



Cooperation in defence against a predator

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ABSTRACT

The origin and the evolutionary stability of cooperation between unrelated individuals is one of the key problems of evolutionary biology. In this paper, a cooperative defence game against a predator is introduced which is based on Hamilton's selfish herd theory and Eshel's survival game models. Cooperation is altruistic in the sense that the individual, which is not the target of the predator, helps the members of the group attacked by the predator and during defensive action the helper individual may also die in any attack. In order to decrease the long term predation risk, this individual has to carry out a high risk action. Here I show that this kind of cooperative behaviour can evolve in small groups. The reason for the emergence of cooperation is that if the predator does not kill a mate of a cooperative individual, then the survival probability of the cooperative individual will increase in two cases. If the mate is non-cooperative, then—according to the dilution effect, the predator confusion effect and the higher predator vigilance—the survival probability of the cooperative individual increases. The second case is when the mate is cooperative, because a cooperative individual has a further gain, the active help in defence during further predator attacks. Thus, if an individual can increase the survival rate of its mates (no matter whether the mate is cooperative or not), then its own predation risk will decrease.

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1. Introduction

A prerequisite to the emergence of cooperation is that individuals live together. The “selfish herd” theory of Hamilton (1971) claims that the evolutionary force behind the formation of a group is predation, since the best shelter is in the centre of a group during each predator's attack if there is no refuge nearby. In other words, individuals reduce their predation risk at the expense of others. Thus, it is natural to investigate the emergence of altruistic defence against the predator in a “selfish herd”. Clearly, altruistic defence against a predator increases the survival probability of the attacked individual and decreases that of the helper individual (Wilson, 1975). For instance, alarm call is considered as one of altruistic traits which benefit other group members at some cost to the caller (Krebs and Davies, 1978, p. 142; Edmunds, 1974, p. 254). Another example is mobbing (Krebs and Davies, 1978, p. 147; Edmunds, 1974, p. 204) when the prey individuals approach the predator within dangerous distance. Moreover, active frightening behaviour is also well known when the prey attacks the predator (Edmunds, 1974, p. 151). For example, musk oxen (*Ovibus moschatus*) form defensive ring when treated by a pack of wolves, and the cows and calves are in the centre of the ring. Furthermore, elephants (*Loxodonta africana*) actively defend themselves and their young

against lions (*Panthera leo*) whereas buffalo (*Syncerus caffer*) can kill lions (Hayward and Kerley, 2005).

Eshel and Weinshall (1988) considered a sequence of survival games with two players. The rules randomly changed from one encounter to another. There were two types of games: the first one was a prisoner's dilemma game in which defection is the best strategy, while in the second game cooperation is of immediate self reward. They showed that there are cases when total cooperation is the best behaviour even in the prisoner's dilemma as well, since the opponent (if alive) will cooperate in the future. Eshel and Shaked (2001) found that partnership¹ may evolve in a random supergame of survival. Supergame contains a continuum of events, in each event each pair of individuals plays a prisoner dilemma game, in which the pay-off matrix contains the survival probabilities which change according to a time independent distribution. The survival rate of single individuals may be higher than that of a non-fully cooperative pair. The pay-off function is the life time of each individual. Eshel and Shaked (2001) (using a little bit similar method to the well-known inclusive fitness method), found that in a class of supergame cooperation can evolve.

¹ Partnership is a relation between at least two individuals when it is their best interest to help each other since by doing so they increase the probability of being together in the future and they continue to help each other.

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The aim of this paper is to “combine” Hamilton’s and Eshel et al.’s ideas. For this purpose, the main assumptions of these theories must be combined. In Hamilton’s scenario, the predator attack is asymmetric in the sense that only one individual from a huge herd is attacked. There is no such kind of asymmetry between two players in Eshel’s models. Hamilton considered only one predator attack, while Eshel considered a continuum of events. In the situation considered here, a predator can attack only one individual at a time and each individual must survive an average number of attacks.

Let us consider a large enough asexual population, in which unrelated individuals have no information on their mate’s behaviour during random group formation.² Every individual has the same ability to defend itself against the predator, to recognize the stalking predator and has the same payoff functions. They all have a genetically fixed (perhaps mixed) behaviour phenotypes³ and no memory.⁴ Furthermore, in the biological case considered here there is neither social nor dominant structure.⁵

Naturally, the size of the group determines defensive ability. If the size of the group decreases then the defensive ability of the group also decreases, thus the survival probability of any member of the group also decreases (Wilson, 1975). In this paper, the simplest possible case is considered in which only two individuals constitute each randomly formed group and when a member of a pair dies then new pair formation from the survived members is not possible.

From a mathematical point of view, I use elementary stochastic methods to calculate the average survival probabilities and then I consider this survival rate as pay-offs. Thus, my approach is a deterministic one, for instance, the stochastic fixation process of any strategy is not investigated.

