



Is envy one of the possible evolutionary roots of charity?

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ABSTRACT

We introduce an evolutionary game in which envy and charity can be considered as a consequence of Darwinian competition, i.e. individuals aim at increasing their own proportion rather than their absolute contribution to the next generation, and other-regarding-preference is a “method” for that. If the damage is additive and its cost is low, an envious strategy defeats a neutral strategy (rational strategy maximizing its own income). If damage is multiplicative, then coexistence of neutral and envious strategists is possible. Envy is a conditional spiteful strategy, thus in envious groups there is less damage than in spiteful groups, so envy decreases the total cost of spiteful competition. Although envy can be selected out in a mixed population of envious, neutral and spiteful individuals when damage is additive, the envious-spiteful strategists (envious within its kin and spiteful outside its kin) outperform neutral and spiteful ones in a simple kin-selection scenario. Furthermore, Clytemnestra's strategy, namely donating to richer people to evokes envious attacks on them, can spread through an envious group. Moreover, the envious-donor strategy (giving to the poorest and damaging the richer individuals) can spread in the envious group. Charity is a “buy-off” behaviour, since the donor can decrease its own damage from envy, thus charity further decreases the total cost of spiteful competition.

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1. Introduction

Egalitarian people have other-regarding preference, that is they alter others' incomes at their own cost (Dawes et al., 2007): they reduce above-average earners' income (costly taking) (Zizzo, 2003) and increase below-average earners' income (costly giving). We propose three evolutionary games which can explain a possible origin for other-regarding preference. One form of other-regarding preference is inequity aversion, i.e. people resist inequitable outcomes (Fehr and Schmidt, 1999). Not only humans (Dawes et al., 2007) but also capuchin monkeys (Brosnan and de Wall, 2003; Takimoto et al., 2009), chimpanzees (Brosnan et al., 2005) and dogs (Range et al., 2009) show different levels of inequity aversion.

From the point of view of the basic premise of economical game theory (claiming that humans are rational players maximizing their own income), the origin of other-regarding preference of egalitarian humans is not clear (Dawes et al., 2007). Moreover, costly taking and costly giving are not rational since both reduce the income of the rational player without direct benefit. Economists have introduced a utility function (a combi-

nation of their own income and the others' incomes Lehmann, 2001; Goel and Thakor, 2005) to describe other-regarding preference.

In evolutionary game theory the fitness (average offspring number of a given behaviour type) measures evolutionary success exclusively. There is an essential difference between the approach of “utility function” and that of “biological fitness”. In economy, other-regarding preference is built using the payoff function of players (it is a linear combination of the payoff of opponents). In general, there is no reason to accept this setup in asexual evolutionary game theory. In our paper, we propose a different model: other-regarding preference is “built in” the phenotype (strategy) by us. The individuals' behaviour will depend either on the success of its opponent or on the relationship between the focal individual and its opponents. To make it clear, in our setup the focal individual behaviour does not depend on what its opponent has done with the focal individual (direct reciprocity), and/or what the opponent has done to others (indirect reciprocity) (Nowak, 2006; Nowak and Sigmund, 2005a,b), but the focal individual's behaviour does depend on the success difference between opponents or on the relationship of opponents. Clearly, this kind of behaviour determines the fitness of phenotypes, which is just our payoff function (it does not need to be a linear combination of the opponents' fitness). In other words, in the proposed model the average fitness of the phenotype determines evolutionary success.

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The basic tenet of Darwinian theory declares that in a given state of population (denoted by x), i -type spreads if the average individual fitness of i -type (denoted by $W_i(x)$) is larger than the average individual fitness of the whole population (denoted by $W(x)$) (Maynard Smith and Price, 1973). Based on this, the relative advantage of i -type is defined as

$$R_i(x) = W_i(x) - W(x), \quad (1)$$

which determines the evolutionary success of i -type (Garay, 2007), since i -type spreads if it has positive relative advantage over the whole population. It means that those phenotypes will spread which have more offspring than the average offspring number of the whole population. We would like to emphasize that the intuitive background of the original definition of evolutionarily stable strategy (ESS) by Maynard Smith is the relative advantage (see, e.g. Hofbauer and Sigmund, 1998). Recall that a strategy is a strict ESS if it has positive advantage in each state of the population, so the abundance of strict ESS always increases. We will also say that different strategies coexist if there exists a neighbourhood of an equilibrium (i.e. a frequency distribution of different strategies, at which they have the same fitness), in which the strategy that becomes rare has positive advantage. Thus, frequencies of different strategies come back to the equilibrium. For simplicity, in all our calculations we use relative advantage (1) to specify which state will be the final state of Darwinian evolution, since our simple games do not require game dynamics.

