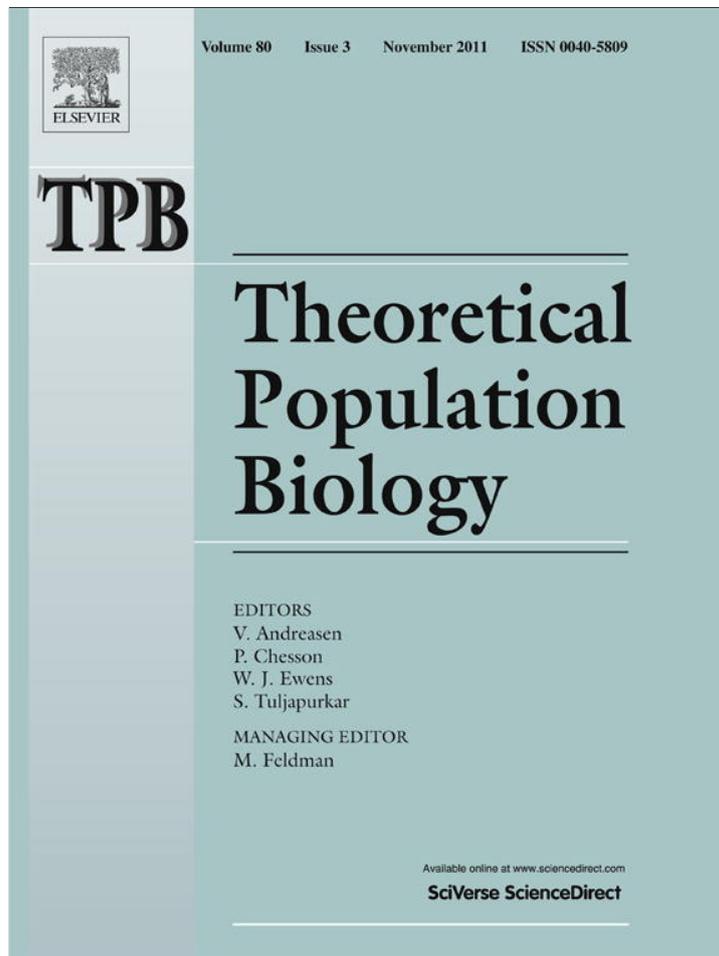


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Survivor's dilemma: Defend the group or flee?

József Garay^{a,*}, Zoltán Varga^b^a Research Group of Theoretical Biology and Ecology of the Hungarian Academy of Sciences and Department of Plant Taxonomy and Ecology, L. Eötvös University, Pázmány P. sétány 1/C, H-1117 Budapest, Hungary^b Institute of Mathematics and Informatics, Szent István University, Páter K. u. 1., H-2103, Gödöllő, Hungary

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ABSTRACT

We consider a survival game of gregarious individuals, in which the aim of the players is survival to reproductive age under predator attacks. The *survivor's dilemma* (shortly: SVD) game consists in the following: a group member either surely survives alone by fleeing, while its defensive mate may be killed; or tries to save its mate's life, risking to get killed. The dilemma is that, in every single attack, fleeing ensures maximal survival probability, but if its mate survives by fighting both, and they remain together, its risk to be killed at the next attack will be lower. We show that, if defense is successful enough, then the one-attack game is a prisoner's dilemma (PD), where fleeing is the strict ESS. We have additively decomposed the SVD game, according to the survival of the group mate of the focal prey, into two games: the aim of the "*collective game*" is survival of the group of prey. Counter-wise, the aim of the "*hostile game*" is survival alone (focal prey survives and its mate is killed by the predator). We obtain the following results: if the attack number is large enough, the multi-attack SVD game is dominated by the "*collective game*" in the sense that each individual can ensure its own maximal survival probability by maximizing the group survival probability in each attack. In the hostile game, the only strict ESS is the fleeing strategy. In the collective game there are two different cases: either defense is a unique strict ESS, or the collective game is bistable, i.e. fleeing and defense are local strict ESS's. If defense is the only strict ESS in the collective game, and the attack number is large enough, defense replaces fleeing strategy in the multi-attack SVD game. However, in the bistable case, defense cannot invade into the fleeing population. It is shown that, if the interaction between relatives is frequent enough, than defense can replace fleeing strategy, in spite of the fact that in the well-mixed population the collective game is bistable.

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1. Introduction

In this paper we consider the biological situation in which a small pack (band, group) of territorial prey is under predator's attacks. A member of a herd can successfully defend against the predator; however, the fleeing individual is more safe when the others defend against predator (Cant et al., 2001; Clutton-Brock et al., 1999a,b; Gilchrist, 2004; Rood, 1983; Waterman, 1997, 2002). In a recent paper (Garay, 2009) we considered a minimal group of two "omniscient" prey individuals; this means that the non-attacked prey is aware of its safety. In this paper we have dropped this assumption, supposing that the group members have no information on which of them is the target of the predator, and the preys have two options: defense against the predator or flee away. In the framework of this generalization, we will see that the one-attack survivor's dilemma (SVD) game is a prisoner's dilemma

(PD), if defense is successful enough. After that we will consider the case when each individual can breed only if it has survived T attacks of predator. For this situation we will use the term T -attack SVD game as proposed in Garay (2009). Lima (1989) studied survival games, assuming that (a) there are two attacks, and (b) both players are aware that the second attack is the last one. Unlike these assumptions, we consider (a') arbitrary but fixed number of attacks, and (b') the players are not aware of this number. There are also further survival games in the literature (e.g. Yaniv and Motro (2005)), but the novelty of our setup is that the predation pressure is defined by the number of attacks suffered before breeding.

The one-attack SVD is a special form of the iterated PD between two individuals, see Axelrod and Hamilton (1981) and the papers citing it. However, we will assume that individuals have genetically fixed behavior phenotypes, thus in this paper we will not consider conditional strategies.

For our present treatment we decompose the SVD game. To our knowledge, only Fletcher and Doebeli (2009) partitioned the individual payoff according to the "interaction environment" in the framework of an N -person public goods game. Our decomposition

* Corresponding author.

E-mail addresses: garayj@ludens.elte.hu (J. Garay), Varga.Zoltan@gek.szie.hu (Z. Varga).

of SVD game is quite different, since this depends on the stochastic survival process, and does not on the strategy of other individuals. We additively decompose the SVD game into two games: the aim of the “collective game” is the survival of the group of prey. Counter-wise, the aim of the “hostile game” is survival alone (focal prey survives and its mate is killed by the predator). Using the decomposition method, we will characterize the evolutionary stability of the SVD game.

In order to see when defense can replace fleeing, we will consider non-well-mixed interaction distributions when the collective game is bistable, i.e. fleeing and defense are local strict ESS's. We will use Grafen's (1979) model of game between relatives. This idea goes back to Hamilton's “viscous populations” (Hamilton, 1964) in which offspring will tend to be close to their parents (cf. Van Baalen and Rand (1998)). We give a threshold for the proportion of all contests between members of the same clone (non-random interactions between relatives), above which defense can replace fleeing strategy in spite of the fact that the collective game is bistable, i.e. in the well mixing population defense and fleeing are local strict ESS's.

2. Predation process

Let us consider an asexual gregarious prey population large enough, and suppose that each individual before reaching reproductive age, is exposed to several predator attacks. Every prey individual has the same ability to defend itself against predator, to recognize the stalking predator and has the same payoff function. We assume that there is no difference between preys with respect to fleeing and defense abilities. They all have a genetically fixed behavior phenotype¹ and no memory.² Furthermore, in the biological case considered here, there is neither social nor dominance structure.³ Now, the simplest possible case is considered in which each group is formed by only two individuals, and unrelated individuals have no information on their mate's behavior. Furthermore, when a member of a pair dies then new pair formation from the survived member is not possible. This is the case when the prey species is territorial, thus the owners of the territory do not form a group with intruders.

We will consider two situations. In the first one, the interaction between individuals is well-mixed during random group formation i.e. each individual interacts with each phenotype, proportionally to the relative frequency of the latter.⁴ In the second situation, we will consider a non-well-mixed interaction distribution.