2. One-attack game

Now let us describe an attack by a predator. Let us assume that the predator chooses randomly one individual from its target pair, thus the probability of being chosen is 0.5 per individual, i.e. each prey has the same predation risk. Each attacked individual must defend itself against the predator. In other words, the attacked individual cannot shift the attack to the other. A non-attacked individual has two pure strategies: the first pure strategy is *altruistic*, i.e. it helps the attacked mate and during this altruistic defence the helper individual may die. Cooperation in defence is an altruistic action, since it decreases the lifetime of helper while increases that of recipient at each predator attack.⁶ With altruistic help there are the following four probabilities of the possible events. Let β_1 denote the probability of survival of both individuals, β_2 be the probability that the attacked individual dies and the helper survives, β_3 be the probability that the attacked individual survives and the helper dies and β_4 denote the probability that both individuals are killed by the predator. Clearly

² Under these assumptions, kin selection (Hamilton, 1964), group selection (Nowak, 2006) and group formation on phenotypic similarity (Burtsev and Turchin, 2006) cannot be used.

³ Since the genetically fixed behaviour is not conditional—i.e. an individual cannot change its behaviour according to the behaviour of others—neither direct (Brandt and Sigmund, 2004) nor indirect reciprocity (Ohtsuki and Iwasa, 2004; Nowak and Sigmund, 2005) can be applied.

⁴ Thus, punishment is not possible in the present model (Fehr and Gächter, 2002; Rockenbach and Milinski, 2006).

⁵ The altruistic defence 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).

⁶ This altruistic help is not considered as a by-product benefit, since the helper is not attacked and its help in defence is not an incidental consequence of a selfish action in each predators attack (Sachs et al., 2004).

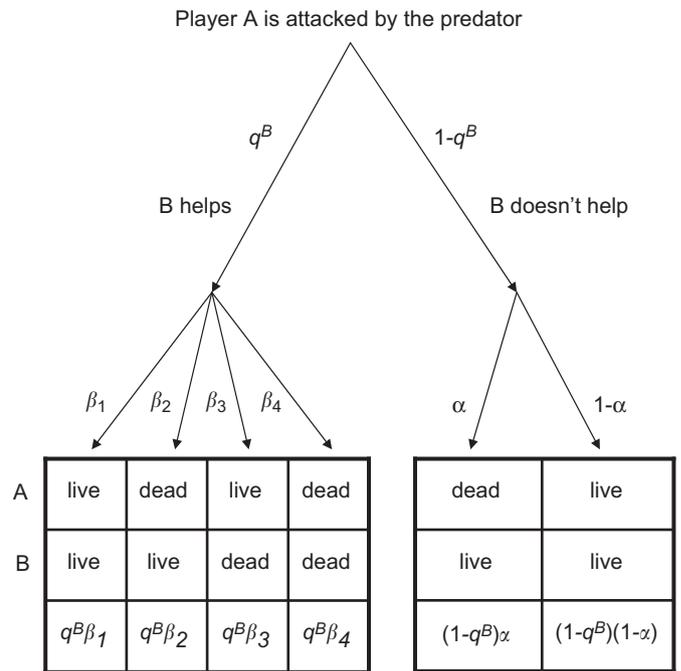


Fig. 1. A-prey is attacked by predator. The boxes at the leaves of the tree contain the elementary events with probabilities. For instance, if A-prey is attacked and the B-prey helps with probability q_B , then $q_B\beta_1$ is the probability that both A- and B-prey survive, etc. Similar process takes place when B-player is attacked by predator.

$\sum_{i=1}^4 \beta_i = 1$. In the case when the helper individual survives with higher probability than the attacked one ($\beta_2 > \beta_3$), help is considered “altruistic”; but in the case when the helper individual survives with lower probability than the attacked one ($\beta_3 > \beta_2$), help is considered as a “self-sacrificing” action. The following results are true in both cases.

The second pure strategy is the *non-altruistic* strategy, i.e. not to help. In this case, the non-attacked individual is not injured and certainly survives. Without altruistic help, let α denote the probability that the attacked individual dies, thus $1 - \alpha$ is the survival probability of the attacked individual.

In the sequel I assume that $\beta_2 < \alpha$ (i.e. altruism increases the survival probability of the attacked individual)⁷ and $\beta_1 > (1 - \alpha)$ (i.e. altruistic defence also increases the survival of the group). If $\beta_1 > 2(1 - \alpha)$, the two individuals together are more successful against the predator than either alone so that there is a “synergistic effect” of altruism (Kun et al., 2006).

For transparency, let one member of the group be called the A-prey and the other one the B-prey. Let $q_A \in [0, 1]$ be the (probably mixed)⁸ strategy of A-prey, i.e. with probability q_A A-prey will help the attacked B-prey. Similarly, $q_B \in [0, 1]$ is the cooperation strategy of B-prey.

Fig. 1 summarizes all possible events with the probabilities of a predator attack.

