



Under multilevel selection: “When shall you be neither spiteful nor envious?”



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HIGHLIGHTS

- We study the egalitarianism-game in multilevel selection situation.
- Egalitarianism-game determines the number of juveniles and their survival depends on the size of their group.
- We apply the standard definition of ESS to a structured population.
- When the survival has a massive effect on the fitness, then donator has evolutionary advantage over envious and spiteful.

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ABSTRACT

In this paper, we study the egalitarianism-game in multilevel selection situation. The individuals form reproductive groups. In each group, an egalitarianism-game determines the number of juveniles of different phenotypes (spiteful, envious, neutral and donator). Before the juveniles form the next reproductive group, they have to survive either predators' attacks or a fight between two groups. We adopt the ESS definition of Maynard Smith to multilevel selection. Based on the “group size advantage” assumption (which claims that each juvenile's survival rate depends on the size of his own group, supposing that either the survival rate under predators' attacks is higher in larger groups, or in inter-group aggression usually the larger group wins) we found that when the survival probability has a massive effect on the average fitness, then “group fitness maximizing behavior” (in our case, either neutral or donator) has evolutionary advantage over “competitive behavior” (in our case, either spiteful or envious).

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1. Introduction

The origin of cooperation has always attracted a great interest (e.g., the seminal paper by Axelrod and Hamilton (1981) has received more than 22,000 citations), while the evolution of spite is a little bit neglected (e.g., the seminal paper by Hamilton (1970) has less than 600 citations), despite that, from a theoretical viewpoint, spite and altruism are two sides of the same coin (cf. Hamilton, 1971b; Lehmann et al., 2006; Vickery et al., 2003). A spiteful strategist costly destroys resource and/or kills the offspring of others (damages anyone), while an envious¹ one is conditionally spiteful, only damaging the more successful rivals. In

the framework of the egalitarian-game (Garay and Móri, 2011) we have shown that if there is no kin preference and the degree of damage is larger than the cost of damage then the spiteful strategy wins in Darwinian “struggle for existence”.

However, it is widely accepted that spite is rare in nature (Jensen, 2010). From the point of human perspective, envy is prohibited in monotheistic religions (as expressed, for example, in the Ten Commandments). Thus, our basic question arises: *is there any selection situation in which spite and envy are outperformed by Darwinian natural selection?* In other words: is there any Darwinian base of forbidding envy and spite?

In this paper, we propose multilevel selection (Okasha, 2006) evolutionary games. In the multilevel selection scenario, a phenotype's success is determined by two factors: the first one takes place within the group; the second one takes place between groups.² In our case,

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¹ Szolnoki et al. (2011), in the framework of the snowdrift, the stag-hung and the prisoner's dilemma games, defined envy and goodwill by the probability of cooperation with a more or less successful neighbor. From a game theoretical viewpoint, their notion of envy is a little different from ours, since the egalitarian game does not consider cooperation. It is shown that punishing according to payoff

(footnote continued)

difference (egalitarian punisher) is an effective strategy in a model of cooperation with not totally well informed individuals (Scheuring, 2010).

territorial individuals reproduce in separate groups where an egalitarianism-game determines the offspring number of parents within the group. Before the juveniles form the new reproductive group, they have to survive. Our simplifying assumption is that these two levels are mathematically independent.

We will concentrate on egalitarianism-game within groups. In the egalitarianism-game, the individuals aim at increasing their own proportion in the next generation rather than their absolute contribution to it. In games that correspond to cooperative behavior, the individuals aim at increasing their own income from a resource (Archetti & Scheuring, 2011).

We consider the following two possible selection forces³ between groups, which are the widely accepted reasons why individuals form groups.⁴ The first one goes back to Hamilton's selfish herd theory (Hamilton, 1971a): individuals form a group to decrease the individual's predation risk. Decrease of predation risk occurs for several reasons such as the "dilution" effect (Dehn, 1990); the "many eyes" hypothesis (Treves, 2000); by confusing predators (Smith and Warburton, 1992); and by mounting a cooperative defense to fight off the predator (Garay and Varga, 2011). For simplicity, we have not built the survival game at the group level, i.e., all members of the group have the same anti-predator behavior, although altruistic defense against predators may evolve if the common defense is successful enough (Garay, 2009). The second selection force is territory deference. Several animal species, e.g. chimpanzee (see Mitani et al., 2010), African lion (see Heinsohn and Packer, 1995), collectively defend their territory, and during "fight", group members are sometimes killed by members of the opponent group. Moreover, the impact of inter-group competition among humans is definitely lethal (Bowles, 2006; Dutton et al., 2005). Theoretical studies pointed out that whenever there is "war" between separate groups, multi-level selection can guarantee the evolutionary stability of altruism if the survival probability of a group depends on the level of altruism within the group (Boza and Számadó, 2010; Bowles, 2006, 2009; Choi and Bowles, 2007; Pacheco et al., 2006; Scheuring, 2009, 2010; Traulsen and Nowak, 2006). For simplicity, we do not take into account the possible fighting behaviors during territorial defense (cf. Lehmann and Feldman, 2008; Hugh-Jones and Zultan, 2010).

In the present paper, we will concentrate on both selection forces on groups. Our results are based on the "group size advantage" assumption (cf. "augmentation advantage" Kokko et al., 2001; Clutton-Brock, 2002), which claims that the larger group "wins" (bigger group, bigger survival rate): either the survival rate under predators' attacks is higher in larger groups; or as in inter-group aggression it is usually supposed: each juvenile's survival rate depends on the difference between the sizes of fighting groups.

Our study is built on the concept of evolutionary stability (Maynard Smith and Price, 1973), but the whole population is not well-mixed, since individuals form separate (live and breed) groups. According to our knowledge, we are the first to apply Maynard Smith's ESS concept to the multilevel selection situation. Using evolutionary stability we

² The group structure has an important effect on the evolution of altruism, as Wilson and Wilson (2007) write: "Selfishness beats altruism within group. Altruistic groups beat selfish groups." However, the original theory of group selection considers the case when there is no direct interaction between groups (Wilson, 1975), but involves competition for representation in the next generation.

³ We do not consider the case when the reason of gregarious behavior is to find a partner to cooperate (e.g. Powers et al., 2011). For instance, we do not study the cooperating breeding, when the (unrelated, subdominant) individuals provide alloparental care and often suppress their own reproduction (Kokko et al., 2001). In our case, the parents feed only their own offspring and parents interact during breeding, e.g. the colonial nestling.

⁴ We mention that the importance of these two factors is already emphasized in the models of cooperation (e.g. Kun et al., 2006, where other advantage of group living is mentioned).

can characterize in what way the "group size advantage" can modify the final state of evolution of the egalitarian game within a group in a multilevel evolutionary scenario.

In Section 2, we define the considered selection situation. In Section 3, we simplify our original egalitarianism-game within a group. In Sections 4 and 5, we consider the case when juveniles have to survive predation and a fight between groups. Finally, we give a summary and some conclusions drawn from our results.

2. Relative advantage and selection situation

We consider an asexual population with non-overlapping generations and pairwise interactions.

2.1. Relative advantage

Our aim is to study evolutionary stability for multilevel selection situation, based on the concept of evolutionary stability, due to Maynard Smith and Price (1973). Namely, the resident phenotype is a ESS (in our case *ML-ESS*), if all possible rare mutant phenotypes have a lower average fitness than the resident one; formally, $\overline{W}_R > \overline{W}_M$. In other words, Darwinian relative advantage of the resident over the mutant is strictly positive, when the mutants are rare enough.

$$R_{RM} := \overline{W}_R - \overline{W}_M > 0. \quad (1)$$

This definition is strictly based on Darwinian tenet: the phenotype having larger average fitness will spread.

2.2. Selection situation

In our terminology "selection situation" determines the calculation of the average fitness of phenotypes. Present selection situation is given by the following 5 points.

1. *Reproductive stage within group.* Individuals form reproducing groups of n members each.⁵ During reproduction, there are interactions within groups only, and this kind of interaction can be described by an evolutionary game. Let R stand for resident, and M for mutant. Suppose the mixed group contains $n_R > 0$ resident and $n_M = n - n_R$ mutant individuals. In the purely resident group the resident average individual fecundity is denoted by $w_R(n, 0)$. In the mixed group (containing residents and mutant(s) as well) the averages of resident and mutant individual fecundity values are $w_R(n_R, n_M)$ and $w_M(n_R, n_M)$, respectively (see Appendix A).
2. *Survival stage.* We assume that the survival process is independent from the game in the reproductive stage, and each juvenile of a given group has the same survival probability. Before juveniles form the new reproductive group, they have to survive
 - a. either the predators' attack, where the survival probability depends only on the size of the group attacked; formally, $P : n_i \mapsto [0, 1]$, where n_i denotes the size of the i -th attacked group;
 - b. or the fight between two groups, where the survival probability depends on the size of the two fighting groups; formally, let $\Pi : (n_1, n_2) \mapsto [0, 1]$ be the survival probability of a group of size n_1 when fighting against a group of size n_2 .

