \frac{2s}{1 - \sqrt{s}}\right) = \frac{3 - \sqrt{s}}{2 - \sqrt{s}} sz,$$
$$\varrho_0 = \varrho_0^*\left(\frac{\varrho_0^*}{\varrho_0}\right)^{-1} = \frac{\sqrt{s}}{1 + sz}, \text{ and finally, by (16),}$$
$$\vartheta = \left(1 - \frac{\sqrt{s}}{1 + sz}\right)\left(1 + sz - \frac{3 - y - z}{3 - y + z} - \frac{3 - \sqrt{s}}{2 - \sqrt{s}} sz\right)$$
$$= \left(1 - \frac{\sqrt{s}}{1 + sz}\right)\left(\frac{2}{3 - y + z} - \frac{s}{2 - \sqrt{s}}\right) z$$
$$= \frac{1 - \sqrt{s} + sz}{1 + sz}\left(\frac{2}{1 - \sqrt{s} + sz} - \frac{1}{2 - \sqrt{s}}\right) sz.$$

Dividing (13) by ϱ_0, and plugging the expressions above into it we get the following stability condition to check.

$$(1 + sz)\left(\frac{3 - \sqrt{s}}{2 - \sqrt{s}} sz + 1 - sz\right)$$
$$> \frac{1 - \sqrt{s} + sz}{1 + sz}\left(\frac{2}{1 - \sqrt{s} + sz} - \frac{1}{2 - \sqrt{s}}\right)sz(1 + sz) + 1.$$

After some calculus this can be transformed into the inequality

$$\frac{2(sz)^2}{2 - \sqrt{s}} > 0,$$

which is obviously satisfied.

A.2.2 Prisoner's dilemma under time constraint

In our second example let

$$\tau_0 = 2, \quad A = \begin{bmatrix} 3 & 1 \\ 4 & 2 \end{bmatrix}, \quad T = \begin{bmatrix} 1 & 1 \\ t & t \end{bmatrix},$$

where $t > 0$. Again, we will find evolutionarily stable strategies of the form $p^* = [y, 1 - y]^\top$, $0 \le y \le 1$ for every fixed t.

We will prove the following facts.

– If $0 < t \le t_1 = \dfrac{9 + \sqrt{5}}{6} = 1.872\ldots$, then $y = 0$ is the only ESS.

– If $t \ge t_2 = 3 + \sqrt{3} = 4.732\ldots$, then $y = 1$ is the only ESS.

– If $t_1 < t < t_2$, then both $y = 0$ and $y = 1$ are ESS (and no other ESS exists).

For the proof let p and z denote the same as in A.2.1. Let us fix $y \in [0, 1]$ and try to find all values of t for which p^* is ESS.

Since $T = \begin{bmatrix} 1 \\ t \end{bmatrix}[1, 1]$, we have $Tp = Tp^* = \begin{bmatrix} 1 \\ t \end{bmatrix}$, thus

$$p^{*\top} Tp^* = p^{*\top} Tp = y + t(1 - y) = t - (t - 1)y,$$
$$p^\top Tp^* = p^\top Tp = t - (t - 1)x = t - (t - 1)y - (t - 1)z.$$

Furthermore,

$$p^{*\top} Ap^* = 3y^2 + 5y(1 - y) + 2(1 - y)^2 = 2 + y,$$
$$p^\top Ap^* = 3xy + x(1 - y) + 4(1 - x)y + 2(1 - x)(1 - y)$$
$$= 2 + 2y - x = 2 + y - z,$$

23

and, by symmetry,

$$p^\top A p = 2 + x = 2 + y + z, \quad p^{*\top} A p = 2 + 2x - y = 2 + y + 2z.$$