Assuming that the predator attacks the group but the group members have no information on which one is the target of the predator, and the only difference between individuals is in their strategies. It will turn out that the following simplifying condition establishes a connection between the conditions of different games: *in one attack a predator can kill at most one member of the prey group.*

For concreteness, let one member of the group be called *A*-prey and the other one *B*-prey. Preys have two options: defend against

the predator (δ_I) or flee (φ_I), where *I* is either *A* or *B*. Then, we have the following four events, according to the behavior of the prey.

Both prey individuals defend. According to our assumptions $p_{A0}(\delta_A, \delta_B) = p_{0B}(\delta_A, \delta_B)$ (the index of *p* indicates which prey survived); and both survive with probability $p_{AB}(\delta_A, \delta_B)$. Since the predator can kill only one prey at a time, we have $p_{AB}(\delta_A, \delta_B) = 1 - 2p_{A0}(\delta_A, \delta_B)$.

A-prey defends against the predator, B-prey flees. Both preys survive with probability *b*, *A*-prey is killed with probability $p_{0B}(\delta_A, \varphi_B) = 1 - b$, while *B*-prey surely survives, i.e. $p_B(\delta_A, \varphi_B) = 1$, which means that in this case only *A*-prey could be killed, while *B*-prey flees, so it surely survives.

B-prey defends against the predator, A-prey flees. Since this situation is the opposite to the previous one, *B*-prey survives with probability *b*, *B*-prey is killed with probability $p_{A0}(\varphi_A, \delta_B) = 1 - b$, while *A*-prey surely survives, i.e. $p_A(\delta_A, \varphi_B) = 1$.

Both preys flee. The predator kills only one prey with the same probability: $p_{A0}(\varphi_A, \varphi_B) = p_{0B}(\varphi_A, \varphi_B)$, so the probability that both preys survive is $p_{AB}(\varphi_A, \varphi_B) = 1 - 2p_{A0}(\varphi_A, \varphi_B)$.

Assume that all individuals survive to breeding age and have the same number of offspring. This simplifying assumption ignores, in particular, that the fitness decreases at the cost of defense and injury during attacks.

2.1. One-attack game: survivor's dilemma⁵

Each individual has to maximize its survival probability. *A*-prey survives in two cases: either both preys survive or *A*-prey survives and *B*-prey is killed. Now, the *survivor's dilemma* (SVD) consists in the following: a group member either surely survives alone by fleeing, while its mate may be killed; or tries to save its mate's life, risking to get killed. The dilemma is that, in every single attack, fleeing ensures maximal survival probability, but if its mate survives by fighting both, and they remain together, its risk to be killed at the next attack will be lower.

To see the connection between SVD game and PD let us consider one attack. Using the above notation, for each individual we have a survival matrix, which is the payoff matrix of *A*-prey:

$$A := \begin{pmatrix} a & b \\ 1 & d \end{pmatrix},$$

defense flee away
 defense *a* *b*
 flee away 1 *d*,

where $a := p_{AB}(\delta_A, \delta_B) + p_{A0}(\delta_A, \delta_B)$ and $d := p_{AB}(\varphi_A, \varphi_B) + p_{A0}(\varphi_A, \varphi_B)$. We note that $a = 1 - p_{A0}(\delta_A, \delta_B)$ and $d = 1 - p_{A0}(\varphi_A, \varphi_B)$. Clearly, payoff matrix **A** defines an evolutionary matrix game.

First, we consider the case when

$$1 > a > d > b > 0. \tag{1}$$

Since the predator can kill only one prey at a time (i.e. $p_{AB}(S, S) + 2p_{A0}(S, S) = 1$, where $S \in \{\delta, \varphi\}$), (1) can be rewritten as

$$1 > p_{AB}(\delta_A, \delta_B) > p_{AB}(\varphi_A, \varphi_B) > 2b - 1; \tag{2}$$

or equivalently,

$$0 < p_{A0}(\delta_A, \delta_B) < p_{A0}(\varphi_A, \varphi_B) < 1 - b < 1.$$

Second, we assume

$$2a > 1 + b. \tag{3}$$

We emphasize that (1) and (3) define the well-known iterated PD game. However there are four differences between these games: In the SVD game, 1. the entries of the pay-off matrix are

⁵ Clearly “defense” is the “cooperator” and fleeing is the “defector” strategy.

¹ Since the genetically fixed behavior is not conditional – i.e. an individual cannot change its behavior according to the behavior of others – neither direct (Brandt and Sigmund, 2004) nor indirect reciprocity (Ohtsuki and Iwasa, 2004; Nowak and Sigmund, 2005) can be applied.

² Thus, in the present model there is no punishment (Fehr and Gächter, 2002; Rockenbach and Milinski, 2006).

³ The altruistic defense is not in order to allow an individual to stay in the group, and altruism is not considered as a result of the “pay-to-stay” hypothesis (Kokko et al., 2002).

⁴ In this situation, under these assumptions, kin (Hamilton, 1964), group (Nowak, 2006) selection and group formation based on phenotypic similarity (Burtsev and Turchin, 2006) cannot be used.

probabilities (and not fitness values), or sums of probabilities of disjoint events (see definition of a and d); 2. if the attack number increases the survival probabilities are calculated multiplicatively (and not additively); 3. If a mate is killed by the predator, in the future, the probability for the survivor to get killed increases based on two factors: first, in a smaller group the probability that a member will be the target of the predator increases; second, the success of defense decreases with the number of defending members of group. 4. Unlike the iterated PD game, in the SVD game, the sequence of the single (different) games may stop at random (“game over” for the focal prey).

Based our assumption that a predator can kill only one prey in one attack, (3) can be formulated as

$$p_{AB}(\delta_A, \delta_B) = 1 - 2p_{A0}(\delta_A, \delta_B) > b. \quad (4)$$

In our survival game the above inequalities have the following biological interpretations.

- $a > d$ means that defense is more successful than common fleeing.
- $d > b$ means that, for the defending individual, common fleeing is more successful than the single one.
- Inequality (3) means that from the point of view of common survival, common defense is more successful than one defending and one fleeing. In other words, the average number of survived individuals of common defense is higher if both preys defend, not only one.

It is well-known that under condition (1), fleeing is an ESS in the SVD game. In other words, independently from the strategy of B -prey, fleeing guarantees the maximal survival probability to A -prey.

2.2. Multi-attack game

Now let us calculate the probability of attaining the reproductive age. For simplicity, let us consider the simplest type of predation. Predation is assumed to be a random process, thus a prey individual can never be sure if an attack occurs. T denotes the average number of attacks.⁶ Assume that the predator can encounter solitary individuals and pairs of prey with the same chance and when the predator meets any of them; it always tries to get it. This assumption rules out that the predator is a player, since it does not have preference regarding the solitary versus the grouped individuals. For instance, the predator may be totally opportunistic (Cressman and Garay, 2011; Garay and Móri, 2010). Based on this assumption, we can suppose that each solitary and each group have to survive the average number of predator's attack (T).

Let $\mathbf{q}_A \in S_2 := \{x \in R^2 : x_i \geq 0; x_1 + x_2 = 1\}$, $\mathbf{q}_A := (q_A, 1 - q_A)$ (with $q_A \in [0, 1]$) be the strategy of A -prey, i.e. with probability q_A A -prey defends against the predator and with probability $1 - q_A \in [0, 1]$ flees away. Similarly, $\mathbf{q}_B \in S_2$, $\mathbf{q}_B := (q_B, 1 - q_B)$ (with $q_B \in [0, 1]$) for B -prey. We emphasize that a prey may use mixed strategies, too.