The main mathematical difference between the predator- and the fight-determined survival is that fight defines a mathematical game between two groups: the strategy of the group is the

⁵ Of course, the size of the reproductive group is determined by the carrying capacity (ecological condition) of the territory. For simplicity, we assume that all reproductive groups contain exactly the same number of parents.

total fecundity of the group, and the survival function Π can be considered as a pay-off function.

We emphasize that in our model the loser group does not disappear, as usually assumed in models of cooperation (e.g. Pacheco et al., 2006; Traulsen and Nowak, 2006). Our model is closer to Scheuring's (2009, 2010) ones, in which the loser group's members merge into the winner group and can keep their phenotype. We think that in human population the winner group abducts the females of the loser group, since for each human male the number of his female partners determines his fitness, thus the genetic material of the loser group does not disappear.

3. *New group formation process.* It is well known that the “assortment” of cooperative mutants helps the coexistence of cooperators (Szathmáry, 2011). Since we are only interested in evolutionary stability, i.e., when the rare mutant will die out, the group formation process does not have any effect.

4. *Mutation process.* Mutation is rare enough. At the first glance, the mutant-mutant interaction within a group is questionable. To shed light on this question, let us consider G groups of size n , and assume that the mutation rate is μ . Thus, the mutants' number in a given group follows the binomial distribution $Binom(n, \mu)$, namely, the probability that in a given group there are exactly m mutants is given by $q_m = \binom{n}{m} \mu^m (1-\mu)^{n-m}$. When μ is very small compared to n , namely, $\mu < (1/(n+1))$, then $q_0 > q_1 > \dots > q_n$. In biological terms, it is most likely that the group does not contain mutants at all, and in general, the more mutants are supposed to exist in the group, the less is the probability of the corresponding event. However, when the number G of groups is high enough, we do not neglect the cases when the number of mutants in a given group is larger than one. On the contrary, if G and n are not so large, then we can neglect the case when the number of mutants is larger than two.

5. *Selection neighborhood.* During the calculation of the average fitness of phenotypes, we have to define the number of groups which determines the average fitness. The complication is that the arbitrarily large territorial population should live on a two dimensional surface. If mutation is rare, we can assume that groups containing mutants are separated, i.e., mixed groups are far from each other. Let us divide the whole population into disjoint sub-populations, such that each sub-population contains only one group with mutants, if there are any mixed groups at all. Let K denote the average number of resident groups in the neighborhood of a mixed group. Clearly, K depends also on the mutation rate. Since $G(1-\mu)^n$ and $G(1-(1-\mu)^n)$ are the average number of groups without and with mutants, respectively, we have $K \approx K_\mu = (1-\mu)^n / (1-(1-\mu)^n)$. Now another ecological complication arises: if the whole population is bounded, e.g., they live on an island, then G and n are relatively small, and if μ is close to zero, it may happen that $K_\mu \gg G$.⁶ However, this problem can be got over by taking conditional expectation with the condition that not all groups are resident. Let ξ denote the number of mixed groups; it follows binomial distribution of order G and parameter $1-(1-\mu)^n$. Then we get the following, better approximation for K .

$$K \approx \frac{E(G-\xi|\xi > 0)}{E(\xi|\xi > 0)} = \frac{G}{E(\xi|\xi > 0)} - 1 = \frac{GP(\xi > 0)}{E\xi} - 1 = \frac{G(1-(1-\mu)^{nG})}{G(1-(1-\mu)^n)} - 1 = (1-\mu)^n + (1-\mu)^{2n} + \dots + (1-\mu)^{(G-1)n}.$$

here the right-hand side is less than $G-1$.

⁶ In the spatial simulation models the neighborhood of the focal individual (or group contains) 1–16 individuals (or groups) (e.g. Boza and Számadó, 2010; Szabó and Tóke, 1998; Számadó et al., 2008).

Since we have no information on K , we will concentrate mainly on the two extreme cases. Firstly, we suppose that K is arbitrarily large, the mixed group contains an arbitrary number of mutants, and we consider general games within the group. Though, when considering a territorial population living on a two-dimensional surface, then K should not be too large: a group cannot interact with too many neighboring groups. However, if we want to compare the mathematical details of original ESS with that of multilevel ESS, we have to allow arbitrarily large population and group sizes, since Maynard Smith considered arbitrarily large populations. Secondly, we assume that $K=1$, under “rare mutation” we mean that there are only few (one or two) mutants in mixed groups (cf. Wilson, 2003, p. 34–35), and we will consider the egalitarian game.

3. Egalitarianism-game within groups

The egalitarianism-game (Garay and Móri, 2011) has three stages in fixed order: at the first stage, the “basic incomes” of individuals are drawn randomly from the same distribution,⁷ which means that the territory capacity is high enough for individuals to have no direct food competition. For simplicity, we assume that there are only two possible basic income values $a_1 < a_2$, with equal probability. At the second, “giving stage”, donators (by giving some valuable resource or service) increase the fecundity of less successful individuals. At the third, “taking stage”, envious individuals apply an envy rule, decrease the fecundity of more successful individuals by acting harmfully on them, and spiteful individuals unconditionally damage others in the group.⁸

We consider the following four behavior types: spiteful, envious, neutral and donator. We define “spiteful” as a behavior which unconditionally and anonymously⁹ causes costly damage to other individuals without benefit to itself. “Envious” strategy reduces the fecundity of the partner at cost to the envious individual if and only if the fecundity of the first is higher than that of the second¹⁰; the probability of envious damage increases with fecundity difference. The probability of damage is $p(X, Y)$, where X and Y denote the fecundity of the attacker and that of the victim, respectively. Envy increases with the difference between individuals (Dawes et al., 2007). We use our envy rule introduced earlier, which is the following increasing function:

$$p(X, Y) = \begin{cases} 0 & \text{if } X \geq Y \\ q(Y-X)^\alpha & \text{if } X < Y \end{cases} \quad (2)$$

where X, Y are drawn randomly from two different values $a_1 < a_2$. Here q denotes the probability of secret damage. By increasing α , one can make the damaging mechanism more and more sensitive to larger differences. However, envy is an expensive passion: a successful attack costs $c(X, Y)$, which can be constant: $c(X, Y) = c$, for simplicity. We assume that an envious individual tries to attack all richer ones but only once each at a taking stage. The degree of damage is $d(X, Y)$, and for simplicity we assume that the damage is a

⁷ It is well-known that kin competition can strongly antagonize the benefit of kin cooperation and inhibit the evolution in viscous population (e.g. West et al., 2002). In our model the individuals do not compete for food, since the basic incomes come from lottery (Garay and Móri, 2011), which does not depend on the size of the group.

⁸ We do not consider the pathogen-mediated version of Hamiltonian spite (Rózsa, 2000).

⁹ Anonymity is a usual experimental condition (Dawes et al., 2007), which rules out the revenge punishment.

¹⁰ Envy (Smith and Kim, 2007) arises when we compare our own property with others' property. The envious person tries to keep the damage in secret (Schoeck, 1966).

fixed proportion of the victim's fecundity $d(X, Y) = : d$. Here c, d, q, α are nonnegative parameters. We consider the case when the damage is additive: the effects of simultaneous attacks are based on the original fecundity of the victim. The "neutral" individuals have no other-regarding-preference, since they never alter others' fecundity. Charity is a costly giving which increases the below-average individuals' income (e.g. food) and it is an altruistic behavior, i.e., an individual increases the fecundity of others by decreasing its own fecundity.¹¹ Now, we assume that the cost b of the successful "donation" is less than the received benefit B of the unsuccessful acceptor: e.g., if unsuccessful individuals starve, then the quantity of donated food can increase the fecundity of the unsuccessful acceptor more than it decreases the donator's.

According to our sequential game, an individual can donate at the giving stage, and after that the same individual can also be envious or spiteful in the taking stage. For simplicity, in the present paper we will only consider pure strategists introduced above, i.e., spiteful and envious ones only make damage and never give "food"; and the donators only give "food" and never cause damage. These strategies can open the simplest possibility to study the problem: when will the spiteful, the envious, the neutral or the donator phenotype be the evolutionary final state within groups. In Appendix A we give the fecundities for all group compositions used.