From (38) it follows that

$$\frac{\varrho_0^*}{\varrho_0} = 1 - (\varrho_0^*)^2 (t-1) z.$$

By this, inequality (11) is strict if and only if

$$1 - (\varrho_0^*)^2 (t-1) z > \frac{2 + y - z}{2 + y} = 1 - \frac{z}{2 + y} \, ;$$

that is,

$$\left(\frac{1}{2 + y} - (\varrho_0^*)^2 (t-1) \right) z > 0.$$

If $y = 0$ then $z > 0$, hence the condition is $(\varrho_0^*)^2 (t-1) < \frac{1}{2}$. Using that $(\varrho_0^*)^2 = (1 - \varrho_0^*)/t$, we get $2(1 - \varrho_0^*)(t-1) < t$. This obviously holds for $t \le 2$, thus we can suppose $t > 2$. By (14)

$$\varrho_0^* = \frac{2}{1 + \sqrt{1 + 4t - 4(t-1)y}} = \frac{2}{1 + \sqrt{1 + 4t}},$$

therefore the condition is equivalent to the inequality

$$\sqrt{1 + 4t} < \frac{3t - 2}{t - 2} \, .$$

Taking squares we arrive at the cubic inequality $4t(t^2 - 6t + 6) < 0$, which yields $t < 3 + \sqrt{3} = t_2$.

Next, let $y = 1$. Then $z < 0$, and we need $(\varrho_0^*)^2 (t-1) > \frac{1}{3}$. This time $\varrho_0^* = \dfrac{2}{1 + \sqrt{5}}$, consequently $y = 1$ is a strict NE if and only if $t > \dfrac{9 + \sqrt{5}}{6} = t_1$.

Finally, let y be arbitrary, and suppose (12) is satisfied. We will show that in (13) the opposite inequality is valid, thus in this way no ESS can be obtained.

Indeed, by (12) we have

$$\frac{\varrho_0^*}{\varrho_0} = 1 - \frac{z}{2 + y}, \quad \varrho_0 = \frac{(2 + y)\varrho_0^*}{2 + y - z},$$

$$\vartheta^* = \frac{1 - \varrho_0^*}{2 - \varrho_0^*} \left(1 - \frac{z}{2 + y} - 1 \right) = -\frac{(1 - \varrho_0^*)z}{(2 - \varrho_0^*)(2 + y)},$$

$$\vartheta = \left(1 - \frac{(2 + y)\varrho_0^*}{2 + y - z} \right) \left(1 - \frac{z}{2 + y} + \frac{(1 - \varrho_0^*)z}{(2 - \varrho_0^*)(2 + y)} - 1 \right)$$

$$= -\left(1 - \frac{(2 + y)\varrho_0^*}{2 + y - z} \right) \frac{z}{(2 - \varrho_0^*)(2 + y)} \, .$$

24

Hence the condition to be checked is

$$\left(1 - \frac{z}{2+y}\right)\left(-\frac{(1-\varrho_0^*)z}{(2-\varrho_0^*)(2+y)}(2+y) + (2+y+2z)\right)$$
$$> -\left(1 - \frac{(2+y)\varrho_0^*}{2+y-z}\right)\frac{z(2+y-z)}{(2-\varrho_0^*)(2+y)} + (2+y+z).$$

After cancellation and rearrangement it reduces to the inequality

$$-\frac{\varrho_0^* z^2}{(2-\varrho_0^*)(2+y)} > 0,$$

which is obviously false.

Remark 3. For every $t \in [t_1, t_2]$ there exists a unique $y \in [0, 1]$ such that (12) is satisfied. In this way we obtain a one to one correspondence between the two intervals. These strategies are unstable Nash equilibrium points.