Based on Fig. 1, it is easy to see that if the predator attacks A-prey then the survival probability of B-prey is $P(B \text{ survives} | A) = q_B(\beta_1 + \beta_2) + (1 - q_B)$. According to the condition $\beta_1 + \beta_2 < 1$, this survival probability function strictly decreases in q_B , so that it reaches its maximum at $q_B = 0$. (From biological point of view, this means that a non-attacked non-cooperative individual surely

⁷ If $\beta_2 > \alpha$, then the non-attacked individual hinders the survival of the attacked one, thus this action is not a help.

⁸ A q_A -strategist does not have to be either full altruistic all the time or full selfish. Rather it has a probability of playing altruistic (with q_A) or the non-altruistic with (with $1 - q_A$) of these pure strategies at any given predator attack.

survives while a cooperative one has a risk in survival.) Thus, if the predator attacks A-prey then the best choice of B-prey is the non-altruistic strategy. Clearly, similar statement holds for A-prey based on symmetrical reasoning.

Now let us take into account that the predator attacks every member of the group with the same probability. If the predator's target choice and the survival of the target prey are independent events then we get

$$P_{AB}(q_A, q_B) := P(A \text{ survives} \ \& \ B \text{ survives}) \\ = (1 - \alpha) - \frac{1}{2}(q_A + q_B)[1 - \alpha - \beta_1], \quad (1)$$

$$P_{A0}(q_A, q_B) := P(A \text{ survives} \ \& \ B \text{ dies}) = \frac{1}{2}[\alpha + q_A(\beta_2 - \alpha) + q_B\beta_3], \quad (2)$$

$$P_{0B}(q_A, q_B) := P(A \text{ dies} \ \& \ B \text{ survives}) = \frac{1}{2}[\alpha + q_A\beta_3 + q_B(\beta_2 - \alpha)], \quad (3)$$

$$P_{00}(q_A, q_B) := P(A \text{ dies} \ \& \ B \text{ dies}) = \frac{1}{2}(q_A + q_B)\beta_4. \quad (4)$$

The survival probability for A-prey is

$$P_A(q_A, q_B) := P_{AB}(q_A, q_B) + P_{A0}(q_A, q_B) = 1 - \frac{1}{2}\alpha + \frac{1}{2}q_A(\beta_1 + \beta_2 - 1) \\ + \frac{1}{2}q_B(\alpha + \beta_1 + \beta_3 - 1).$$

Since $\beta_1 + \beta_2 < 1$, the maximum survival probability of A-prey is guaranteed by $q_A = 0$. Clearly, similar statement holds for B-prey. Thus, also a non-altruistic strategy guarantees maximum survival rate on the average in each predator attack.

In summary, the non-altruistic behaviour is the best one (i.e. strict evolutionarily stable strategy, ESS) from a game theoretical point of view in one-attack game for all prey. On the other hand, if $1 - \alpha < \beta_1$, then the survival probability of pair (1) attains its maximum at $q_A = q_B = 1$. This means that the group survives with maximum probability if both prey are totally altruistic.

Finally, I emphasize that when group size is higher than two and there is only one predator attack, the predictions of this model remain valid, whenever the cooperative help has a risk.

3. Many-attacks game

The aim of this game is to survive a given number of predator attacks and to attain the age of reproduction. Now let us calculate the probability to attain 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 when an attack might occur. T denotes the mean of the distribution of attack numbers.⁹ Assume that the predator can find solitary individuals and pairs of prey with the same probability 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 the predator does not have preference regarding the solitary versus the grouped individuals. Furthermore, since it is already assumed that the predator finds with the same probability solitary animals and pairs of prey, each solitary and each group must survive the average number of predator's attack (T). The latter is an advantage for individuals of a group, since each prey in a group has half the predation risk. In the literature, this effect is called the "dilution effect" (Foster and Treherne, 1981). In the present model, predation risk is described by the predation success in each attack and by the average number of predator attacks.

In this game, the smallest group (with two members) is considered for simplicity. However, in two-member groups Hamilton's selfish herd theory does not work since there is no

centre of the group where a prey is safe. Nevertheless, the "selfish herd" theory is one of the most important starting points of this paper for the following reasons. Firstly, a non-cooperative individual can decrease its predation risk at the expense of its mate. Secondly, the predator attacks the nearest prey only, strictly one of the two ones. Thirdly, the results of the present model may be generalized to small groups when predation pressure is large enough.¹⁰

Another simplifying condition is that after a successful attack, the surviving prey do not form a new group. If the solitary survivor after a successful attack easily and immediately finds another solitary survivor to form a new pair, then it means that the population would be very dense. In other words, the prey stays in a huge but not too compact group. Now I consider another extreme case, namely when the density is very low thus each member of a group, which survives a successful attack, will be a solitary prey, i.e. the survived prey cannot form a new pair. Another case is when the prey are territorial: then the territorial defence hinders the solitary individuals' forming a new group. I do emphasize that this simplifying assumption (namely, solitary remains solitary) rules out that a non-cooperative individual, changing groups, finally finds a group in which the relative frequency of cooperative individuals is high.