Since the phenotypes' average fitness must be calculated differently for predation and fight, we will deal with these cases separately.

4. Multilevel ESS for predation on group

In this section, we consider the case when the juveniles have to survive a predator attack before reproduction. We assume that increase in the number of juveniles in a group increases the survival probability of each group member. Now let us consider the average fitness of the different phenotypes when predation determines survival.

$$\overline{W}_R := \frac{KnP(w_{RT})w_R(n, 0) + n_R P(w_{MT})w_M(n_R, n_M)}{Kn + n_R}, \quad (3)$$

$$\overline{W}_M := \frac{P_M(w_{MT})n_M w_M(n_R, n_M)}{n_M} = P_M(w_{MT})w_M(n_R, n_M). \quad (4)$$

here $w_{RT} := n w_R(n, 0)$ and $w_{MT} := n_R w_R(n_R, n_M) + n_M w_M(n_R, n_M)$ denote the total fecundity in the resident and the mixed group, respectively. Observe that here fitness is the average number of descendants of the different phenotypes in the next, non-overlapping generation. Indeed, the denominator of (3) is the number of resident parents in $K + 1$ groups, and the numerator of (3) is the total number of surviving descendants of the resident phenotype from the resident and mixed groups.

Resident phenotype is *ML-ESS for predation on group* when the relative advantage of the resident over all mutants is positive, i.e., inequality (1) is valid for all possible mutants. Formally,

$$Kn[P(w_{RT})w_R(n, 0) - P(w_{MT})w_M(n_R, n_M)] + n_R P(w_{MT})[w_R(n_R, n_M) - w_M(n_R, n_M)] > 0 \quad (5)$$

¹¹ Altruistic food-sharing is well-known phenomenon within primates (Burkart et al., 2007; Kasper et al., 2008) well explained by many (Fruth and Hohmann, 2002). Charity does not expect a direct or indirect (Nowak and Sigmund, 2005) material income in the future (Garay, 2009); it is not considered as a consequence of kinship since recipients are not necessarily related to the donator; it is not a by-product of altruism, since it is not an "incidental" consequence of the selfishness of the donator (Fruth and Hohmann, 2002) and donator does not breed cooperatively with recipient (Burkart et al., 2007).

4.1. General game with arbitrarily large K

First, we assume that the mutant is arbitrarily rare and K is large enough (in mathematical terms: we can assume that $K \rightarrow +\infty$), thus inequality (5) is equivalent to the following two conditions:

- (i) *Equilibrium condition of ML-ESS for predation.* For all possible mutants

$$P(w_{RT})w_R(n, 0) - P(w_{MT})w_M(n_R, n_M) \geq 0. \quad (6)$$

- (ii) *Stability conditions of ML-ESS for predation.* If for a given mutant there is equality in equilibrium condition (i), then for this mutant we have

$$w_R(n_R, n_M) - w_M(n_R, n_M) > 0. \quad (7)$$

Observe that equilibrium condition (i) requires that the resident group ensures higher fitness for its resident member than the mixed group for its mutant member. Furthermore, since the survival probability function is strictly increasing with the group size, thus mutant cannot increase its own and its group's total fecundity at the same time. Stability condition (ii) requires that the fecundity of a resident is higher than that of a mutant within the group. Surprisingly, if the group size is large enough, then stability condition (ii) coincides with the starting point of mathematical formulation of the classical ESS.

In Appendix B we will show that, if the mutation rate is arbitrarily small and K is arbitrarily large, then for all possible game within group there exists a survival rate P , which is strictly increasing and guarantees that the group size maximizing strategy is ML-ESS. There are two main points here. Firstly, phenotype maximizing the group's total fecundity is not automatically ML-ESS, since ML-ESS is determined by the relative ratio of the survival probabilities and fecundities. Secondly, there is a possible survival function, when the ESS, phenotype maximizing the "welfare of the group", is ML-ESS. From our perspective it means that if donator strategy maximizes the total fecundity of the group, and the survival has a larger effect on fitness than the phenotype fecundity does, then donator outperforms spiteful, envious and neutral strategies alike.

4.2. Egalitarian game with finite K

Now the question arises: what happens when mutation rate is not arbitrarily small, and the total population size is not arbitrarily large; in mathematical terms, when the mutation rate does not converge to zero. Since Darwinian tenet (a phenotype spreads when it has higher fitness than the other one) does not depend on the mutation rate, so inequality (5) can be used directly.

However, the predation process is quite complicated. We need a simple theoretical survival probability function depending on a parameter that measures the predation pressure. We will consider the following survival probability function.

$$P(w_T) := \frac{1}{1 + \exp(-(w_T - \beta))},$$

where w_T is the total fecundity of the focal group and the positive parameter β corresponds to the group size where 50% of the members survive. Observe that the survival probability is a decreasing function of β when the size is fixed. In other words, when β is increased, the same survival probability is guaranteed by a larger group. In conclusion, parameter β characterizes the intensity of predation press. So as to illustrate that not only the predation press determines the final state of evolution we give two Example 1 the first one, the benefit of donation is not so large.

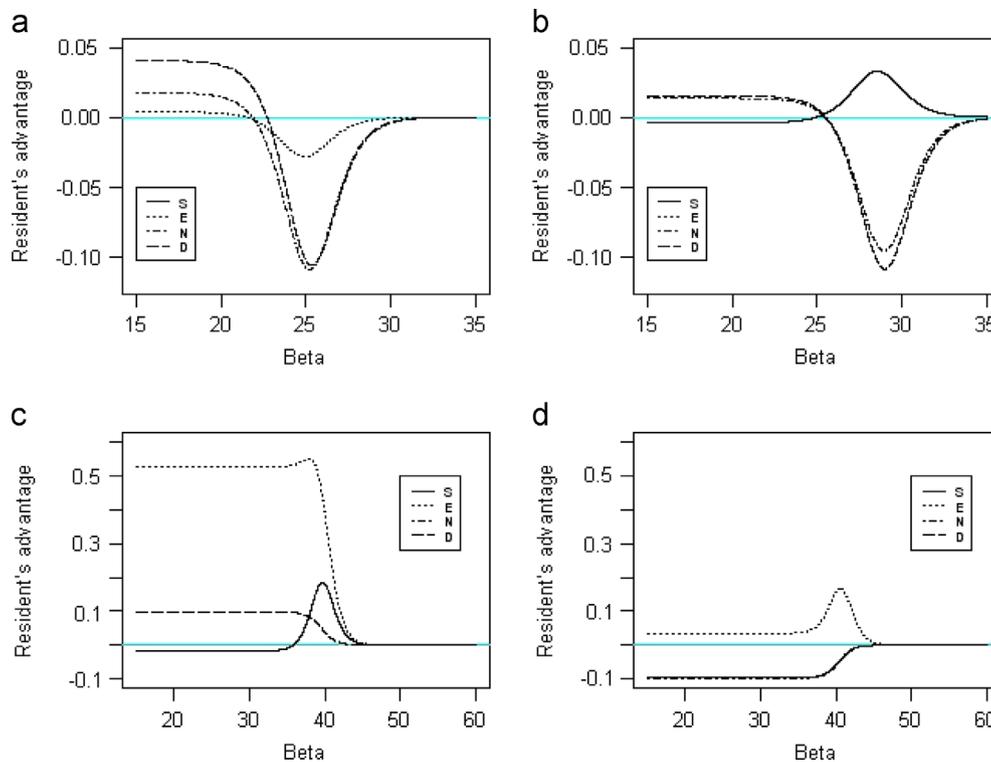


Fig. 1. (a) shows the relative advantage of resident spiteful strategy over the other rare mutants (envious, neutral, donor). We found that spiteful strategy is a strict local ML-ESS, when the predation intensity $\beta \in (0, 21.46)$. (b) shows the relative advantage of resident envious strategy over the other rare mutants (spiteful, neutral, donor). Observe that envious strategy is a strict local ML-ESS, when the predation intensity $\beta \in (24.94, 25.48)$. (c) shows the relative advantage of resident neutral strategy over the other rare mutants (spiteful, envious, donor), and that neutral strategy is a strict local ML-ESS, when the predation intensity $\beta > 35.82$. (d) shows the relative advantage of resident donor strategy over the other rare mutants (spiteful, envious, and neutral). Also shows that with the chosen parameters, donor strategy is never strict local ML-ESS. (a) Resident strategy: spiteful, (b) resident strategy: Envious, (c) resident strategy: Neutral and (d) resident strategy: Donator.