Indeed, (12) implies

$$\frac{1}{2+y} = (\varrho_0^*)^2(t-1) = \frac{(1-\varrho_0^*)(t-1)}{t - (t-1)y}.$$

Note that t must be greater than 1. For the sake of convenience introduce $u = \frac{3}{2}t - 1$ and $v = t - (t-1)y$. Then $1 \le v \le t$. By some algebra we arrive at the equation

$$\sqrt{1+4v} = \frac{u}{u-v}.$$

If u is negative, the right hand side is less than 1, while the left hand side is greater than 1. Thus $u > v$ is required. Taking squares and rearranging leads to

$$v\left[4v^2 - (8u-1)v + (4u^2 - 2u)\right] = 0,$$

from which

$$v = \frac{8u - 1 - \sqrt{16u+1}}{8}, \quad \text{that is,} \quad y = \frac{9 - 4t + \sqrt{24t - 15}}{8(t-1)}$$

(the other root of the quadratic equation is greater than u.)

From condition $1 \le v$ we get $u \ge \dfrac{5 + \sqrt{5}}{4}$, that is, $t \ge t_1$. On the other hand, $v \le t = \frac{2}{3}(u+1)$ is equivalent to $u \le \dfrac{7 + 3\sqrt{3}}{2}$, that is, $t \le t_2$. Since

$$\frac{dv}{du} = 1 - \frac{1}{\sqrt{16u+1}} > 0,$$

the correspondence $u \leftrightarrow v$ is one to one, and the same holds for $t \leftrightarrow y$.

References

[1] B. Allen, and M.A. Nowak, *Games on graphs*, EMS Surv. Math. Sci., 1 (2014), pp. 113–151. doi:10.4171/EMSS/3

[2] M. Broom, M.L. Crowe, M.R. Fitzgerald, and J. Rychtář, *The stochastic modelling of kleptoparasitism using a Markov process*, J. Theor. Biol., 264 (2010), pp. 266-272. doi:10.1016/j.jtbi.2010.01.012

[3] M. Broom, R.M. Luther, G.D. Ruxton, and J. Rychtář, *A game-theoretic model of kleptoparasitic behavior in polymorphic populations*, J. Theor. Biol., 255 (2008), pp. 81–91. doi:10.1016/j.jtbi.2008.08.001

[4] M. Broom, R.M. Luther, and J. Rychtář, *Hawk-Dove game in kleptoparasitic populations*, J. Comb. Inf. Syst. Sci., 4 (2009), pp. 449–462. doi:10.1080/09720502.2009.10700621

[5] M. Broom, and G.D. Ruxton, *Evolutionarily Stable Stealing: Game Theory applied to Kleptoparasitism*, Behavioral Ecology, 9 (1998), pp. 397–403. doi:10.1093/beheco/9.4.397

[6] M. Broom, and J. Rychtář, *Game-Theoretical Models in Biology*, Boca Raton, FL: CRC Press/Taylor & Francis Group, 2013. ISBN-13: 978-1439853214

[7] E.L. Charnov, *Optimal foraging: Attack strategy of a mantid*, Am. Nat., 110 (1976), pp. 141–151. doi:10.1086/283054

[8] E.L. Charnov, *Optimal foraging: The marginal value theorem*, Theor. Pop. Biol., 9 (1976), pp. 129–136. doi:10.1016/0040-5809(76)90040-X

[9] J. Garay, R. Cressman, F. Xu, Z. Varga, and T. Cabello, *Optimal Forager Against Ideal Free Distributed Prey*, Am. Nat., 186 (2015), pp. 111–122. doi:10.1086/681638

[10] J. Garay, Z. Varga, M. Gámez, and T. Cabello, *Functional response and population dynamics for fighting predator, based on activity distribution*, J. Theor. Biol., 368 (2015), pp. 74–82. doi:10.1016/j.jtbi.2014.12.012

[11] A. Granas, and J. Dugundji, *Fixed Point Theory*, Springer Monographs in Mathematics, New York: Springer, 2003. ISBN 978-0-387-21593-8

[12] C. Hadjichrysanthou, and M. Broom, *When should animals share food? Game theory applied to kleptoparasitic populations with food sharing*, Behavioral Ecology, 23 (2012), pp. 977–991. doi:10.1093/beheco/ars061