In Darwinian “struggle for existence” (and perhaps in economy as well Hansen and Samuelson, 1988; Schaffer, 1989; Guth and Peleg, 2001) the fitness (profit) maximizing preference does not always guarantee maximum relative advantage (Garay and Varga, 2005). For instance, Hamilton (1970, 1971) pointed out that when a spiteful individual (which harms itself and its competitor as well) decreases his own fitness less than that of its competitor, spite may evolve if damage occurs between individuals of lower than average relatedness. We do not use Hamilton’s kin selection approach in all introduced games, since firstly, discrimination between kin and non-kin is not necessary for the evolution of spite (Knowlton and Parker, 1979); secondly, envy occurs within a family (e.g. Cain’s slaying of Abel); and thirdly, children without siblings showed much more costly sharing behaviour than children with siblings (Fehr et al., 2008). Following the standard setup of evolutionary game theory, we consider only asexual populations (Maynard Smith and Price, 1973), and individuals with the same genetically fixed strategy have the same payoff. This means that there is no difference between players (in strength, aggressivity, damage causing ability). The envious and spiteful individual causes damage to its partners. To do damage is a costly action which decreases the fitness of the recipient, for instance, destroys the collected food or kills the offspring of the target individual. The main point is that damage does not increase the fitness of anybody.

Nowadays, the origins of human generosity have been explored by using biological, psychological, anthropological and sociological evidence (see Komter, 2010 and references therein). One kind of generosity is charity, which is an altruistic behaviour, i.e. an individual increases the fitness of others at the price of its own fitness. Altruistic food-sharing is a well-known phenomenon among 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, 2005a) material reward in the future (Garay, 2009); it is not considered as a consequence of kinship since recipients are not necessarily related to the donor; it is not a by-product of altruism, since it is not an “incidental” consequence of the selfishness of the donor (Fruth and Hohmann, 2002) and the donor does not breed cooperatively with the recipient (Burkart et al., 2007).

For other-regarding preference, it is a prerequisite that players know the success of others (e.g. amount of accumulated food, offspring number). We consider more than two individuals in an interacting group. Although inequity aversion plays a key role in the evolution of cooperation in humans (Fehr and Fischbacher, 2003; Taylor et al., 2007; Johnson et al., 2009), we will start from a simpler situation in which each player’s basic income (score) is drawn randomly from the same distribution (Dawes et al., 2007; Lehmann, 2001). Moreover, for simplicity, we consider a non-repetitive game, thus there is no possibility to revenge (either reward, Li et al., 2010 or punishment, Scheuring, 2010b) in the future, and there is no possibility for norms (Ohtsuki and Iwasa, 2006) to evolve.

We emphasize that the above observations are only motivation for this paper, and we do not aim to model the following experiment. In a human experiment (Dawes et al., 2007), two egalitarian motives are observed: a below average earner damages an above average earner; and an above average earner gives score to a below average earner. However, there are two types of behaviour which are inconsistent with egalitarian motives: firstly, in 12% of cases of costly taking, a below average earner damages a below average earner, which makes both of them poorer. Secondly, in 17% of cases of costly giving, a below average earner gives score to an above average earner, which makes the rich richer and the poor poorer. We shall show that Darwinian theory can shed light on all four observations. For this purpose, we will introduce the simplest evolutionary games giving an insight into a possible evolutionary background of the above four observations. For the sake of simplicity, we do not aim to model human behaviour, for instance, we will consider non-repetitive games, where human memory has no role. Moreover, we use the standard asexual evolutionary game theory setup. Thus, in our model, we do not deal with the sex dependent human envy, i.e., men’s envy is motivated by financial resource, status and sexual power, conversely, women’s envy is motivated by sexual attractivity (clothes, makeup) (Hill and Buss, 2006).