Example 1. In Fig. 1, the relative advantages (5) are given as functions of β . The parameters of egalitarian-game are $n = 20$, $n_2 = 3$, $a_1 = 1$, $a_2 = 3$, $q = 0.1$, $c = 0.003$, $d = 0.15$, $\alpha = 1$, $b = 0.01$ and $B = 0.06$.

In summary, when predation determines the survival of juveniles, we found that for $\beta \in (0, 21.46)$ spitefulness is strict pure ML-ESS. For $\beta \in (24.94, 25.48)$ envy is strict pure ML-ESS. The neutral is pure ML-ESS, when $\beta > 35.82$. Here, donor strategy is never strict pure ML-ESS, since the benefit of donation is relatively small. Furthermore, observe that there is a bistable case: when $\beta \in (21.46, 24.94)$, both spitefulness and envy are strict pure ML-ESS. Moreover, when $\beta \in (25.48, 35.82)$, there is no strict pure ML-ESS.

Example 2. In the second example, if the benefit of donation is large enough and the predation press is high enough, then donor strategy is strict pure ML-ESS. In Fig. 2, the relative advantages (5) are given as functions of β . All other parameters being the same as for Fig. 1.

We found that when the predation intensity $\beta \in (0, 23.68)$ then the spiteful; when $\beta \in (26.35, 27.88)$ then the envious; when $\beta \in (35.52, 38.92)$ then the neutral; and finally when $\beta > 43.22$, then the donor strategy is a strict local ML-ESS.

4.3. Results on predation

We tried to change the value of some parameters one by one, to check how robust our findings were. While keeping all other parameters fixed (as in the Figures) and increasing a_2 , the spiteful strategy ceases to be best for any predation intensity. That is, the envious is the best strategy for low values of the predation intensity β . The neutral and donor strategies remain the best for larger and larger β values. Similarly, if we start increasing c (keeping all other

parameters fixed), first the spiteful, then the envious strategy ceases to be the best for any predation intensity. If c is large enough, then the neutral strategy is the best for small values of β , and the donor strategy is the best for large values of β . Finally, we experimented with increasing the value of B . We found that, qualitatively, the only change is that the envious strategy ceases to be the best for any predation intensity. To sum up, under predation the neutral and donor strategies seem quite robust with respect to parameter variation, while the spiteful and the envious strategies need a very careful balance of parameter values to be optimal.

The “basic trend of evolution” is the same: when the survival rate has no massive effect on the average fitness of the phenotypes, then the spite is ML-ESS; when this effect increases, then envious, neutral and donor will be ML-ESS. However, the relation between survival rate and fecundity determines what will happen (see Figs. 1 and 2). Our results are robust in the sense that we get the same “basic trend” if we change slightly the parameters of the egalitarian games.

5. Multilevel ESS for fight between groups

Since we assume that only two groups fight, we have three different survival probabilities according to the fighting groups: $\Pi(w_{RT}, w_{RT})$, $\Pi(w_{RT}, w_{MT})$ and $\Pi(w_{MT}, w_{RT})$ denote the survival probability for a resident group against another resident group, against a mixed group, and that of a mixed group against a resident group, respectively. Thus, the average fitness of the resident is

$$\bar{w}_R = \frac{(K-1)n\Pi(w_{RT}, w_{RT})w_R(n, 0) + n\Pi(w_{RT}, w_{MT})w_R(n, 0) + n\Pi(w_{MT}, w_{RT})w_R(n_R, n_M)}{Kn + n_R} \tag{8}$$

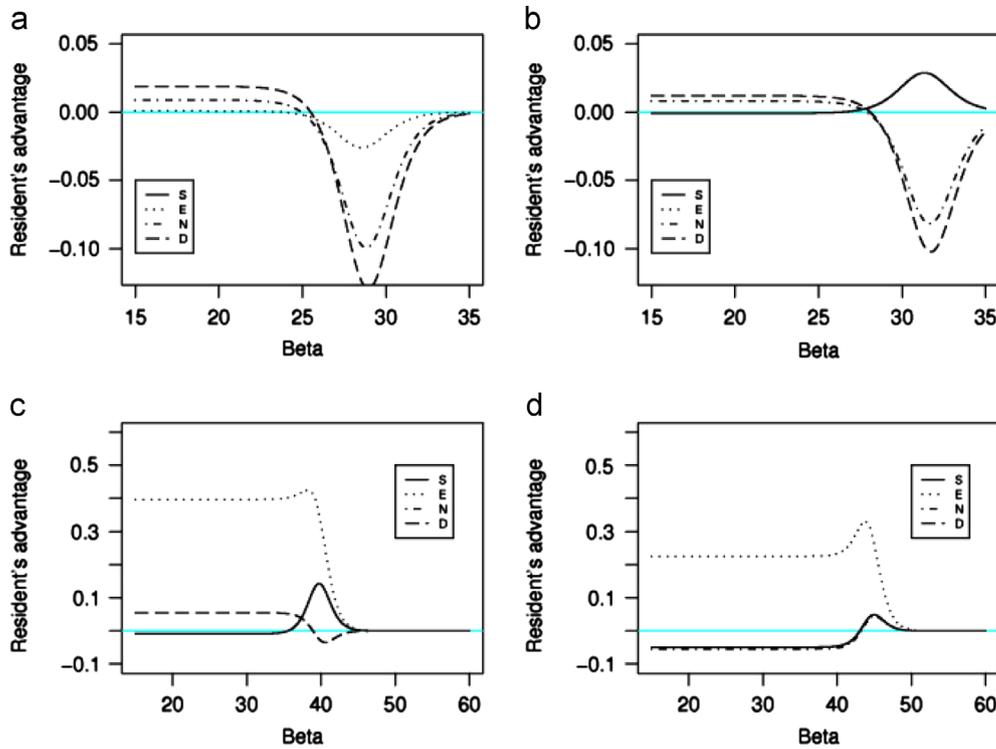


Fig. 2. (a) shows the relative advantage of resident spiteful strategy over the other rare mutants (envious, neutral, donator). We found that spiteful strategy is a strict local ML-ESS, when the predation intensity $\beta \in (0, 23.68)$. (b) shows the relative advantage of resident envious strategy over the other rare mutants (spiteful, neutral, donator). Observe that envious strategy is a strict local ML-ESS, when the predation intensity $\beta \in (26.35, 27.88)$. (c) shows the relative advantage of resident neutral strategy over the other rare mutants (spiteful, envious, donator), and that neutral strategy is a strict local ML-ESS, when the predation intensity $\beta \in (35.52, 38.92)$. (d) shows the relative advantage of resident donator strategy over the other rare mutants (spiteful, envious, and neutral). Also shows that donator strategy is a strict local ML-ESS, when the predation intensity $\beta > 43.22$. (a) Resident strategy: Spiteful, (b) Resident strategy: Fnvious, (c) Resident strategy: Neutral and (d) Resident strategy: Donator.

since the numerator of (8) is the total number of surviving descendants of the resident phenotype from the resident groups fighting with other resident groups; from the resident group fighting with the mixed group and from the mixed group fighting with a resident group, respectively. The average fitness of mutant phenotype is the following,

$$\overline{W}_M : = \Pi(w_{MT}, w_{RT})w_M(n_R, n_M) \quad (9)$$

Resident phenotype is ML-ESS for fight between groups, when the relative advantage of the resident over all mutants is positive; i.e., inequality (1) is valid for all possible mutants. Formally,

$$(K-1)n\Pi(w_{RT}, w_{RT})w_R(n, 0) + n\Pi(w_{RT}, w_{MT})w_R(n, 0) + n_R\Pi(w_{MT}, w_{RT})w_R(n_R, n_M) - (Kn + n_R)\Pi(w_{MT}, w_{RT})w_M(n_R, n_M) > 0 \quad (10)$$

5.1. General game with arbitrarily large K

Here we assume again that $K \rightarrow +\infty$. Then inequality (10) is equivalent to the following two conditions:

(iii) *Equilibrium condition of ML-ESS for fight.* For all possible mutants

$$\Pi(w_{RT}, w_{RT})w_R(n, 0) - \Pi(w_{MT}, w_{RT})w_M(n_R, n_M) \geq 0, \quad (11)$$

(iv) *Stability conditions of ML-ESS for fight.* If there is equality in (9) for a given mutant, then for that mutant we have

$$\frac{n\Pi(w_{RT}, w_{MT})w_R(n, 0) + n_R\Pi(w_{MT}, w_{RT})w_R(n_R, n_M)}{n + n_R} - \Pi(w_{MT}, w_{RT})w_M(n_R, n_M) > 0 \quad (12)$$

Observe that the “basic logic” of equilibrium condition of classical matrix game ESS remains valid, since both equilibrium conditions (i) and (iii) compare the fitness of a resident when interacting another resident with the fitness of a mutant interacting a resident. However, the basic logic of the stability conditions (ii) and (iv) changes, although both stability conditions compare the average fitness of a resident with that of a mutant, but now these pay-offs do not come from resident–mutant and mutant–mutant interaction, as the stability condition of classical ESS.