Let $P(\mathbf{q}_A, \mathbf{q}_B)$ denote the average probability of collective survival of A -prey and B -prey:

$$P(\mathbf{q}_A, \mathbf{q}_B) := q_A [q_B p_{AB}(\delta_A, \delta_B) + (1 - q_B) b] + (1 - q_A) [q_B b + (1 - q_B) p_{AB}(\varphi_A, \varphi_B)]. \quad (5)$$

Furthermore, $Q(\mathbf{q}_A, \mathbf{q}_B)$ denotes the average probability that A -prey survives while B -prey is killed:

$$Q(\mathbf{q}_A, \mathbf{q}_B) := q_A q_B p_{A0}(\delta_A, \delta_B) + (1 - q_A) [q_B (1 - b) + (1 - q_B) p_{A0}(\varphi_A, \varphi_B)]. \quad (6)$$

Let η be the survival probability of a solitary prey. A -prey can survive T attacks in two ways: either B -prey also survives T attacks (collective survival) or B -prey dies at some, say t -th attack ($t = 1, 2, \dots, T$) while A -prey survives; and then the solitary A -prey survives $T - t$ predator attacks. Thus the average survival rate of A -prey is given by

$$P_A(\mathbf{q}_A, \mathbf{q}_B) := P(\mathbf{q}_A, \mathbf{q}_B)^T + \sum_{t=0}^{T-1} P(\mathbf{q}_A, \mathbf{q}_B)^{T-1-t} Q(\mathbf{q}_A, \mathbf{q}_B) \eta^t. \quad (7)$$

In another form,

$$P_A(\mathbf{q}_A, \mathbf{q}_B) = P(\mathbf{q}_A, \mathbf{q}_B)^T + Q(\mathbf{q}_A, \mathbf{q}_B) \frac{P(\mathbf{q}_A, \mathbf{q}_B)^T - \eta^T}{P(\mathbf{q}_A, \mathbf{q}_B) - \eta}. \quad (8)$$

We easily obtain a similar formula for $P_B(\mathbf{q}_A, \mathbf{q}_B)$. In this way, we get a *nonlinear 2-person T -attack SVD game*, in which the strategies are $\mathbf{q}_A \in S_2$, $\mathbf{q}_B \in S_2$, and payoff functions are $P_B(\mathbf{q}_A, \mathbf{q}_B)$, $P_A(\mathbf{q}_A, \mathbf{q}_B)$.

We note that if $T = 1$ then (7) can be written as $\mathbf{q}_A \mathbf{A} \mathbf{q}_B = P(\mathbf{q}_A, \mathbf{q}_B) + Q(\mathbf{q}_A, \mathbf{q}_B)$, so we get back the one-attack game.

If $P(\mathbf{q}_A, \mathbf{q}_B)$ and $Q(\mathbf{q}_A, \mathbf{q}_B)$ are “optimal” at the same strategy, this strategy ensures the maximal survival probability of T attacks. However, the situation is more complicated, when $P(\mathbf{q}_A, \mathbf{q}_B)$ and $Q(\mathbf{q}_A, \mathbf{q}_B)$ are “optimal” at different strategies. In the latter case we will see that $P(\mathbf{q}_A, \mathbf{q}_B)$ dominates the SVD game in the sense that there is a \bar{T} such that for each $T > \bar{T}$, the maximum of $P(\mathbf{q}_A, \mathbf{q}_B)$ also implies the maximum of the final survival probability $P_A(\mathbf{q}_A, \mathbf{q}_B)$. The intuition behind this is quite clear: since each individual only once can benefit from killing its mate, but in the long term, it can benefit from their joint survival of T attacks.

Thus, when T is large enough, the common survival probability dominates the T -attack survival game.⁷

Now the question arises: What is the threshold for the attack number which guarantees this dominance?

The “final” survival probability of A -prey, (8), can be rewritten in the following form

$$P_A(\mathbf{q}_A, \mathbf{q}_B) = \left[\frac{P(\mathbf{q}_A, \mathbf{q}_B) + Q(\mathbf{q}_A, \mathbf{q}_B) - \eta}{P(\mathbf{q}_A, \mathbf{q}_B) - \eta} \left[\frac{P(\mathbf{q}_A, \mathbf{q}_B)}{\eta} \right]^T - \frac{Q(\mathbf{q}_A, \mathbf{q}_B)}{P(\mathbf{q}_A, \mathbf{q}_B) - \eta} \right] \eta^T.$$

In what follows, we assume $b > \eta$, implying $P(\mathbf{q}_A, \mathbf{q}_B) > \eta$ for all $\mathbf{q}_A, \mathbf{q}_B \in [0, 1]$. This assumption means that living in a group guarantees higher survival probability. Thus $P_A(\mathbf{q}_A, \mathbf{q}_B)$ takes its maximum when

$$\frac{P(\mathbf{q}_A, \mathbf{q}_B) + Q(\mathbf{q}_A, \mathbf{q}_B) - \eta}{P(\mathbf{q}_A, \mathbf{q}_B) - \eta} \left[\frac{P(\mathbf{q}_A, \mathbf{q}_B)}{\eta} \right]^T - \frac{Q(\mathbf{q}_A, \mathbf{q}_B)}{P(\mathbf{q}_A, \mathbf{q}_B) - \eta} \quad (9)$$

has a maximum. In the Appendix we have proved that for T large enough ($T > \bar{T}$), the maximal survival probability under T attacks is guaranteed by maximal $P(\mathbf{q}_A, \mathbf{q}_B)$.

Finally, we note that $\frac{P(\mathbf{q}_A, \mathbf{q}_B) + Q(\mathbf{q}_A, \mathbf{q}_B) - \eta}{P(\mathbf{q}_A, \mathbf{q}_B) - \eta}$ and $\frac{Q(\mathbf{q}_A, \mathbf{q}_B)}{P(\mathbf{q}_A, \mathbf{q}_B) - \eta}$ have biological meaning: $P(\mathbf{q}_A, \mathbf{q}_B) + Q(\mathbf{q}_A, \mathbf{q}_B) - \eta$ is the difference between survival probabilities of living in group and living solitary. Furthermore, $P(\mathbf{q}_A, \mathbf{q}_B) - \eta$ is the difference between survival probabilities of collective and solitary survivals.

⁶ To avoid unnecessary complications, T is considered deterministic. If the minimal attack number is large enough, our predictions remain valid for the case when T is a random variable.

⁷ We mention that if the group size is larger than 2, for instance 100, and the attack number is also high, e.g. 100 000, than this intuitive picture remains valid.

3. Decomposition of survivals' dilemma

The SVD game can be decomposed into two games, according to the dilemma: either fleeing, which ensures maximal survival rate at each attack; or defense, which increases the survival probability of group mates, but decreases the defender's individual survival probability. The basis of the additive decomposition is the fact that the possible outcomes of a single attack are disjoint events.

In this section two conditions will play a crucial rule. The first one is

$$1 + b > 2d. \tag{10}$$

The biological interpretation of (10) is that common fleeing guarantees higher average number of surviving individuals than the case when one prey defends against the predator while the other prey flees. Using our assumptions, (10) can be rewritten as

$$p_{AB}(\varphi_A, \varphi_B) = 1 - 2p_{A0}(\varphi_A, \varphi_B) < b. \tag{11}$$

This inequality is independent from the well-known inequalities of survivals' dilemma (1) and (3), and plays no role in the PD games.

The second condition important for this section concerns the sign of

$$p_{AB}(\delta_A, \delta_B) + p_{AB}(\varphi_A, \varphi_B) - 2b. \tag{12}$$

The biological interpretation of the sign of (12) is the following: synchronized joint actions can imply higher or lower survival than the non-synchronized ones. We emphasize that the sign of (12) is not determined by the conditions of iterated PD (i.e. by inequalities (1) and (3)).

If the prey has no information on which attack is the last one, in each attack *A*-prey has to decide, whether $P(\mathbf{q}_A, \mathbf{q}_B)$ or $Q(\mathbf{q}_A, \mathbf{q}_B)$ should be maximized in each attack to provide maximal average survival probability after T attacks. However, both probabilities depend on the behavior of both preys. Observe that $P(\mathbf{q}_A, \mathbf{q}_B)$ and $Q(\mathbf{q}_A, \mathbf{q}_B)$ define the following two games. These games are named according to the aim (payoff function) of the games, instead of the characteristic properties of the payoff matrix, which is the usual way to name matrix games.