Let η be the survival probability of solitary prey. According to the "many eyes" hypothesis, which claims that the group observes the stalking predator earlier than the solitary prey (see e.g. Treves, 2000), and the "confusion effect" (i.e. when confronted with a group of their prey, predators often become confused and less successful in their attacks see e.g. Jeschke and Tollrian, 2007), it is probable that $1 - \alpha > \eta$.

Fig. 2 summarizes the random process of survival of A-prey.

Based on Fig. 2, it is easy to see that the average survival probability of A-prey in a group, which contains (q_A, q_B) , strategy is¹¹

$$P_A(q_A, q_B) := P_{AB}(q_A, q_B)^T + P_{A0}(q_A, q_B) \frac{P_{AB}(q_A, q_B)^{(T-1)} - \eta^{(T-1)}}{P_{AB}(q_B, q_B) - \eta} \eta. \quad (5)$$

Using (1)–(4), (5) will have the following form:

$$P_A(q_A, q_B) = [(1 - \alpha) - \frac{1}{2}(q_A + q_B)[1 - \alpha - \beta_1]]^T \\ + \frac{1}{2}(\alpha + q_A(\beta_2 - \alpha) + q_B\beta_3) \\ \times \frac{[(1 - \alpha) - \frac{1}{2}(q_A + q_B)[1 - \alpha - \beta_1]]^{(T-1)} - \eta^{(T-1)}}{(1 - \alpha) - \frac{1}{2}(q_A + q_B)[1 - \alpha - \beta_1] - \eta}. \quad (6)$$

For simplicity, let us assume that each prey, reaching the reproduction age, has the same number of offspring. In this case, natural selection favours individuals that reach the reproduction age with higher probability. This assumption is a worst case one

¹⁰ Furthermore, if there is no fixed geometry of the herd (the herd is well mixed), then the individuals in danger zone always change and if there are many predator attacks then the peripheral effect is not so important. Indeed, assume that a predator only attacks individuals in danger zone. Let m be the number of individuals in danger zone out of a group of size n , thus $1/m$ is the probability of attacks upon them. Moreover, in the centre of the group the attack probability is zero. If the group is well mixed, then the probability of an individual staying in danger zone or in the safe centre is m/n and $n - (m/n)$, respectively. Thus, the average attack probability in an average encounter is given by $(1/m)(m/n) + 0(1/(n - m))(n - m/n) = 1/n$, which equals to the risk coming from dilution effect. In other words, in each attack the geometrical effect is very important (since the individual risk is either $1/m$ or 0), but in well-mixed groups under many attacks it is not a modifying factor. Of course, when the group has a fixed geometrical structure (e.g. a nest colony) this reasoning does not work.

¹¹ Use $1 + s + s^2 + \dots + s^{n-1} + s^n = (s^n - 1)/(s - 1)$! Moreover, Eq. (5) has meaning if and only if $P_{AB}(q_A, q_B) - \eta \neq 0$, for all $(q_A, q_B) \in [0, 1] \times [0, 1]$, which is guaranteed by conditions $1 - \alpha > \eta$ and $\beta_1 > 1 - \alpha$.

⁹ To avoiding unnecessary complications, I do not consider the distribution of attack numbers. If the minimal attack number is high, my predictions remain valid.

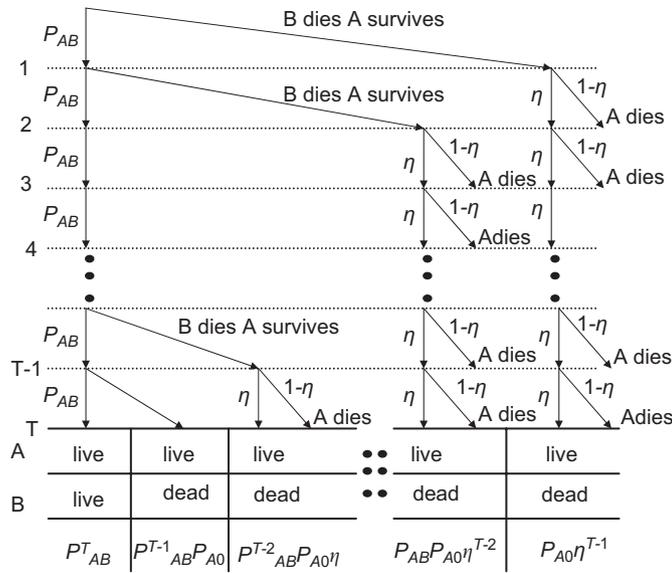


Fig. 2. A-prey attains reproductive age. A-prey survives either in group or as solitary. If B-player dies at attack $T - k$, then the possibility that A-prey survives is $P_{AB}^{T-k-1}P_{A0}^k$. The probability that A-prey attains reproductive age equals the sum of the probabilities of all possible elementary events given at the leaves of the tree. Similar process takes place for B-player.

for groups, since if we take into account the cost of defence against a predator; then each solitary individual must have higher cost than non-solitary ones. For instance, according to the dilution effect a solitary prey is attacked more often, thus the cost (e.g. energy cost of escape and/or injuring risk) of its defence is higher. Moreover, a given level of vigilance is more costly for solitary individuals.