[13] J. Hofbauer, and K. Siegmund, *The Theory of Evolution and Dynamical Systems*, Cambridge: Cambridge University Press, 1988. ISBN-13: 978-0521358385

[14] C.S. Holling, *The components of predation as revealed by a study of small-mammal predation of the European pine sawfly*, The Canadian Entomologist, 9 (1959), pp. 293–320. doi:10.4039/Ent91293-5

[15] R.M. Luther, and M. Broom, *Rapid convergence to an equilibrium state in kleptoparasitic populations*, J. Math. Biol., 48 (2004), pp. 325–339. doi:10.1007/s00285-003-0237-3

[16] J. Maynard Smith, *Evolution and the Theory of Games*, Cambridge: Cambridge University Press, 1982. ISBN: 0-521-28884-3

[17] J. Maynard Smith, and G.R. Price, *The logic of animal conflict*, Nature, 246 (1973), pp. 15–18. doi:10.1038/246015a0

[18] J.R. Norris, *Markov Chains*, 2nd Ed., Cambridge Series in Statistical and Probabilistic Mathematics, Cambridge: Cambridge University Press, 1999. ISBN: 978-0521633963

[19] M.A. Nowak, *Five Rules for the Evolution of Cooperation*, Science, 314 (2006), pp. 1560–1563. doi:10.1126/science.1133755

[20] M.A. Nowak, S. Bonhoeffer, and R.M. May, *More Spatial Games*, Internat. J. Bifur. Chaos Appl. Sci. Engrg., 4 (1994), pp. 33–56. doi:10.1142/S0218127494000046

[21] M.A. Nowak, and R. May, *The spatial dilemmas of evolution*, Internat. J. Bifur. Chaos Appl. Sci. Engrg., 3 (1993), pp. 35–78. doi:10.1142/S0218127493000040

[22] J.M. Pacheco, A. Traulsen, and M.A. Nowak, *Coevolution of Strategy and Structure in Complex Networks with Dynamical Linking*, Phys. Rev. Lett., 97 (2006), 258103. doi:10.1103/PhysRevLett.97.258103

[23] J.M. Pacheco, A. Traulsen, and M.A. Nowak, *Active linking in evolutionary games*, J. Theor. Biol., 243 (2006), pp. 437–443. doi:10.1016/j.jtbi.2006.06.027

[24] F.C. Santos, and J.M. Pacheco, *Scale-free networks provide a unifying framework for the emergence of cooperation*, Phys. Rev. Lett., 95 (2005), 098104. doi:10.1103/PhysRevLett.95.098104

[25] F.C. Santos, J.F. Rodrigues, and J.M. Pacheco, *Graph topology plays a determinant role in the evolution of cooperation*, Proc. R. Soc. B, 273 (2006), pp. 51–55. doi:10.1098/rspb.2005.3272

[26] E. Sirot, *An evolutionarily stable strategy for aggressiveness in feeding groups*, Behavioral Ecology, 11 (2000), pp. 351–356. doi:10.1098/rspb.2005.3272

[27] G. Szabó, and G. Fáth, *Evolutionary games on graphs*, Phys. Rep., 446 (2007), pp. 97–216. doi:10.1016/j.physrep.2007.04.004

[28] G. Szabó, J. Vukov, and A. Szolnoki, *Phase diagrams for an evolutionary prisoner's dilemma game on two-dimensional lattices*, Phys. Rev. E, 72 (2005), 047107. doi:10.1103/PhysRevE.72.047107

[29] E. Szathmáry, *To group or not to group?*, Science, 334 (2011), pp. 1648–1649. doi:10.1126/science.1209548

[30] G.E. Yates, and M. Broom, *A stochastic model of kleptoparasitism*, J. Theor. Biol., 248 (2007), pp. 480–489. doi:10.1016/j.jtbi.2007.05.007