In Appendix C we will show that if the mutation rate is arbitrarily small and K arbitrarily large, then for all possible games within group there is a strictly increasing survival rate function Π , which can guarantee that the group size maximizing strategy is ML-ESS. This statement claims that if the donator strategy maximizes the total fecundity of the group, and survival has a larger effect on fitness than phenotype fecundity does, then the donator outperforms spite, envy, and neutral strategy.

5.2. Egalitarian game with finite K

Now assume that the total population size is not arbitrarily large, so we have to use inequality (10) directly. We need a simple theoretical survival probability function in which there is a parameter determining the survival probability of two fighting groups. In this section, we will use the following expression for the survival probability of juveniles. Consider a group of size w_{G_1T} fighting with a group of size w_{G_2T} . All members of this group have the same survival probability

$$\Pi(w_{G_1T}, w_{G_2T}) : = \frac{(w_{G_1T})^\kappa}{(w_{G_1T})^\kappa + (w_{G_2T})^\kappa},$$

Observe that the positive parameter κ determines the level of group largeness advantage; we will call this advantage *the fight*

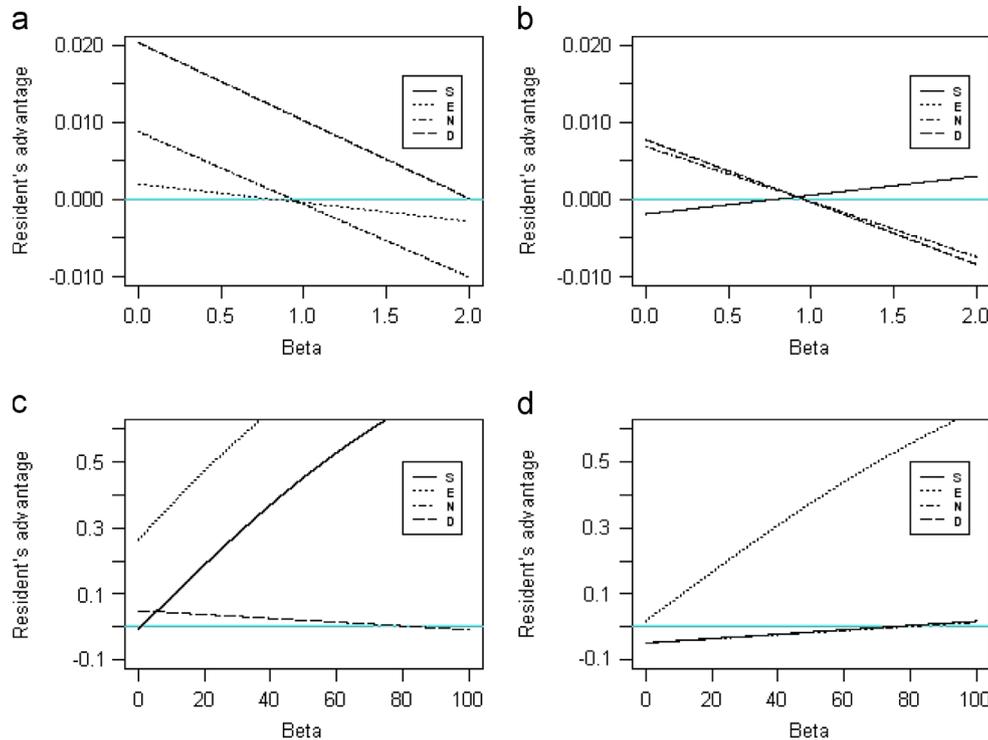


Fig. 3. (a) shows the relative advantage of resident spiteful strategy over the other rare mutants (envious, neutral, donator). We found that spiteful strategy is a strict local ML-ESS, when the fight intensity $\beta \in (0, 0.806)$. (b) shows the relative advantage of resident envious strategy over the other rare mutants (spiteful, neutral, donator). Observe that envious strategy is a strict local ML-ESS, when the fight intensity $\beta \in (0.797, 0.950)$. (c) shows the relative advantage of resident neutral strategy over the other rare mutants (spiteful, envious, donator), and that neutral strategy is a strict local ML-ESS, when the fight intensity $\beta \in (0.885, 85.215)$. (d) shows the relative advantage of resident donator strategy over the other rare mutants (spiteful, envious, and neutral). Also shows that donator strategy is a strict local ML-ESS, when the fight intensity $\beta \geq 77.373$. (a) Resident strategy: Spiteful, (b) Resident strategy: Envious, (c) Resident strategy: Neutral and (d) Resident strategy: Donator.

intensity.¹² As κ increases, the survival probability in the larger group is increasing, while the survival probability in the smaller group is decreasing, thus the difference between these two survival rates is also increasing.

Let us consider the payoff functions (8)–(9) in the case when the players' juvenile offspring sizes are given by the above egalitarianism-game within groups. Now we are looking for strict pure ML-ESS, thus at a fixed fight intensity κ we consider the cases where the whole population follows the same strategy (either spiteful, envious, neutral or donator), and we aim at finding out which one will be strict ML-ESS. In other words, in a monomorphic population of one of the pure strategies the other pure phenotype cannot invade, when mutation is rare enough.

Example 3. We wish to see when the pure strategies (spiteful, envious, neutral and donator) can establish ML-ESS populations. We consider small groups ($n=20$), thus in Fig. 3 it is assumed that there is only one mutant. The parameters of the egalitarian-game are set as follows: $a_1 = 1$, $a_2 = 3$, $q = 0.1$, $c = 0.001$, $d = 0.2$, $\alpha = 1$, $b = 0.02$ and $B = 0.03$. In Fig. 3, the relative advantages (3) are given as functions of b .¹³

In summary, we found that, when fight intensity increases, first the spiteful, then the envious, after that the neutral, and finally the donator strategy becomes pure ML-ESS. Moreover, in some cases

there are more than one strict local ML-ESS: when $b \in (0.797, 0.806)$ then both spiteful and envious; when $b \in (0.885, 0.950)$, then both envious and neutral; when $b \in (77.373, 85.215)$, then both neutral and donator strategies are pure ML-ESS.

We remark that, if there are two mutants in one of the groups, then the spiteful strategy is not strict ML-ESS. The reason for that is the following: the basic advantage of spiteful strategy is that nobody injures itself, thus each spiteful individual may suffer one less spiteful attacks than each mutant does. This advantage of spitefulness disappears easily during fight in our model.

5.3. Results on fight

We tried to change the value of some parameters one by one, to check how robust our findings were. While keeping all other parameters fixed (as in the figures) and increasing a_2 , first the spiteful, then the envious strategy cease to be the best for any fight intensity κ . The same phenomenon is observed if we increase c instead. That is, if a_2 (or c) is large enough, then the neutral strategy is the best for small values of κ , and the donator strategy is the best for large values of κ . Finally, increasing the value of B , we found – as in the case of predation – that qualitatively the only change is that the envious strategy ceases to be the best for any fight intensity. To sum up, under group fight, the neutral and donator strategies seem quite robust with respect to parameter variation, while the spiteful and the envious strategies still need a very fragile balance of parameter values to be optimal.

6. Conclusions

From game theoretical point of view we can say that in the multilevel selection model the final stage of selection depends on

¹² Similar "survival" probability function is used in studies of origin of cooperation (e.g. Nowak et al., 1994). Although the exponent is called either as "degree of stochasticity" or "strength of selection" (see Nowak et al., 1994); in our case the fitness is determined by two levels and we do not consider the stochastic process, therefore we use a different name of β .

¹³ The mathematical details of calculation for the relative advantage functions are found in Appendix B. Since we consider only four phenotypes, we have three relative advantage functions for each resident phenotype.

the juveniles' survival probability as well. In this paper, we assume that the survival probability increases with the total number of juveniles in the group. Thus, in our multilevel selection model, the fitness of a given phenotype depends on the fecundity of the other phenotypes as well, since the total fecundity of the whole group is a sum of the fecundity of the interacting phenotypes within the group.