3.1. Collective game

Means that the aim is the groups survival together, so the payoff function $P(\mathbf{q}_A, \mathbf{q}_B)$ is generated by the payoff matrix

$$\mathbf{B} := \begin{pmatrix} p_{AB}(\delta_A, \delta_B) & b \\ b & p_{AB}(\varphi_A, \varphi_B) \end{pmatrix}.$$

Indeed, $P(\mathbf{q}_A, \mathbf{q}_B) = \mathbf{q}_A \mathbf{B} \mathbf{q}_B$. We emphasize that payoff matrix \mathbf{B} is symmetric, so this game is a partnership game, in which both players share their payoff equally (Hofbauer and Sigmund, 1998).

3.1.1

Assume that $p_{AB}(\delta_A, \delta_B) + p_{AB}(\varphi_A, \varphi_B) > 2b$ and $p_{AB}(\varphi_A, \varphi_B) < b$. In this case there is no interior equilibrium and only defense $\mathbf{e}_1 := (1, 0)$ is a global strict ESS. Inequality $p_{AB}(\varphi_A, \varphi_B) < b$ means that defense alone is more successful than common fleeing.

3.1.2

Assume that $p_{AB}(\delta_A, \delta_B) + p_{AB}(\varphi_A, \varphi_B) < 2b$ and $p_{AB}(\varphi_A, \varphi_B) < b$. In this case there is no interior equilibrium and again only defense \mathbf{e}_1 is a global strict ESS.

Thus, we have

$$P(\mathbf{e}_1, \mathbf{e}_1) > P(\mathbf{e}_1, \mathbf{q}) = P(\mathbf{q}, \mathbf{e}_1) > P(\mathbf{q}, \mathbf{q}) \tag{13}$$

for $q \in S_2 \setminus \{\mathbf{e}_1\}$.

3.1.3

Assume $p_{AB}(\varphi_A, \varphi_B) > b$, which means that the common fleeing is more successful than defense alone. We emphasize that $p_{AB}(\varphi_A, \varphi_B) > b$ implies $p_{AB}(\delta_A, \delta_B) + p_{AB}(\varphi_A, \varphi_B) > 2b$. Now there is an unstable mixed equilibrium $(\frac{p_{AB}(\varphi_A, \varphi_B) - b}{p_{AB}(\delta_A, \delta_B) - 2b + p_{AB}(\varphi_A, \varphi_B)}, \frac{p_{AB}(\delta_A, \delta_B) - b}{p_{AB}(\delta_A, \delta_B) - 2b + p_{AB}(\varphi_A, \varphi_B)})$, and defense \mathbf{e}_1 and fleeing $\mathbf{e}_2 := (0, 1)$ are local strict ESS's for the collective game. Formally, defense is a strict ESS if

$$P(\mathbf{e}_1, \mathbf{e}_1) > P(\mathbf{q}, \mathbf{e}_1) \quad \text{for all } q \in S_2, \mathbf{q} \neq \mathbf{e}_1. \tag{14}$$

Furthermore, fleeing $\mathbf{e}_2 = (0, 1)$ is a strict ESS if

$$P(\mathbf{e}_2, \mathbf{e}_2) > P(\mathbf{q}, \mathbf{e}_2) \quad \text{for all } q \in S_2, \mathbf{q} \neq \mathbf{e}_2. \tag{15}$$

Observe that \mathbf{e}_1 dominates in the bistable case in the sense that it guarantees higher group survival mean than \mathbf{e}_2 ; if common defense guarantees higher common survival, then common fleeing (i.e. $p_{AB}(\delta_A, \delta_B) > p_{AB}(\varphi_A, \varphi_B)$) implies $\mathbf{e}_1 \mathbf{B} \mathbf{e}_1 = P_{AB}(\delta_A, \delta_B) > P_{AB}(\varphi_A, \varphi_B) = \mathbf{e}_2 \mathbf{B} \mathbf{e}_2$.

3.2. Hostile game

In this game the aim is survival alone (e.g. *A*-prey survival and *B*-prey is killed by the predator). The payoff function is $Q(\mathbf{q}_A, \mathbf{q}_B)$, which is generated by the following payoff matrix

$$\mathbf{C} := \begin{pmatrix} p_{A0}(\delta_A, \delta_B) & 0 \\ 1 - b & p_{A0}(\varphi_A, \varphi_B) \end{pmatrix}.$$

Indeed, $Q(\mathbf{q}_A, \mathbf{q}_B) = \mathbf{q}_A \mathbf{C} \mathbf{q}_B$. It is easy to see that inequality (1) implies that $\mathbf{e}_2 = (0, 1)$ is a unique strict ESS.

We emphasize that fleeing strategy cannot always optimize the payoff functions of collective and hostile games at the same time. Furthermore, the sum of the payoff matrices of the collective game and the hostile game is the same as that of SVD game in Section 2.1, formally $\mathbf{A} = \mathbf{B} + \mathbf{C}$. In this sense the collective and the hostile games provide an additive decomposition of the SVD game, based on the fact that the possible outcomes of a single attack are disjoint random events. Clearly, if a strategy is ESS for both games defined by matrices \mathbf{B}, \mathbf{C} , then it is also ESS for \mathbf{A} .

4. Well mixed population

In the following we will be only interested in this question: Under what condition defense can replace fleeing strategy? We say that *mutant strategy* (defense, \mathbf{e}_1) can replace the resident strategy (fleeing, \mathbf{e}_2), if in any population state the fitness of mutant defense is higher than that of the resident fleeing strategists, i.e. $W_R(\mathbf{e}_2, \mathbf{e}_1 \varepsilon) < W_M(\mathbf{e}_1, \mathbf{e}_2, \varepsilon)$ for all $\varepsilon \in]0, 1]$ (c.f. Garay (2007)).

We have already assumed that $b > \eta$, which implies $P(\mathbf{q}_A, \mathbf{q}_B) > \eta$ for all $\mathbf{q}_A, \mathbf{q}_B \in [0, 1]$. This assumption means that living in group ensures higher survival probability. We have two different cases.

4.1

The collective game has a unique global ESS, namely defense, \mathbf{e}_1 ; and the hostile game has a unique global ESS, namely fleeing, \mathbf{e}_2 . In a multi-attack game defense replaces fleeing, if for all $\varepsilon \in]0, 1]$ the average fitness of defense is higher than that of fleeing, formally,

$$(1 - \varepsilon) P_R(\mathbf{e}_2, \mathbf{e}_2) + \varepsilon P_R(\mathbf{e}_2, \mathbf{e}_1) < (1 - \varepsilon) P_M(\mathbf{e}_1, \mathbf{e}_2) + \varepsilon P_M(\mathbf{e}_1, \mathbf{e}_1).$$

As we have shown in Section 3, for an attack number large enough, the individual survival probability can be maximized by maximizing the collective survival, moreover, in Sections 3.1.1 and

3.1.2 we have seen that collective survival probability is optimized by defense, independently from the group mate's behavior. Hence $P_R(\mathbf{e}_2, \mathbf{e}_2) < P_M(\mathbf{e}_1, \mathbf{e}_2)$ and $P_R(\mathbf{e}_2, \mathbf{e}_1) < P_M(\mathbf{e}_1, \mathbf{e}_1)$ thus the above inequality holds for all $\varepsilon \in]0, 1]$. Summarizing, if the attack number is large enough, defense guarantees the maximal survival probability for A-prey, whatever B-prey does.

4.2

With a parallel reasoning it is easy to see, if collective game is bistable then the T-attack SVD game is also bistable, i.e. both fleeing and defense are local ESS's. Indeed, \mathbf{q}_R (either \mathbf{e}_1 or \mathbf{e}_2) is a strict local ESS, if for every rare mutant strategy \mathbf{q}_M (either \mathbf{e}_2 or \mathbf{e}_1) we have

$$P_R(\mathbf{q}_R, \mathbf{q}_R) > P_M(\mathbf{q}_M, \mathbf{q}_R).$$

However, we have seen that, if T is large enough, then $P_R(\mathbf{q}_R, \mathbf{q}_R) > P_M(\mathbf{q}_M, \mathbf{q}_R)$, whenever $P(\mathbf{q}_R, \mathbf{q}_R) > P(\mathbf{q}_M, \mathbf{q}_R)$, thus fleeing and defense are local ESS's for the T-attack survival game, as well. In other words, under the condition of Section 3.1.3, not only the collective game but also the multi-attack survival game is bistable. Thus in a well-mixed population, increasing the attack number, ESS does not necessarily “switch”, since fleeing is a local pure ESS. However, defense is also a local pure ESS in a T-attack survival game, while the conflict in each attack is described by a SVD.