Cost-benefit analysis is also very insightful in kin selection (Hamilton, 1964); “stakeholder altruism” (Roberts, 2005); and “partnership selection” (Eshel and Shaked, 2001). In the first two cases, the effect of cooperation is “instantaneous”, contrary to “partnership selection” and the present case when the benefit of helping in a given attack will realize in the lifetime. Now I consider only the case when the average predator attack is only $T = 2$. In the first attack, the cost of cooperation is the probability of death of a helper, i.e. $\beta_3 + \beta_4$. For the purpose to define the benefit of helper B, first I calculate the average survival probability of a helper in the next predator attack, which depends clearly on the strategy of the mate of the helper individual. Using the above notation, the average survival probability of a helper is $P_{AB}(q_A, 1)P_B(q_A, 1) + P_{OB}(q_A, 1)\eta$, while the solitary individual’s survival rate is η . Intuitively, the benefit of help is different from the above two survival rates, formally $P_{AB}(q_A, 1)P_B(q_A, 1) + P_{OB}(q_A, 1)\eta - \eta$, since this is increment in survival probability thanks to help in previous defence against predator attack. In the present model, the benefit is higher than cost if

$$P_{AB}(q_A, 1)P_B(q_A, 1) + P_{OB}(q_A, 1)\eta > \eta + \beta_3 + \beta_4. \tag{7}$$

Now assume that $q_A = 0$ so that (7) has the following form:

$$(1 - \alpha + \beta_1)(1 - \alpha + \beta_1 + \beta_2) + 2\beta_2\eta > 4\eta + 4\beta_3 + 4\beta_4. \tag{8}$$

Thus, help in defence increases the helper’s survival rate in the next predator attack whenever (8) holds.

Before I give the condition of ESS for the many-attacks game, I emphasize that if $T = 1$ we get back the one-attack game where the non-altruistic behaviour is ESS.

In order to find an ESS, let us follow the ideas of Maynard Smith, the founder of evolutionary game theory (Maynard Smith, 1982), and consider a large enough Resident prey population and

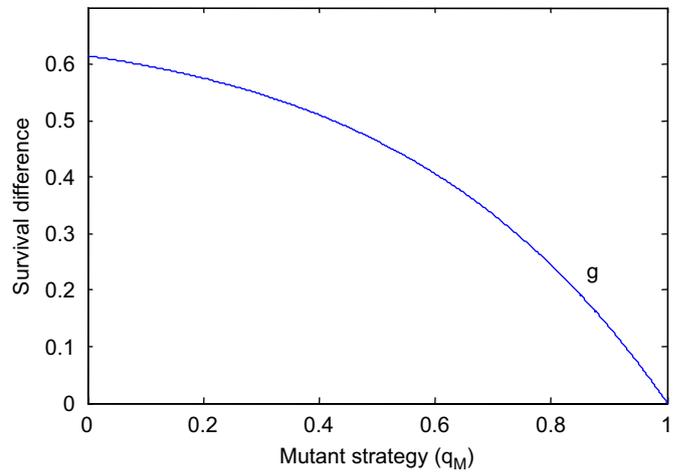


Fig. 3. Altruism is a strict ESS. In this example, $\beta_1 = 0.95$, $\beta_2 = 0.02$, $\beta_3 = 0.01$, $\alpha = 0.6$, $\eta = 0.2$ and $T = 8$. Since the solitary survival rate is 0.2 and survival rate without altruism is 0.4, the “selfish herd” decreases predation risk. Moreover, this is a synergistic case since the altruistic pair survives with a probability of 0.95 while without altruism the survival rate is only 0.4. The function $f(q_M) = P_R(1, 1) - P_M(q_M, 1)$ is positive in $q_M \in [0, 1]$, which means that no mutant can invade into a totally altruistic resident population.

resident strategy by letting $q_R = 1$. Assume that a small new prey subpopulation arises with a Mutant strategy $q_M \neq 1$. If the mutation rate is arbitrarily small, then for the evolutionary stability of total cooperator ($q_R = 1$) it is sufficient that the survival probability of resident is higher than that of mutant (i.e. $P_R(1, 1) > P_M(q_M, 1)$). More precisely, using (6), whenever we have

$$\begin{aligned} & \beta_1^T + \frac{1}{2}(\beta_2 + \beta_3)\gamma \frac{\beta_1^{(T-1)} - \eta^{(T-1)}}{\beta_1 - \eta} - \left[(1 - \alpha) - \frac{1}{2}(q_M + 1)[1 - \alpha - \beta_1] \right]^T \\ & - \frac{1}{2}(\alpha + q_M(\beta_2 - \alpha) + \beta_3)\eta \\ & \times \frac{\left[(1 - \alpha) - \frac{1}{2}(q_M + 1)[1 - \alpha - \beta_1] \right]^{(T-1)} - \eta^{(T-1)}}{(1 - \alpha) - \frac{1}{2}(q_M + 1)[1 - \alpha - \beta_1] - \eta} > 0 \end{aligned}$$

for $q_M \in]0, 1[$, then the totally altruistic strategy is a strict ESS. In Fig. 3, there is an example showing that the altruistic strategy is a strict ESS, i.e. there is no smaller level altruistic strategy which can invade into a totally altruistic population.