6.1. Summary the results

In this paper, we examined which behavior can establish evolutionary stable population in a multilevel selection situation, when the offspring number within a group is determined by egalitarianism-game and the juveniles have to survive (either predator attacks or fight for territory) to reproductive age. The egalitarian game gives a possibility to consider a “scale of group welfare”, since spiteful, envious, neutral and donator strategies do increase the total fecundity of the group, in this given order. In a well-mixed model, the spiteful outperforms the envious, neutral and donator strategists as well (Garay and Móri, 2011). Now we found that, not regarding whether predation or territorial fight determines the survival rate, when the survival rate decreases with respect to fecundity, first the spiteful, then the envious, after that the neutral and finally the donator will be ML-ESS.

Furthermore, we note that, since the average fitness of different behaviors is a highly non-linear function, the existence of a pure strict ML-ESS does not exclude the possibility of coexistence of all types. There are two possible frameworks to investigate possible coexistence: the first one uses a stochastic model, since we have small groups, the stochastic effects may play a role; the second one uses a game dynamics, see e.g. Hofbauer and Sigmund (1998), Cressman (2010). These frameworks can give different predictions, since in finite stochastic models one behavior gets finally fixed (Garay and Móri, 2012); while in replicator dynamics coexistence is most likely. We are planning to return to these investigations in future studies.

Here, we have to note that spite is a costly competition in our model (costly for both actor and recipient). The main difference between our spiteful and Hamiltonian (Hamilton, 1970, 1971b) and Wilsonian (Wilson, 1975) spiteful strategies is the following. When we calculate the fitness of different phenotypes (Gardner and West, 2004a, 2004b; West and Gardner, 2010) we do not consider the genetic relatedness between opponents (Knowlton and Parker, 1979).

6.2. About our ML-ESS definitions

The ESS concepts are based on the relative advantage of resident phenotype over all rare mutants (see Eq. (1)). In different selection situations, we get different detailed versions of relative advantage. In our terminology, “selection situation” is given by the population structure (including new group formation processes), the selection forces (game theoretical conflict within groups, and selection forces on groups) and the mutation process. The presented selection situation is near to the group selection perspective. However, the relative advantage strictly follows Darwinian tenet: a phenotype with higher fitness than the others, will spread. Now the question arises: what is the connection between Darwinian relative advantage-based concept and group (Nowak et al., 2010) or kin (Abbot et al., 2011) selection trends. We hope that the “orthodox” Darwinian view can build a bridge between these two trends (Okasha, 2010) or can synthesize those. In the present paper, we make a connection between Darwinian relative advantage-based concept and group selection trends, since in the presented selection situations the average fitness of phenotypes depends on the survival probability (which is determined by the total group fecundity), and, at the same time, on the fecundity of phenotype (which is determined by a game within group, thus interactions between relatives). In other words, the “welfare of

group” is only one of the components of fitness, thus our theoretical framework is not a pure version of the group selection trend. But the effect of group size on the survival rate (thus on the fitness of phenotypes) is beyond any doubt.

To shed light on a possible synthesis of group and kin selection trends, let us consider a multilevel selection situation when the predator press is high enough for the envious strategy to be a ML-ESS, and, according to our assumption, there is no kin regarding preference (e.g., green beard). Now assume that kin regarding preference appears in this situation (e.g., envy outside of kin and donator within kin), while the predation press does not change. Clearly, this behavior does increase the fecundity of the own phenotype (since there is no envious attack between family members) and increases the total fecundity of group (which increases the survival rate for all members of the juvenile group) at the same time. This kin regarding preference will spread, since we have already shown that at the ML-ESS for predation there is no such behavior which could increase the total fecundity of the whole group and its own fecundity at the same time, provided that the selection neighborhood (measured by K) is arbitrarily large. Thus, these two basic ideas of group and kin selection trend can be built into the same Darwinian model in the future.

Finally, we note that in the egalitarian game (Garay and Móri, 2011), when the behavior depends on the relatedness of components (see envious–spiteful strategy: envy within its family and spiteful outside), envy outcompetes the spiteful.

6.3. About spite

An accepted example of spite is that the western and herring gulls destroy the egg of rivals (or kill the chick without consuming it) if they had lost their own eggs (Pierotti, 1980). As another example, stump-tail macaques interfere with copulating pairs, so that they risk aggression (Breereton, 1994). From our perspective, these examples can be considered as envious behavior, since an unsuccessful individual makes damage to a successful one.

Moreover, it is widely accepted (e.g. Jensen, 2010) that spite (envy) is extraordinarily rare in nature. What is the reason for that? From the classical evolutionary game theoretical point of view, spite has relative advantage over the non-spiteful strategy in well-mixed population, when the cost of making damage is smaller than the damage caused (Garay and Móri, 2011; Vickery et al., 2003). In the present selection situation, envy outperforms the spiteful, when the fight between groups or predation pressure is neither too small (when spiteful wins), nor too high (when neutral or donator wins). Our present result sheds light on the observation that the spiteful is very rare in biology, for we found that spite is ML-ESS if either the predation press or the fight intensity between groups is small. The main point is that spite (and envy) decreases its own fecundity (with the cost of damage) and the total fecundity of its group (with the total degree of damage), but at the same time it increases its relative advantage in fecundity within its group. When survival probability has a massive effect on fitness (in both cases: predation and fight), then spiteful and envious strategies are outperformed more easily. Maybe this is one of the most important reasons, why spite (and envy) is rare in nature in group structured populations. Whereas the altruistic and cooperative behavior can increase the total fecundity of the group, thus these behaviors are more likely to evolve when the survival rate increases with the total fecundity of group. However, the stronger of the two selection factors (group size based survival and phenotype fecundity) determines the outcome of selection.

The human case is more complicated. As we know, human behavior is a mixture, since donation, envious and spiteful (Dawes et al., 2007) behaviors take place at the same time in the same experiment (Another example for the mixed behavior: cooperative and patient and impatient punisher are observed in the same

experiment, see Espín et al., 2012.). In the light of our present results, we claim that, during human evolution, group-based survival exposed a “middle-sized” effect on the phenotype fitness, since if fight is extraordinarily lethal, behaviors decreasing the total fecundity of the group get outperformed by multilevel selection (cf. Bowles, 2006, 2009). Moreover, we also found that egalitarian behavior (envy) is ML-ESS when survival rate has “middle-sized” effect on the phenotype fitness. We mentioned the comparative study of violence in chimpanzees and humans which found that although humans had rates of aggression two and three orders of magnitude less than chimpanzees, they still have similarly high rate of lethal aggression (Wrangham et al., 2006).

Finally, Wilson (2003) has already called attention to the fact that group structure and the environment of humans influences human religions. The moral laws are a part of any religion. Although we are interested in the evolutionary advantage and disadvantage of spite, we have also found that the group structure and ecological background (in our case predation press and territorial behavior) have crucial role in the evolutionary success of spite and envy.

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Appendix A

A.1. Average individual fitness in pure groups

When computing the average individual fitness, we can start from the average basic income, which is $(a_1 + a_2)/2$, and then count all positive or negative modifications coming from interactions within the group. Let us introduce the notation $\Delta = a_2 - a_1$.

Spiteful group. The average cost of damage is $(n - 1)qc$, and the average amount of damage is $(n - 1)qd((a_1 + a_2)/2)$, thus

$$w_S(n) = \frac{a_1 + a_2}{2}(1 - (n - 1)qd) - (n - 1)qc.$$

Envious group. Suppose that exactly Y individuals receive basic income a_1 , then Y follows the binomial distribution $Binom(n, 1/2)$. Each of them acts enviously $n - Y$ times with success probability $\Delta^\alpha q$ in each case, at the cost of c and with damage da_2 . Thus, the average fitness in the envious group is

$$w_E(n) = \frac{a_1 + a_2}{2} - \frac{1}{n}E(Y(n - Y))\Delta^\alpha q(c + da_2) \\ = \frac{a_1 + a_2}{2} - \frac{n - 1}{4}\Delta^\alpha q(c + da_2).$$

Neutral group. Since there is no damage in this group, we have

$$w_N(n) = \frac{a_1 + a_2}{2}.$$

Donator group. Again, let Y denote the number of poor individuals. The poorer individuals get donation from each of wealthier group mates. The effect of donation is B , and this costs b . We suppose that $b < B$, thus the positive effect of donation is larger than its cost. In this way donation is offered $Y(n - Y)$ times, yielding a net benefit of $B - b$ in each case. Hence, the average fitness in the donator group is

$$w_D(n) = \frac{a_1 + a_2}{2} + \frac{1}{n}E(Y(n - Y))(B - b) = \frac{a_1 + a_2}{2} + \frac{n - 1}{4}(B - b).$$

A.2. Average individual fitness in mixed groups

For simplicity, we assume that in every mixed group there are 2 types only, with n_1 and n_2 individuals, $n_1 + n_2 = n$. Let Y_1 and Y_2 denote the number of individuals with basic income a_1 for the two types, respectively. They are independent, and follow the binomial distribution $Binom(n_1, 1/2)$, and $Binom(n_2, 1/2)$, respectively. In the subscript of the average individual fitness function $w_{T_1, T_2}(n_1, n_2)$ the two initials show the subgroup types, and the fitness is computed for the type in the first place. The arguments of the function show the sizes of the subgroups, in the order of subscripts.