In summary, the properties of the collective game are “inherited” by the T-attack survival game. Based on the fact that in a bistable game defense is the dominant ESS, in the following we will be interested in the question, whether in non-well mixed population, defense can replace the fleeing strategy?

5. ESS for a non-well-mixed population: “game between relatives”

Now the question arises which level of non-well mixed interaction distribution between relatives can imply that defense replaces the fleeing strategy in the survival game? To answer this question, now we will focus on games between relatives (Grafen, 1979; Hines and Maynard Smith, 1979).

Let us consider a non-well-mixed asexual population, in which “instead of pairs being randomly formed, . . . a fraction “ $0 < \gamma < 1$,” of all contests are between members of the same clone (and hence between opponents with the same pure or mixed strategy), and a fraction $(1 - \gamma)$ are between random assorted opponents”. In general, frequency $\varepsilon > 0$ of mutants and $0 < \gamma < 1$ together determine the interaction distributions. In what follows, γ will be called *clonal interaction rate*. Now, the interactions are characterized by the following two distributions

$$X_R(\varepsilon, \gamma) := \begin{cases} \mathbf{q}^* \leftrightarrow \mathbf{q}^* & \mathbf{q}^* \leftrightarrow \mathbf{q}_M \\ \gamma + (1 - \gamma)(1 - \varepsilon) & (1 - \gamma)\varepsilon, \end{cases}$$

$$X_M(\varepsilon, \gamma) := \begin{cases} \mathbf{q}_M \leftrightarrow \mathbf{q}^* & \mathbf{q}_M \leftrightarrow \mathbf{q}_M \\ (1 - \gamma)(1 - \varepsilon) & \gamma + (1 - \gamma)\varepsilon, \end{cases}$$

where $X \leftrightarrow Y$ indicates the interaction between X- and Y-strategists, and $\mathbf{q}^*, \mathbf{q}_M \in S_2$ are resident and mutant strategies, respectively. Observe that

$$\gamma + (1 - \gamma)(1 - \varepsilon) + (1 - \gamma)\varepsilon = 1 \quad \text{and} \\ (1 - \gamma)(1 - \varepsilon) + \gamma + (1 - \gamma)\varepsilon = 1.$$

To make this clearer, we note that the usual two basic assumptions of evolutionary games (asexuality and very small mutation rate) together imply that all individuals in a given clone have the same phenotype. Thus, when the interaction is frequent within

clones, interaction between the same strategists is more likely. We emphasize that in this setup the stochastic process, which is the cause of non-well mixing, is not defined. We will deal with this in the Discussion section.

Following Maynard Smith's basic ideas, the terminal state of the evolution in a non-well mixed interaction distribution is characterized by the following inequality:

$$W(\mathbf{q}^*, \mathbf{q}_M, X_R(\varepsilon)) > W(\mathbf{q}_M, \mathbf{q}^*, X_M(\varepsilon)),$$

where $W(\mathbf{q}^*, \mathbf{q}_M, X_R(\varepsilon))$ and $W(\mathbf{q}_M, \mathbf{q}^*, X_M(\varepsilon))$ denote the average fitness of resident and the mutant strategists,⁹ respectively.

In our situation, when the interaction distribution is linear in γ , this inequality has the following special form:

$$[\gamma + (1 - \gamma)(1 - \varepsilon)]V(\mathbf{q}^*, \mathbf{q}^*) + (1 - \gamma)\varepsilon V(\mathbf{q}^*, \mathbf{q}_M) > \\ [\gamma + (1 - \gamma)\varepsilon]V(\mathbf{q}_M, \mathbf{q}_M) + (1 - \gamma)(1 - \varepsilon)V(\mathbf{q}_M, \mathbf{q}^*), \quad (16)$$

where $V(X, Y)$ denotes the payoff of an X-strategist when interacting with Y-strategist. We emphasize that $\gamma = 0$ implies

$$(1 - \varepsilon)V(\mathbf{q}^*, \mathbf{q}^*) + \varepsilon V(\mathbf{q}^*, \mathbf{q}_M) > \varepsilon V(\mathbf{q}_M, \mathbf{q}_M) \\ + (1 - \varepsilon)V(\mathbf{q}_M, \mathbf{q}^*),$$

so we get back the original ESS setup of Maynard Smith.

Clearly, the interaction distribution within and between clones modifies the original ESS condition of Maynard Smith. For instance, the opposite extreme to Maynard Smith's well-mixed population is when individuals interact only with their clone, i.e. $\gamma = 1$. Then \mathbf{q}^* is an ESS with respect to the totally non-mixed interaction distribution, $V(\mathbf{q}^*, \mathbf{q}^*) > V(\mathbf{q}_M, \mathbf{q}_M)$ for all possible mutant strategies, according to inequality (14). This only means that if there is no interaction between two clones, the winner clone has higher fitness. However, we think $\gamma = 1$ is only an extreme case,¹⁰ we assume that $\gamma < 1$. To see what the theoretical consequence of non-well-mixing interaction between relatives is, we make the following remark.

Remark 1. Let us consider a matrix game with $\mathbf{G} \in R^{n \times n}$ and $V(\mathbf{q}, \mathbf{p}) := \mathbf{qGp}$. Assume that there exists a unique mixed ESS $\mathbf{q}^* \in \text{int} S_n$ in the well-mixed population, i.e. $\mathbf{q}^* \mathbf{G} \mathbf{q}^* = \mathbf{qGq}^*$ and $\mathbf{q}^* \mathbf{G} \mathbf{q} > \mathbf{qGq}^*$ for all $\mathbf{q} \in S_n$; and denote by $\mathbf{x}^* \in \text{int} S_n$ the maximum of function \mathbf{qGq} , i.e. $\mathbf{x}^* \mathbf{G} \mathbf{x}^* > \mathbf{qGq}$ for all $\mathbf{q} \in S_n$, $\mathbf{x}^* \neq \mathbf{q}^*$.¹¹ Now the question arises, whether there is such $\gamma \in (0, 1)$, that guarantees that \mathbf{x}^* can replace \mathbf{q}^* .¹² Formally, we are looking for such $\gamma \in (0, 1)$, that

$$[\gamma + (1 - \gamma)(1 - \varepsilon)]\mathbf{x}^* \mathbf{G} \mathbf{x}^* + (1 - \gamma)\varepsilon \mathbf{x}^* \mathbf{G} \mathbf{q}^* > \\ [\gamma + (1 - \gamma)\varepsilon]\mathbf{q}^* \mathbf{G} \mathbf{q}^* + (1 - \gamma)(1 - \varepsilon)\mathbf{q}^* \mathbf{G} \mathbf{x}^*$$

holds for all $\varepsilon \in (0, 1)$. Using $(\mathbf{q}^* - \mathbf{x}^*) \mathbf{G} \mathbf{q}^* = 0$, the above inequality can be written as

$$\gamma \{\mathbf{x}^* \mathbf{G} \mathbf{x}^* - \mathbf{q}^* \mathbf{G} \mathbf{q}^*\} > (1 - \gamma)(1 - \varepsilon) (\mathbf{q}^* - \mathbf{x}^*) \mathbf{G} (\mathbf{x}^* - \mathbf{q}^*).$$

It is well known that if $\mathbf{q}^* \in \text{int} S_n$ is an ESS then $(\mathbf{q}^* - \mathbf{x}^*) \mathbf{G} (\mathbf{x}^* - \mathbf{q}^*) > 0$, so both sides of the above inequality are strictly positive for all $\gamma \in (0, 1)$. For a fix $\gamma \in (0, 1)$, we need the above inequality to hold for $\varepsilon = 0$ and 1 at the same time. For $\varepsilon = 1$,

⁹ E.g. $W(S_1, S_2, X_1(\varepsilon)) := P_1(S_1 \leftrightarrow S_1)V(S_1, S_1) + P_1(S_1 \leftrightarrow S_2)V(S_1, S_2)$, where $P_1(S_1 \leftrightarrow S_i)$ denotes the interaction probability between S_1 and S_i .