Now the question is how can the altruistic strategy invade into a “selfish herd”? Let us consider a large enough, totally non-altruistic resident population ($q_R = 0$), in which a rare mutant strategy ($q_M > 0$) arises. If the frequency of the mutant strategy is arbitrarily small and the survival probability of mutant is higher than that of resident (i.e. $P_R(0, 0) < P_M(q_M, 0)$), then cooperation can invade into the non-altruistic population. More precisely, whenever we have

$$\begin{aligned} & \left[(1 - \alpha) - \frac{1}{2}q_M[1 - \alpha - \beta_1] \right]^T + \frac{1}{2}(\alpha + q_M(\beta_2 - \alpha))\eta \\ & \times \frac{\left[(1 - \alpha) - \frac{1}{2}q_M[1 - \alpha - \beta_1] \right]^{(T-1)} - \eta^{(T-1)}}{(1 - \alpha) - \frac{1}{2}q_M[1 - \alpha - \beta_1] - \eta} \\ & - (1 - \alpha)^T - \frac{1}{2}\alpha\eta \frac{(1 - \alpha)^{(T-1)} - \eta^{(T-1)}}{(1 - \alpha) - \eta} > 0 \end{aligned}$$

for $q_M \in]0, 1[$, then the altruistic strategy invades into the totally non-altruistic selfish herd. An example when altruistic strategy can invade is given in Fig. 4.

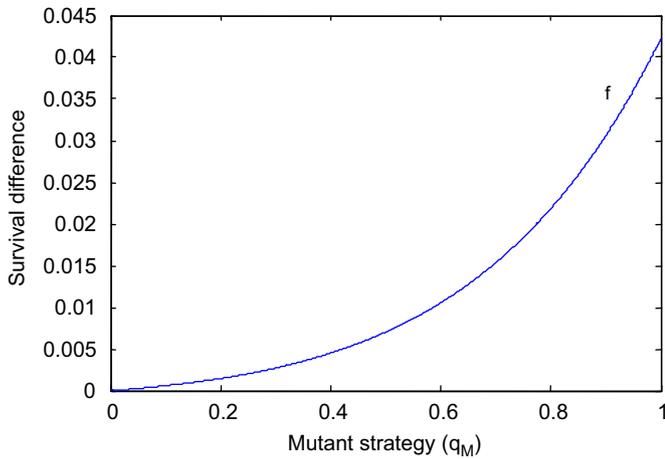


Fig. 4. Altruism invades into a non-altruistic selfish herd. In this example, $\beta_1 = 0.95$, $\beta_2 = 0.02$, $\beta_3 = 0.01$, $\alpha = 0.6$, $\eta = 0.2$ and $T = 8$. The function $g(q_M) = P_M(q_M, 0) - P_R(0, 0)$ is positive in $q_M \in [0, 1]$, which means that the altruistic strategy can invade into a selfish herd.

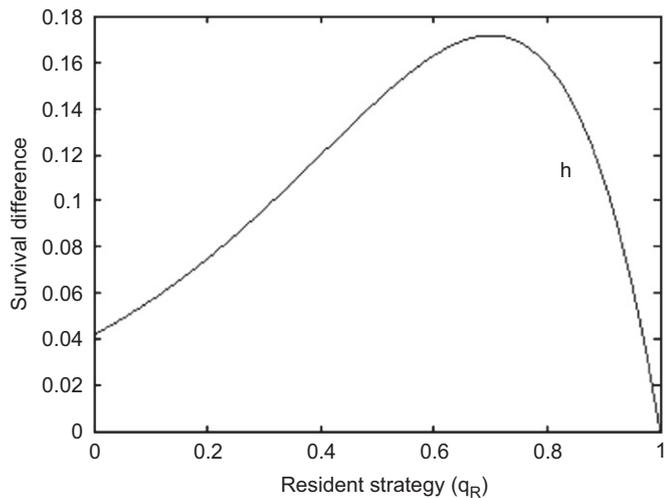


Fig. 5. Total altruism invades into a non-totally altruistic population. In this example, $\beta_1 = 0.95$, $\beta_2 = 0.02$, $\beta_3 = 0.01$, $\alpha = 0.6$, $\eta = 0.2$ and $T = 8$. The function $h(q_R) = P_M(1, q_R) - P_R(q_R, q_R)$ is positive in $q_R \in [0, 1]$, which means that the totally altruistic strategy can invade into a non-totally altruistic population.