1. Spiteful & envious group

Spiteful subgroup. A spiteful individual tries to damage the property of everybody else, and he is attacked by all the other spiteful, but he does not attack himself. This makes an average loss of

$$(n - 1)qc + (n_1 - 1)qd\frac{a_1 + a_2}{2}.$$

In addition, a wealthier spiteful is attacked by the poorer envious group mates too, with probability $\Delta^\alpha q$. Hence the average individual fitness of the spiteful is

$$w_{SE}(n_1, n_2) = \frac{a_1 + a_2}{2} - (n - 1)qc - (n_1 - 1)qd\frac{a_1 + a_2}{2} \\ - \frac{1}{n_1}E((n_1 - Y_1)Y_2)\Delta^\alpha qda_2 \\ = \frac{a_1 + a_2}{2}(1 - (n_1 - 1)qd) - (n - 1)qc - \frac{n_2}{4}\Delta^\alpha qda_2.$$

Envious subgroup. Depending on his basic income, the fitness of any envious individual is decreased by the damage caused the spiteful subgroup. This is $n_1qd((a_1 + a_2)/2)$ in expectation. Besides, a poor envious individual should pay the cost of his attacks on richer group mates. This is $(n - Y_1 - Y_2)\Delta^\alpha qc$ in expectation. Though a rich envious does not harm anybody, but he is still attacked by the poor envious, thus his fitness decreases by further $(n_2 - Y_2)\Delta^\alpha qda_2$.

From all these the average individual fitness of an envious individual is

$$w_{ES}(n_2, n_1) = \frac{a_1 + a_2}{2}(1 - n_1qd) - \frac{1}{n_2}E(Y_2(n - Y_1 - Y_2))\Delta^\alpha qc \\ + Y_2(n_2 - Y_2)\Delta^\alpha qda_2 \\ = \frac{a_1 + a_2}{2}(1 - n_1qd) - \frac{n_1 + n_2 - 1}{4}\Delta^\alpha qc - \frac{n_2 - 1}{4}\Delta^\alpha qda_2 \\ = \frac{a_1 + a_2}{2}(1 - n_1qd) - \frac{n - 1}{4}\Delta^\alpha qc - \frac{n_2 - 1}{4}\Delta^\alpha qda_2.$$

2. Spiteful & neutral group

Spiteful subgroup. The basic income of a spiteful individual decreases by the cost of his attacks on everybody else, and by the damage caused by the other spiteful individuals. Hence, the average individual fitness of a spiteful is

$$w_{SN}(n_1, n_2) = \frac{a_1 + a_2}{2} - (n - 1)qc - (n_1 - 1)qd\frac{a_1 + a_2}{2} \\ = \frac{a_1 + a_2}{2}(1 - (n_1 - 1)qd) - (n - 1)qc.$$

Neutral subgroup. Their basic income is only decreased by the damage they suffer from the spiteful. Thus, their average individual fitness is

$$w_{NS}(n_2, n_1) = \frac{a_1 + a_2}{2}(1 - n_1qd).$$

3. Spiteful & donator group

Spiteful subgroup. The spiteful individuals attack everybody else, and they also suffer damage from other spiteful group mates. In addition, the poor individuals receive donation

$(n_2 - Y_2)B$ from rich donators. Hence the updated fitness of a poor spiteful individual is

$$(a_1 + (n_2 - Y_2)B)(1 - (n_1 - 1)qd) - (n - 1)qc.$$

For a rich spiteful individual this is

$$a_2(1 - (n_1 - 1)qd) - (n - 1)qc.$$

Hence the average individual fitness of the spiteful is

$$\begin{aligned} w_{SD}(n_1, n_2) &= \frac{1}{n_1} E[Y_1(a_1 + (n_2 - Y_2)B)(1 - (n_1 - 1)qd)] \\ &\quad + \frac{1}{n_1} E[(n_1 - Y_1)a_2(1 - (n_1 - 1)qd)] - (n - 1)qc \\ &= \frac{a_1 + a_2}{2} (1 - (n_1 - 1)qd) + \frac{1}{n_1} E(Y_1(n_2 - Y_2)) \\ &\quad \times B(1 - (n_1 - 1)qd) - (n - 1)qc \\ &= \left(\frac{a_1 + a_2}{2} + \frac{n_2 B}{4} \right) (1 - (n_1 - 1)qd) - (n - 1)qc. \end{aligned}$$

Donator subgroup. Their basic income is decreased by the damage caused by the spiteful subgroup. In addition, a poor donator receives $(n_2 - Y_2)B$ from richer donators, while the fitness of a rich donator decreases by $(Y_1 + Y_2)b$. Consequently, a poor donator's updated fitness is

$$(a_1 + (n_2 - Y_2)B)(1 - (n_1 - 1)qd),$$

while for a rich donator it is

$$(a_2 - (Y_1 + Y_2)b)(1 - (n_1 - 1)qd).$$

Hence, the average individual fitness in the donator subgroup is

$$\begin{aligned} w_{DS}(n_2, n_1) &= \frac{1}{n_2} E[Y_2(a_1 + (n_2 - Y_2)B)(1 - (n_1 - 1)qd)] \\ &\quad + \frac{1}{n_2} E[(n_2 - Y_2)(a_2 - (Y_1 + Y_2)b)(1 - (n_1 - 1)qd)] \\ &= \left(\frac{a_1 + a_2}{2} + \frac{n_2 - 1}{4} B - \frac{n - 1}{4} b \right) (1 - (n_1 - 1)qd). \end{aligned}$$

4. Envious & neutral group

Envious subgroup. The only source of loss is envy within the subgroup. Each poor envious tries to do harm to every richer groupmate. This happens $Y_1(n - Y_1 - Y_2)$ times, with an expected loss of $\Delta^\alpha qc$ in each case. In addition, the rich envious individuals must suffer attacks from poorer envious group mates, with an expected loss of $Y_1 \Delta^\alpha qda_2$. Hence the subgroup's average individual fitness is

$$\begin{aligned} w_{EN}(n_1, n_2) &= \frac{a_1 + a_2}{2} - \frac{1}{n_1} E(Y_1(n - Y_1 - Y_2)\Delta^\alpha qc) \\ &\quad + Y_1(n_1 - Y_1)\Delta^\alpha qda_2 \\ &= \frac{a_1 + a_2}{2} - \frac{n - 1}{4} \Delta^\alpha qc - \frac{n_2 - 1}{4} \Delta^\alpha qda_2. \end{aligned}$$

Neutral subgroup. Rich neutrals are the target of envy, and this is the only source of loss. Hence the average individual fitness is

$$\begin{aligned} w_{NE}(n_2, n_1) &= \frac{a_1 + a_2}{2} - \frac{1}{n_2} E(Y_1(n_2 - Y_2)\Delta^\alpha qda_2) \\ &= \frac{a_1 + a_2}{2} - \frac{n_1}{4} \Delta^\alpha qda_2. \end{aligned}$$

5. Envious & donator group

After the giving stage there are $Y_1 + Y_2$ poorer individuals. They have already received an amount of $(n_2 - Y_2)B$ from rich donators, so their income is $a_1 + (n_2 - Y_2)B$ at the moment. The income of rich donators decreased by $(Y_1 + Y_2)b$, hence they have $a_2 - (Y_1 + Y_2)b$ each. The income of rich envious individuals did not change. Thus, the income difference between a poor envious and a rich donator is $\Delta - (n_2 - Y_2)B - (Y_1 + Y_2)b$, and it is $\Delta - (n_2 - Y_2)B$ between a poor and a rich envious. Now, the taking stage follows. Poor envious individuals attack all

richer group mates, but with a smaller probability when the target is a rich donator.