¹⁰ Although in the case of eusocial animals (ants, bees) the cooperation happens between families (nests, swarms), however these examples are special cases.

¹¹ The concavity of the game, i.e. $(\mathbf{q}^* - \mathbf{x}^*) \mathbf{G} (\mathbf{q}^* - \mathbf{x}^*) < 0$, is a necessary condition for existence of both the ESS and the maximum (see e.g. Garay and Varga (1999)).

¹² To our knowledge, we are the first to raise this question.

⁸ Here γ is the same as r of Grafen (1979) and Maynard Smith (1982), we only use different notation since in genetics r usually denotes genetic relatedness between two individuals.

inequality always holds, since \mathbf{x}^* is the maximum point. For $\varepsilon = 0$, let us introduce

$$\check{\gamma} := \frac{(\mathbf{q}^* - \mathbf{x}^*) \mathbf{G} (\mathbf{x}^* - \mathbf{q}^*)}{\mathbf{x}^* \mathbf{G} \mathbf{x}^* - \mathbf{q}^* \mathbf{G} \mathbf{q}^* + (\mathbf{q}^* - \mathbf{x}^*) \mathbf{G} (\mathbf{x}^* - \mathbf{q}^*)}.$$

Clearly $\check{\gamma} \in (0, 1)$ and for all $\check{\gamma} < \gamma < 1$, the maximizing \mathbf{x}^* replaces the mixed ESS \mathbf{q}^* .¹³ In other words, under high clonal interaction rate, in the natural selection such a phenotype will win that maximizes the average fitness of its group (containing mainly its clone). We mentioned that there is a connection between Hamilton's rule and our observation: following Maynard Smith, let us consider an asexual population with very rare mutation rate, and assume that there is a one-to-one correspondence between phenotypes and genotypes; then the relationship between individuals having same phenotype is $r = 1$. Consequently Hamilton's rule claims that if the cost of altruism is smaller than the benefit from it, then altruistic trait will spread. Observe that this is the general definition of altruism. For instance, the basic condition of the iterated survivor's dilemma (inequality (3)) implies that the clones' fitness is maximal at total cooperation. On the other hand, we know only one model (Garay, 2009), in which the cost of altruism is larger than the benefit from it (see the "self-sacrificing" case, when the helper individual survives with lower probability than the attacked one), in spite of the fact that defense ensures the maximal group survival.

Now we will look for a $0 < \bar{\gamma} < 1$, which can guarantee that mutant "defense" strategy, \mathbf{e}_1 , can replace the resident "fleeing" strategy, \mathbf{e}_2 , i.e. we need a threshold $0 < \bar{\gamma} < 1$ such that for all $\bar{\gamma} < \gamma < 1$ and $\varepsilon \in (0, 1]$, we have

$$W_R(\mathbf{e}_2, \mathbf{e}_1, X_R(\varepsilon, \gamma)) < W_M(\mathbf{e}_1, \mathbf{e}_2, X_M(\varepsilon, \gamma)). \quad (17)$$

Statement 1. If a matrix $\mathbf{G} := \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}$ defines the payoff and we have a linear interaction distribution, \mathbf{e}_1 can replace the resident fleeing strategy \mathbf{e}_2 whenever

$$[\gamma + (1 - \gamma)(1 - \varepsilon)]a_{22} + (1 - \gamma)\varepsilon a_{21} < (1 - \gamma)(1 - \varepsilon)a_{12} + [\gamma + (1 - \gamma)\varepsilon]a_{11}$$

holds for all $0 < \gamma < 1$ sufficiently close to 1 and all $\varepsilon \in]0, 1]$, which is equivalent to

$$a_{22} - a_{12} - \varepsilon(a_{11} - a_{12} - a_{21} + a_{22}) < \gamma(a_{11} - a_{12} - \varepsilon(a_{11} - a_{12} - a_{21} + a_{22})). \quad (18)$$

Observe that in both sides of inequality (18), there are two linear functions of $\varepsilon \in [0, 1]$. Thus inequality (18) holds for all $\varepsilon \in [0, 1]$, when it holds for $\varepsilon = 0$ and $\varepsilon = 1$ at the same time. Thus $\mathbf{e}_1 = (1, 0)$ can replace the resident fleeing strategy $\mathbf{e}_2 = (0, 1)$, when there exists $0 < \bar{\gamma} < 1$ such that for all $\bar{\gamma} < \gamma < 1$ the following two inequalities hold at the same time:

$$a_{22} - a_{12} < \gamma(a_{11} - a_{12}) \quad \text{and} \\ a_{21} - a_{11} < \gamma(a_{21} - a_{22}). \quad (19)$$

From the point of view of the present paper, there are two important games: SVD and collective games. In the following we will investigate, when the defense can replace fleeing in both games:

Example 1. In our SVD game, inequalities (19) hold with threshold $\bar{\gamma}_1 := \max\{\frac{a-b}{a-b}, \frac{1-a}{1-d}\}$. By inequality (1), we have $0 < \bar{\gamma}_1$. In biological terms, if each individual form a pair interaction with its kin (with same phenotype) with probability higher than $\bar{\gamma}_1$, then in the SVD game defense replaces the fleeing strategy.

¹³ This result is not surprising, since one of the basic assumptions of Maynard Smith's ESS model is that the interaction between opponents is well-mixed.

Finally, we note that, since by the assumption that a predator can kill only one prey in one attack, we have

$$\bar{\gamma}_1 = \max\left\{ \frac{(p_{AB}(\varphi_A, \varphi_B) + 1) - 2b}{(p_{AB}(\delta_A, \delta_B) + 1) - 2b}, \frac{2 - (p_{AB}(\delta_A, \delta_B) + 1)}{2 - (p_{AB}(\varphi_A, \varphi_B) + 1)} \right\}.$$

Example 2. Let us consider a general collective game. According to the sign of $p_{AB}(\delta_A, \delta_B) - b$ we have two cases:

1. Assume that $p_{AB}(\varphi_A, \varphi_B) - b > 0$. Then the first inequality of (19) holds for all γ with $0 < \bar{\gamma}_2 < \gamma < 1$, where $\bar{\gamma}_2 := \frac{p_{AB}(\varphi_A, \varphi_B) - b}{p_{AB}(\delta_A, \delta_B) - b}$. The second inequality of (19) holds for all $0 \leq \gamma \leq 1$.

2. Assume that $p_{AB}(\varphi_A, \varphi_B) - b < 0$. Then both inequalities of (19) hold for all $0 \leq \gamma \leq 1$.

Thus, if the collective game is bistable, the non-well-mixed interaction can guarantee that the dominant ESS will be unique. Furthermore, when there is only one global strict ESS, then both in the well-mixed and in the non-well-mixed populations, the strict ESS remains ESS.

Now the question arises whether the collective or the SVD game has lower clone interaction rate threshold, in other words which is the larger, $\bar{\gamma}_1$ or $\bar{\gamma}_2$? Using inequalities (1) and (4), an easy calculation shows that $\frac{p_{AB}(\varphi_A, \varphi_B) + 1 - 2b}{p_{AB}(\delta_A, \delta_B) + 1 - 2b} > \frac{p_{AB}(\varphi_A, \varphi_B) - b}{p_{AB}(\delta_A, \delta_B) - b}$. Thus the SVD game has higher clone interaction rate threshold. Therefore, at lower level of clonal interaction rate, in the collective game defense can replace the fleeing strategy. This implies that under lower level of clonal interaction rate, in the T -attack SVD game, defense replaces the fleeing strategy, while with the same mixing level, in SVD defense cannot invade.

It is well-known that non-well-mixedness alone can guarantee that in SVD game the defense strategy is an ESS. However, there is a low level of clonal interaction rate, at which cooperation can evolve in a T -attack SVD game, while at this level in the non-well-mixed population, in a single SVD game, fleeing remains a classical ESS.