The final question is that how can the totally altruistic strategy invade into a non-totally altruistic population? Consider a non-totally altruistic resident population ($0 < q_R < 1$), in which a rare totally altruistic mutant strategy ($q_M = 1$) arises. Whenever the survival probability of mutant is higher than that of resident (i.e. $P_R(q_R, q_R) < P_M(1, q_R)$), then the totally altruistic strategy can invade into the non-totally altruistic population. More precisely, whenever we have

$$\begin{aligned} & \left[(1 - \alpha) - \frac{1}{2}(1 + q_R)[1 - \alpha - \beta_1] \right]^T - [(1 - \alpha) - q_R[1 - \alpha - \beta_1]]^T \\ & + \frac{1}{2}(\beta_2 + \beta_3 q_R) \frac{\left[(1 - \alpha) - \frac{1}{2}(1 + q_R)[1 - \alpha - \beta_1] \right]^{(T-1)} - \eta^{(T-1)}}{(1 - \alpha) - \frac{1}{2}(1 + q_R)[1 - \alpha - \beta_1] - \eta} \\ & - \frac{1}{2}(\alpha + q_R(\beta_2 + \beta_3 - \alpha)) \frac{[(1 - \alpha) - q_R[1 - \alpha - \beta_1]]^{(T-1)} - \eta^{(T-1)}}{(1 - \alpha) - q_R[1 - \alpha - \beta_1] - \eta} \eta > 0 \end{aligned}$$

for $q_R \in]0, 1[$, then the totally altruistic strategy invades into the non-totally altruistic population, in other words the totally

altruistic strategy is *invader stable*, sensu Apaloo (1997, 2006). An example for this case is given in Fig. 5.

4. Discussion

Any behaviour which decreases the fitness of possessor while increases the fitness of possible competitors is not favoured by natural selection. Thus, altruistic help in defence must have a fitness advantage with respect to the lifetime. The example above demonstrated that although for a single attack the non-altruistic strategy ensures maximum survival rate, on the long run the altruistic one is superior in the following three senses.

1. Non-altruistic strategy cannot invade into altruistic population; in other words altruistic help in defence against predator is an ESS. The intuitive reason is that the less altruistic strategy decreases the survival probability of the group, although the less altruistic partner will survive with a higher average probability than its altruistic mate, but then as a solitary, less altruistic prey will have a higher predation risk. Taken together, the less altruistic individual has a lower survival probability.

2. Altruistic help in defence against predator can evolve in a non-altruistic population. The intuitive reason for that is the “dilution effect”: altruistic strategy increases the survival rate of group mates, thus an altruistic individual has a lower chance of becoming target during the next attack. From a theoretical viewpoint, here “interdependence” (Roberts, 2005) takes place, since a cooperator is benefited as a secondary consequence of altruistic help towards its recipients, no matter whether recipient will reciprocate or not. Namely, existence of the helper partner reduces predation risk of helper in future predator attacks. However, in Roberts’s set up a part of benefit of recipient increases the pay-off of helper. This kind of pay-off re-distribution cannot occur in the game proposed here, which can be considered as a new type of “stakeholder altruism” (Roberts, 2005).

3. The totally altruistic strategy is *invader stable*, since it can invade into all other strategies.

The proposed evolutionary scenario is based strictly on the assumption that the altruistic defence against predators is successful, i.e. under high predation pressure the survival rate of the group strictly increases with the increase of the number of altruistic members of that group. Moreover, the existence of a saved individual decreases the probability that the helper will become a target in the future, which is guaranteed by small group size. The point is that whenever the number of prey is less than the highest possible number of prey killed by predator (i.e. an individual’s predation risk is high), then it is worthwhile to save the life of a group mate, according to the present model. However, whenever the number of prey is much higher than the highest possible number of prey killed by predator (i.e. individual’s predation risk is not so high), the hazardous help has not any effect on the survival rate of helper in the future, according to the “selfish herd” theory. Thus, during “group augmentation” (Brown, 1987) the non-altruistic individual’s survival probability increases and the cooperation disposition in defence must decrease in huge enough groups. Based on that, the group augmentation explanation applies to a small herd.

Although the small groups are formed on the kin relation in general, the results of this paper call our attention to the fact that the altruistic defence against predator can be understood based the on selfish interest of members of a group. For instance, banded mongoose (*Mungos mungo*) lives in groups with size 3–36 and the members of the group are not necessarily relatives (Gilchrist, 2004). Mongoose groups have successful defence against the predator by its harassment (Rood, 1975). Another example, unrelated male Cape ground squirrels (*Xerus inauris*) live in

groups, and only two males drove reptilian predators away by mobbing (Waterman, 1997). Predation seems to be the most important selective factor leading to sociality for mongoose and squirrel (Waterman, 1997; Rood, 1983). A final example is the cooperatively breeding brown treecreeper (*Climacteris picumnus*) which has three to eight individuals in a group to actively defend themselves, to protect adults as well as the nest (Doerr and Doerr, 2006). Obviously, the model proposed here does not apply to the problem of cooperative breeding directly; since the cooperative defence is only one aspect of cooperative breeding (Brown, 1987; Couckburn, 1998). However, predation, as an ecological constraint (Emlen, 1982), plays an important role in cooperative breeding, because in many species helpers engage in anti-predator defence (e.g. mammals: Clutton-Brock et al., 2003; birds: Maklakov, 2002; fishes: Heg et al., 2004).