Envious subgroup. The loss of a poor envious individual is $[(n_1 - Y_1)(\Delta - (n_2 - Y_2)B)^\alpha + (n_2 - Y_2)(\Delta - (n_2 - Y_2)B - (Y_1 + Y_2)b)^\alpha]qc$,

while the loss of a rich envious individual is

$$Y_1(\Delta - (n_2 - Y_2)B)^\alpha qda_2.$$

This makes an average individual fitness of

$$\begin{aligned} w_{ED}(n_1, n_2) &= \frac{a_1 + a_2}{2} - \frac{1}{n_1} E(Y_1(n_1 - Y_1)[\Delta - (n_2 - Y_2)B]^\alpha qc) \\ &\quad - \frac{1}{n_1} E(Y_1(n_2 - Y_2)[\Delta - (n_2 - Y_2)B - (Y_1 + Y_2)b]^\alpha qc) \\ &\quad - \frac{1}{n_1} E((n_1 - Y_1)Y_1[\Delta - (n_2 - Y_2)B]^\alpha qda_2) \\ &= \frac{a_1 + a_2}{2} - \frac{n_1 - 1}{4} E([\Delta - (n_2 - Y_2)B]^\alpha q(c + da_2)) \\ &\quad - \frac{1}{n_1} E(Y_1(n_2 - Y_2)[\Delta - n_2 B + (B - b)Y_2 - bY_1]^\alpha qc). \end{aligned}$$

It is hard to find a closed form of $w_E(n_1, n_2)$ for a general α , but in the simplest case of $\alpha = 1$ we have

$$\begin{aligned} w_{ED}(n_1, n_2) &= \frac{a_1 + a_2}{2} - \frac{n_1 - 1}{4} \left(\Delta - \frac{n_2 B}{2} \right) q(c + da_2) - \frac{n_2}{4} (\Delta - n_2 B) qc \\ &\quad - \frac{n_2(n_2 - 1)}{8} (B - b) qc + \frac{(n_1 + 1)n_2}{4} b qc. \end{aligned}$$

Donator subgroup. A poor donator receives $(n_2 - Y_2)B$ from rich donators. A rich donator gives $(Y_1 + Y_2)b$ to the poor, and suffers further

$$Y_1[\Delta - (n_2 - Y_2)B - (Y_1 + Y_2)b]^\alpha qd(a_2 - (Y_1 + Y_2)b)$$

damage by the poor envious group mates. Thus, the average individual fitness is

$$\begin{aligned} w_{DE}(n_2, n_1) &= \frac{a_1 + a_2}{2} + \frac{1}{n_2} E(Y_2(n_2 - Y_2)B) - \frac{1}{n_2} E((n_2 - Y_2)(Y_1 + Y_2)b) \\ &\quad - \frac{1}{n_2} E(Y_1(n_2 - Y_2)[\Delta - (n_2 - Y_2)B \\ &\quad - (Y_1 + Y_2)b]^\alpha qd[a_2 - (Y_1 + Y_2)b]) \\ &= \frac{a_1 + a_2}{2} + \frac{n_2 - 1}{4} B - \frac{n - 1}{4} b \\ &\quad - \frac{1}{n_2} E(Y_1(n_2 - Y_2)[\Delta - n_2 B + (B - b)Y_2 \\ &\quad - bY_1]^\alpha [a_2 - (Y_1 + Y_2)b]) qd. \end{aligned}$$

For $\alpha = 1$ we have

$$\begin{aligned} w_{DE}(n_2, n_1) &= \frac{a_1 + a_2}{2} + \frac{n_2 - 1}{4} B - \frac{n - 1}{4} b - \frac{n_1}{4} \left(a_2 - \frac{n_2 B}{2} \right) (\Delta - n_2 B) qd \\ &\quad - \frac{n_1(n_2 - 1)}{8} \left(a_2 - \frac{n + 1}{2} b \right) (B - b) qd + \frac{n_1(n_1 + 1)}{8} \\ &\quad \times \left(a_2 - \frac{n + n_1 + 2}{2} b \right) b qd. \end{aligned}$$

6. Neutral & donator group

Neutral subgroup. The only change with respect to the basic income is the donation from rich donators to poor neutrals. Thus, the average individual fitness is

$$w_{ND}(n_1, n_2) = \frac{a_1 + a_2}{2} + \frac{1}{n_1} E(Y_1(n_2 - Y_2))B = \frac{a_1 + a_2}{2} + \frac{n_2 B}{4}.$$

Donator subgroup. Donation within the subgroup yields a net increase of $Y_2(n_2 - Y_2)(B - b)$. Donation to the poor neutrals takes $Y_1(n_2 - Y_2)b$. Hence, the average individual fitness is

$$\begin{aligned} w_{DN}(n_2, n_1) &:= \frac{a_1 + a_2}{2} + \frac{1}{n_2} E(Y_2(n_2 - Y_2)(B - b) - Y_1(n_2 - Y_2)b) \\ &= \frac{a_1 + a_2}{2} + \frac{n_2 - 1}{4} (B - b) - \frac{n_1 b}{4} = \frac{a_1 + a_2}{2} + \frac{n_2 - 1}{4} B - \frac{n - 1}{4} b. \end{aligned}$$

Appendix B

Statement 1. If the mutation rate is arbitrarily small and K is arbitrarily large, for all possible game within group there exists a strictly increasing survival rate function P , which can guarantee that the strategy maximizing the group size is ML-ESS.

For simplicity, we consider here a special case, with a finite set S of phenotypes, $S := \{M_1, M_2, \dots, M_L, R\}$. Assume that the resident phenotype maximizes the total fecundity of the group, i.e. $w_{RT} > w_{MT}$ for all mutants. Consider a mutant M_F which can optimize its own fecundity against this resident phenotype within group, i.e., $w_{M_F}(n_R, n_{M_F}) - w_R(n_R, n_{M_F})$ is maximal with respect to the set of mutants $\{M_1, M_2, \dots, M_L\}$. Furthermore, consider a mutant M_T , for which $w_{RT} - w_{M_T}$ is minimal over the set of mutants. As we see, when mutation rate is small enough, then the stability condition (i) guarantees that the resident is ML-ESS. Thus, for each fixed game theoretical conflict within groups we are looking for strictly increasing survival rate functions for which

$$P(w_{RT})w_R(n, 0) > P(w_{M_T})w_{M_F}(n_R, n_{M_F}).$$

Observe that for the fixed game theoretical conflict this inequality is sufficient for $P(\cdot)$ to be the desired survival function, since the mutant types M_T and M_F are determined by the game theoretical conflict within groups. From biological point of view, the above inequality requires that the survival rate between w_{M_T} and w_{RT} increases “radically”. Let us try to find such a survival rate function in the form $P(x) := (x/w_{RT})^\nu$, where $x \in [0, w_{RT}]$ is the total size of the focal group. From the sufficient inequality above it follows that $w_R(n, 0)/w_{M_F}(n_R, n_{M_F}) > (w_{M_T}/w_{RT})^\nu$, that is, $\ln w_R(n, 0) - \ln w_{M_F}(n_R, n_{M_F}) < (\ln w_{M_T} - \ln w_{RT})\nu$. Note that the right-hand side is negative. Thus, for all exponents ν satisfying

$$\nu > \frac{\ln w_{M_F}(n_R, n_{M_F}) - \ln w_R(n, 0)}{\ln w_{RT} - \ln w_{M_T}},$$

the group size maximizing strategy is ML-ESS. ■

Appendix C

Statement 2. If the mutation rate is arbitrarily small and K is arbitrarily large, then for all possible games within group there exists a strictly increasing survival rate function Π , which can guarantee that the group size maximizing strategy is ML-ESS.

With the notations of Statement 1, we need a survival function Π such that

$$\Pi(w_{RT}, w_{RT})w_R(n, 0) > \Pi(w_{M_T}, w_{RT})w_{M_F}(n_R, n_{M_F}).$$

Again, from biological point of view the above inequality needs that the survival rate between w_{M_T} and w_{RT} can increase steeply. This time we are looking for a survival rate function of the form $\Pi(x, y) := x^\kappa/(x+y)^\kappa$. Then the above inequality reads

$$\frac{w_{RT}^\kappa}{(w_{RT} + w_{RT})^\kappa} w_R(n, 0) > \frac{w_{M_T}^\kappa}{(w_{M_T} + w_{RT})^\kappa} w_{M_F}(n_R, n_{M_F}).$$

Thus for all exponents κ for which

$$\kappa > \frac{\ln w_{M_F}(n_R, n_{M_F}) - \ln w_R(n, 0)}{\ln(w_{M_T} + w_{RT}) - \ln 2w_{M_T}},$$

the group size maximizing strategy is ML-ESS. ■

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