6. Conclusions

In the cases when survival of individuals to reproductive age depends not only on its own behavior, but also on that of its conspecific group mates, the optimal behavior of an individual is determined by a game with as many persons as the number of group members. There is an essential difference between games concerning number of offspring, and survival games (cf. Hauert et al. (2006) and Parvinen (2010)), namely, in survival games the death of a mate is a single event after which the survival probability of each individual decreases, and so does that of the whole group. Formally, surviving individuals will play a different game, since the number of players is reduced. We gave a threshold for the number of attacks above which the individual survival is optimized by optimizing the group survival probability. This result is valid both for our previous model (where individuals were well informed, each prey individual was aware which of them could be killed by the predator, see Garay (2009)), and for our present model.

Based on the structure of the survival process, there is a natural decomposition of the repetitive SVD game into "hostile" and "collective" games. The "aims" of these games are different. In the hostile game the payoff function is the probability that focal individual survives and the group mate is killed by the predator, while in the collective game the payoff function is the probability that a focal individual survives together with its mate. These two games provide the additive decomposition of a SVD. The collective game is a partnership game, there is no conflict between the "group" interest and the individual based selection. In the collective game we found two possibilities: first, only defense is a unique strict ESS (as in Garay (2009)); second, the game is bistable: "fleeing" and "defense" are local strict ESS-s in the well-mixed population. In the hostile game only fleeing is the unique ESS.

We have shown the following: if the attack number is large enough, and the individual wants to maximize its survival probability in the T -attack survival game, then it can optimize its own survival probability, maximizing the collective survival probability. In other words, in each predation attack, each individual maximizes the group survival and does not the individual survival rate. However, there is an essential difference concerning the property of the collective game. In the case, when in the collective game defense is the only strict ESS, in well-mixed interaction distribution, when the attack number is high enough, defense is also a strict ESS in the many-attack survival game, in spite of the fact that in the one-attack game fleeing is the strict ESS. In the case when the collective game is bistable, many-attack survival game is also bistable in a well-mixed population.

To ensure that a bistable state evolves to a dominant ESS we followed the setup of Grafen's (1979) game between relatives. We considered an asexual population with very low mutation rate, in which individuals have genetically fixed pure phenotypes and all members of the clone have the same strategy. We focused only on territorial species, in which a group of individuals maintain (reserve) a territory. When the group splits, or the group formation is not a well-mixed process, the relative frequencies of interaction within relatives increase, so finally the advantage of defense against a predator comes from the kinships of interacting individuals. We emphasize that this reasoning goes back to Hamilton's idea on "viscous population". The novelty in our investigation is that we are interested in the level of clone interaction rate implying that defense can replace fleeing strategy, when in the well-mixing population defense and fleeing are local strict ESS-s. We gave a threshold such that, if the interaction probability within the clone is higher than this value, then the dominant ESS of the completely mixed population will be the only global ESS for the non-well mixed population. Non-well-mixed interaction alone can imply that defense is able to replace fleeing in the SVD game. However, under higher level of clone interaction rate, in the collective game defense replaces the fleeing strategy, while with the same mixing level in the SVD game, defense cannot invade. Summing up, in an SVD game, higher level of clone interaction rate can guarantee that defense replaces fleeing. Finally, we do not forget about the fact, that frequent interaction between relatives is only needed to guarantee that defense replaces fleeing, when the collective game is bistable. However, in the case when in the collective game defense is a strict ESS, in well-mixed interaction, defense is also the unique ESS in the multi-attack survival game. In this case the frequent interaction within the clone is not needed for the evolutionary advantage of defense.

We want to emphasize that not only the game between relatives is the only process where the interaction within a clone is more likely. We think that the following non-well-mixing processes can also guarantee that in the bistable case defense replaces fleeing. Without a complete overview, there are lots of different theoretical cases when the interaction distribution is not well-mixed, e.g. spatial structure caused by limited dispersal (Czárán and Hoekstra, 1992; Nowak and May, 1992; Killingback et al., 2006; Számádó et al., 2008); network reciprocity (Szabó and Fáth, 2007; Kun and Scheuring, 2009); or when each individual interacts only with a subset of the whole population (see e.g. Tarnita et al. (2009) and Maynard Smith and Szathmry (1995)); group selection (Wilson and Wilson, 2007; Traulsen and Nowak, 2006); partially random partnerships (e.g. Szabó and Vukov (2004)); complex network with dynamical linking (Pacheco et al., 2006). Our conjecture is that the above mentioned non-well mixing, stochastically interacting processes would also guarantee the evolutionary success of defense. In our simple selection situation (when asexual clones without mutation are considered), group selection and game between relatives are very close to

each other from mathematical point of view, since both processes yield non-well mixed interaction distribution. This agrees with the observation made by Nowak (2006) that "payoff matrix for group selection is structurally identical to the payoff matrix for kin selection". We feel that the above mentioned different stochastic processes result in a non-well mixed interaction distribution in which interaction between clones is more likely compared to well-mixing populations. For instance, Számádó et al. (2008) pointed out that dispersal (mixing process) and neighborhood size (c.f. Ifti et al. (2004)) together determine the advantage of cooperators and the interaction distribution, as well. Not only theoretical works point out that limited dispersal does not favor cooperation, but when individuals disperse in groups then cooperation evolves in *Pseudomonas aeruginosa* (Kümmerli et al., 2009).

There are at least two kinds of prey groups: the first one is small compared to the number of predator attacks, the relationship between herd members is strong and the different groups do not mix. In this kind of group, as we have seen, altruistic defense may evolve. We emphasize that maximizing collective survival is the only "tool" for the phenotypes to maximize their own survival probability. Intuitively, in a multi-attack survival game, the group mate is a "source" of higher survival probability and not only a competitor. The second kind of prey group is a large herd in which the average relationship between herd members is very weak, and the herd mixes arbitrarily. Now the question arises, why the altruistic defense is rare in a large, well-mixed group. We feel that our game decomposition may shed light on this question. Let us define a behavior "selfish" if the individual maximizes its own survival probability (defined by SVD game); a "hostile" behavior means maximization of the probability to survive alone while other prey dies; finally, the behavior of group member is called "altruistic" if the group survival rate is maximized at the cost of the other group member. From Darwinian point of view, it seems that the "best" competitor behavior is the hostile one; since it can increase its relative advantage over the population by letting killed its competitor belonging to a different clone. However, this kind of advantage can only work when the group size is large enough compared to the number of predator attacks, and the group is well mixed, i.e. the killed individual belongs to another phenotype. Finally, we emphasize that selfish behavior determines the outcome of the natural selection.

Now, we mention a few concrete biological examples, in which our theoretical result may be applicable: predation seems to be the most important selective factor leading to sociality for mongoose and squirrel (Waterman, 1997; Rood, 1983). Furthermore, our non-well mixed interaction distribution (in our case group formation) may happen in the nature, since the small groups are formed based on the kin relation, in general. The first example, banded mongoose (*Mungos mungo*) lives in groups with size from 3 to 36, and the members of the group are usually relatives, but not necessarily (Gilchrist, 2004). Mongoose groups have successful defense against the predator by their harassment (Rood, 1975). Furthermore, mongoose packs also split, and when both males and females were evicted from a pack at the same time, the dispersing animals immediately separated into same-sex groups and went separate away, and finally a male and a female packs form a new pack (Cant et al., 2001), in which the males are not relative with females. Second example, unrelated male Cape ground squirrels (*Xerus inauris*) live in groups, and only two males drove reptilian predators away by mobbing (Waterman, 1997). However, it is unlikely that male bands contain closely related individuals (Waterman, 1995), but matrilineal kin bands split into smaller groups (Waterman, 2002). Third example, cooperative meerkats (*Suricata suricatta*) also display cooperative defense against predator, the females form groups based on kinship (Clutton-Brock et al., 1999a,b), and female meerkats are more likely to breed in their natal group than males (Clutton-Brock et al., 2002).