Some readers may think that the following two simplifying assumptions of this paper are very restricted, namely, that a group contains only two members and that solitary individuals remain solitary. Now, I will argue that the results may be valid to larger though not too huge groups as well. Based on the results of Clutton-Brock et al. (1999a, b) on cooperative meerkats (*Suricata suricatta*), a theoretical example will be given to argue that these assumptions may be weakened.

The model assumes a maximum group size of just two. The reader may think that the death of a single individual in a pair makes big difference regarding the survivorship of the remaining individual. However, in a more realistic situation of groups of more than two (e.g. banded mongoose live in groups of up to 36), the death of one individual would not have as profound an effect on predator dilution. Thus, in a large group the cost of altruism might not outweigh the benefit of one individual's contribution to the dilution effect. To give an example, in a group of two (as in this model) there is a probability of 0.5 that the predator will, at a given time step, attack any individual in the group. So the death of one individual that means the probability of attack on the remaining individual doubled. With 20 individuals there is a probability of 0.05 of attack on each individual. This means that the loss of one individual increases each remaining individual's probability of being attacked by less than 0.003. But let us consider high predation pressure, for instance $T = 100$ (e.g. roughly, every three days there is one predator attack during a year) and groups can go extinct by predation. In this case, although at the first successful predation dilution does not change drastically, after 11 successful attacks the probability of extinction of the group drastically increases. For instance, Clutton-Brock et al. (1999a) found that all groups at size of 9 animals or below became extinct. One of the two most important conditions of my model is that the extinction probability of a group strictly increases when the size of the group decreases. The main point is that group size and predation pressure together determine the results of my model. On the other hand, in a huge group Hamilton's "selfish herd" theory and the dilution effect must work, and risky help does not evolve when the predator can kill only a small part of the huge herd.

The second simplifying assumption of my model is that individuals do not form new groups after their mate is killed. The reader may think that if individuals found new mates then it would no longer make sense for them to risk themselves to maintain the dilution effect as it could be gained cost-free by joining another lone individual. However, if predation pressure is large enough and cooperative defense is synergetic (very successful), then the possibility of new group formation does not change the prediction. Let us consider the following theoretical example, with three kinds of groups: the first with two cooperative individuals, the second with one cooperative and one non-cooperative individuals, and the third with two non-

cooperative individuals, for which the survival probability are $\sqrt[100]{0.9}$, and $\frac{1}{2}$ and $\frac{1}{4}$, respectively, in the case of one predator attack. Let the solitary survival rate be $\frac{1}{10}$ in the case of one predator attack. If the average attack number is 100, then it is expected that only the cooperative group can survive 100 attacks, no matter of there is new group formation or not. The second of the two most important conditions of my model is that predation pressure must be high enough (i.e. a predator can kill all prey, in other words, if prey density is less than the predation "capacity" of predators) and cooperation is successful (i.e. each cooperative group has a high enough survival rate).

Observe that in the above two theoretical examples altruism is a prerequisite to survive, thus it may be evolutionary stable, but in this case the development of altruism is not possible. However, a possible scenario is the following: first a selfish herd appears (in this case the dilution, peripheral and confusion effects with high level of vigilance keep the individual survival probability at high level). Then, the carrying capacity of the field decreases (lower group size) while predation pressure does not change or increases to a level where the predator can kill the overwhelming majority of the non-cooperative groups. In this situation, altruistic help may evolve if the appearance of only one altruistic individual in a group increases the survival probability of the group in question. For instance, Clutton-Brock et al. (1999a, b) found that during over 2000 h of observation, no raised guards were attacked or killed by predators, probably because sentinels were usually the first to detect predators and they took up position very near to burrow thus they were usually among the first animals below ground. However, alarm call clearly increases of survival probability of other individuals in the group (while cooperative behavior does not decrease the survival probability of helper).

In summary, altruism can evolve under circumstances when the partner is a "source" rather than a competitor, which is guaranteed by the following three assumptions: the predator pressure is high; the individual's predation risk is a steeply decreasing function of group size and finally cooperative defence is successful. In the proposed model, the group member is considered as a "shelter against predator". From this point of view, altruism is a cost of keeping its mate, its "shelter" alive.

I introduced a new family of survival games in which there is a two-person game for any number of predator attack (T). When predation risk is low ($T = 1$), then the non-altruistic strategy is strict ESS, but if predation risk is high ($T = 8$, Figs. 3–5) there exists a case where altruistic help is strict invader ESS. The mathematical reason for this different behaviour is that the survival game is not additive. We should pay attention to the fact that in cooperative phenomena where fitness is not additively obtained from the pay-offs coming from turns of game theoretical conflicts; cooperation may evolve (cf. Eshel and Shaked, 2001).

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