Furthermore, we would like to call the attention to the fact that clone interaction rate (or group formation) can arise not only from predator–prey interaction. First, related primate males (rhesus macaques, velvet monkey) sometimes emigrate together from their natal troops (Gouzoules and Gouzoules, 1987). Contrarily, male chimpanzees remain in their natal community, they cooperate to defend their territory (Mitani, 2009), and during territory defense the resident male sometimes is killed by the intruder group. Furthermore, male lions birthing in the same natal group form a collation and they can occupy females' pride together, furthermore when female lions' prides split, dispersing females invariably settle adjacent to their natal territory (Spong and Creel, 2004; VanderWall et al., 2009). Although in these examples the biological effect is the aggression within species, but during territory defense a member of the group can be killed by other intruder conspecifics, so in these cases the territory defense can define a survival game. Moreover, the power of a group strictly decreases with decreasing group size. Of course, in this case the aggressive interactions may define a game different from SVD considered by us, but the structure of the T -attack survival game may remain valid, so our result may be generalized to these cases.

Finally, we would like to point out that our two basic assumptions may be dropped in the future.

First, we have considered a minimal group with two members. We think that if the group size is not too high compared to the average attack number, then our results remain valid, when the survival probability of the group synergistically increases with the group size (cf. Garay (2009)). However, when the territorial group size is N , the one-attack survival game should be described by an N -person public goods game.

Second, we assume that there is no migration between territorial defending groups. Traulsen and Nowak (2006) pointed out that in a stochastic model of multi-level (group) selection, when the migration between groups is not too high, group selection favors cooperation. In our case, if there are both fleeing and defense strategists in the population, at average, from a fleeing–defense pair, fleeing has a higher chance to survive. Thus, new groups formed by migration are fleeing–fleeing pairs at average having lower survival probability than defense–defense pairs. Therefore, if the attack number is high enough, then the defense–defense pairs have a final evolutionary advantage (cf. Garay (2009)).

The fight for territory between groups is sometime also lethal. If there is “war” between separate groups, the multi-level selection can guarantee the evolutionary stability of altruism, if the survival probability of groups depends on the level of altruism within groups (Boza and Számadó, 2010; Bowles, 2006, 2009; Choi and Bowles, 2007). We think that there is a possible generalization of SVD for this case (Huge-Jones and Zultan, 2010).

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Appendix

Let us assume that for some $0 < \varepsilon < 1 - \eta$, $P, Q : S_2 \rightarrow [\eta + \varepsilon, 1]$ are continuous functions and consider function

$$P_A(\mathbf{q}_A, \mathbf{q}_B) = \left[\frac{P(\mathbf{q}_A, \mathbf{q}_B) + Q(\mathbf{q}_A, \mathbf{q}_B) - \eta}{P(\mathbf{q}_A, \mathbf{q}_B) - \eta} \left[\frac{P(\mathbf{q}_A, \mathbf{q}_B)}{\eta} \right]^T - \frac{Q(\mathbf{q}_A, \mathbf{q}_B)}{P(\mathbf{q}_A, \mathbf{q}_B) - \eta} \right] \eta^T$$

defined on $S_2 \times S_2$. Let us fix $\mathbf{q}_B \in S_2$ and assume that for some $\mathbf{x}_A, \mathbf{y}_A \in S_2, \mathbf{x}_A \neq \mathbf{y}_A$, we have

$$P(\mathbf{x}_A, \mathbf{q}_B) > P(\mathbf{y}_A, \mathbf{q}_B).^{14} \tag{A.1}$$

Statement. There exists $\bar{T} := \bar{T}(\mathbf{x}_A, \mathbf{y}_A, \mathbf{q}_B) \in \mathbb{N}$ such that for all $T > \bar{T}$ we have

$$P_A(\mathbf{x}_A, \mathbf{q}_B) > P_A(\mathbf{y}_A, \mathbf{q}_B). \tag{A.2}$$

Indeed, an easy calculation shows that inequality (A.2) can be written as

$$\left[\frac{P(\mathbf{x}_A, \mathbf{q}_B)}{P(\mathbf{y}_A, \mathbf{q}_B)} \right]^T > \frac{\frac{P(\mathbf{y}_A, \mathbf{q}_B) + Q(\mathbf{y}_A, \mathbf{q}_B) - \eta}{P(\mathbf{y}_A, \mathbf{q}_B) - \eta} + \frac{\frac{Q(\mathbf{x}_A, \mathbf{q}_B)}{P(\mathbf{x}_A, \mathbf{q}_B) - \eta} - \frac{Q(\mathbf{y}_A, \mathbf{q}_B)}{P(\mathbf{y}_A, \mathbf{q}_B) - \eta}}{\left[\frac{P(\mathbf{y}_A, \mathbf{q}_B)}{\eta} \right]^T}}{\frac{P(\mathbf{x}_A, \mathbf{q}_B) + Q(\mathbf{x}_A, \mathbf{q}_B) - \eta}{P(\mathbf{x}_A, \mathbf{q}_B) - \eta}}.$$

Since for all $(\mathbf{q}_A, \mathbf{q}_B) \in S_2 \times S_2$ we have $P(\mathbf{q}_A, \mathbf{q}_B) > \eta$, for the right-hand side of the latter inequality we obtain

$$\frac{\frac{P(\mathbf{y}_A, \mathbf{q}_B) + Q(\mathbf{y}_A, \mathbf{q}_B) - \eta}{P(\mathbf{y}_A, \mathbf{q}_B) - \eta} + \frac{\frac{Q(\mathbf{x}_A, \mathbf{q}_B)}{P(\mathbf{x}_A, \mathbf{q}_B) - \eta} - \frac{Q(\mathbf{y}_A, \mathbf{q}_B)}{P(\mathbf{y}_A, \mathbf{q}_B) - \eta}}{\left[\frac{P(\mathbf{y}_A, \mathbf{q}_B)}{\eta} \right]^T}}{\frac{P(\mathbf{x}_A, \mathbf{q}_B) + Q(\mathbf{x}_A, \mathbf{q}_B) - \eta}{P(\mathbf{x}_A, \mathbf{q}_B) - \eta}} < \frac{\frac{P(\mathbf{y}_A, \mathbf{q}_B) + Q(\mathbf{y}_A, \mathbf{q}_B) - \eta}{P(\mathbf{y}_A, \mathbf{q}_B) - \eta} + \left| \frac{Q(\mathbf{x}_A, \mathbf{q}_B)}{P(\mathbf{x}_A, \mathbf{q}_B) - \eta} - \frac{Q(\mathbf{y}_A, \mathbf{q}_B)}{P(\mathbf{y}_A, \mathbf{q}_B) - \eta} \right|}{\frac{P(\mathbf{x}_A, \mathbf{q}_B) + Q(\mathbf{x}_A, \mathbf{q}_B) - \eta}{P(\mathbf{x}_A, \mathbf{q}_B) - \eta}}.$$

Furthermore, P and Q are continuous functions on S_2 , thus there exists

$$K := \max_{\mathbf{x}_A, \mathbf{y}_A, \mathbf{q}_B \in S_n} \frac{\frac{P(\mathbf{y}_A, \mathbf{q}_B) + Q(\mathbf{y}_A, \mathbf{q}_B) - \eta}{P(\mathbf{y}_A, \mathbf{q}_B) - \eta} + \left| \frac{Q(\mathbf{x}_A, \mathbf{q}_B)}{P(\mathbf{x}_A, \mathbf{q}_B) - \eta} - \frac{Q(\mathbf{y}_A, \mathbf{q}_B)}{P(\mathbf{y}_A, \mathbf{q}_B) - \eta} \right|}{\frac{P(\mathbf{x}_A, \mathbf{q}_B) + Q(\mathbf{x}_A, \mathbf{q}_B) - \eta}{P(\mathbf{x}_A, \mathbf{q}_B) - \eta}} > 0.$$

Hence, for our statement it is enough to find a positive integer \bar{T} , with

$$\left[\frac{P(\mathbf{x}_A, \mathbf{q}_B)}{P(\mathbf{y}_A, \mathbf{q}_B)} \right]^{\bar{T}} > K.$$

Hence, we immediately obtain

$$\bar{T} = \frac{\ln K}{\ln P(\mathbf{x}_A, \mathbf{q}_B) - \ln P(\mathbf{y}_A, \mathbf{q}_B)}.$$

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¹⁴ Observe that this condition is a part of the strict Nash condition for (x_A, q_B) in the sense that if player B does not change his strategy, then player A can only decrease his pay-off by deviating from his strategy x_A .

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