Most evolutionary models on the origin of human altruism consider ancient human populations living in hunter–gatherer groups (e.g. Leimar and Hammerstein, 2001; Scheuring, 2010a). We also think that the direct Darwinian evolutionary scenario was true mainly in the Pleistocene and Holocene when hunter–gatherer human groups went extinct easily (Bowles, 2006). In the ancient past it seemed that wealth led to having more food which led to having more offspring. In contrast to that, in our modern society, wealth may lead to smaller family size, so studies are required to see if there is any possible direct application of the present evolutionary model to modern society (cf. Komter, 2010). For instance, in our asexual model we cannot investigate the relation between envy and sexes.

Finally, during model building, we also emphasize a few possible connections between the presented games and animal behaviour.

2. Envy Is Conditional Spitefulness

To show that envy has an evolutionary connection we recall the following: if a woman is pregnant in a village of Tzintzuntzan, the family will keep it in secret as long as possible, and after the pregnancy becomes known in the village, there are still attempts not to remind others of it, since a baby is considered highly desirable and the mother or the baby might suffer from others’ envy (Foster, 1967). We note that there are female chimpanzees (Townsend et al., 2007; Pusey et al., 2008) that kill the infants of other females. The direct effect of infanticide is that competition for resources declines. The indirect effect is that infanticidal females increase their own proportion in (but not absolute contribution to) the next generation (Dobson et al., 2000).

Envy is well-known in all human societies (Schoeck, 1966). Moreover, envy is prohibited in monotheistic religions (as expressed, for example, in the Ten Commandments), it plays an important role in criminals' behaviour, economy, sociology, social revolutions (Schoeck, 1966), and probably in genocide, since one of its prominent features is the belief that the target group obtained unfair advantage in the past (Dutton et al., 2005).

In Darwinian evolution, success is measured by the offspring number, so damage is either annihilating the gathered food of the target individual, or killing its offspring. We defined "spiteful" as a behaviour which unconditionally causes costly damage to other individuals without benefit to the self. 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). Anonymity is a usual experimental condition (Dawes et al., 2007), which rules out the revenge punishment. Based on these, we define an "envious" strategy as reducing the fitness of the partner at cost to the envious individual if and only if the fitness of the first one is higher than that of the second one, and the probability of damage increases with fitness difference and the damage is done secretly. We note that fitness difference increases the damage not only case of human envy (Vickery et al., 2003). For instance, the more eggs there are, the more conspecific eggs are eaten by cannibal female threespine sticklebacks (FitzGerald, 1992). Moreover, in the Navajo language there are no words for "lucky" or "fortune", but there is one for "envy". In the case when players' basic income follows the same random distribution, we will see that there is a connection between human envy and Darwinian relative advantage.

Now we fix $n > 2$ as the group size, and $0 \leq m \leq n$ denotes the number of envious spiteful strategists, so $n - m$ is the number of neutral individuals (without other-regarding preference), who never alter others' fitness. In our model, neutral strategy can be considered as a rational strategy maximizing its own income.

Is it worth being envious? The answer is positive, if the mean decrease of the fitness of an envious individual is less than that of a neutral strategist. Now we have to introduce some notation. Envious individuals try to damage someone else's property. The probability of damage is $p(X, Y)$, where X and Y denote the fitness of the attacker and that of the victim, respectively. Then envy increases with the difference between individuals (Dawes et al., 2007). Since we have no information on the concrete form of this increasing function we consider

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

For simplicity, we assume that at the beginning all individuals have random values of fitness, independently of each other, and that fitness can take on two different values $a_1 < a_2$. Here q measures the likeliness of the opportunity for 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 $c(X, Y)$; for simplicity let the cost be constant: $c(X, Y) = c$. We assume that an envious individual tries to attack all richer ones but attacks all of those once only. The degree of damage is $d(X, Y)$, and for simplicity we assume that it is a fixed proportion of the victim's fitness, $d(X, Y) = dY$. Here c, d, q, α are nonnegative parameters, the first three are typically small. We emphasize that neither neutrality nor spitefulness decrease the fitness difference between other members of the group average, but envy does, if the cost of damage is less than the degree of damage caused ($c < da_2$), so envy does not produce absolute equality.

3. Envy Against Neutral Strategy

In this section, we consider a well-mixed population of envious and neutral strategists. We consider two different kinds of damage process:

Suppose first that the damage is *additive* (Dawes et al., 2007): the effects of simultaneous attacks are based on the original fitness of the victim. That is, if an individual having fitness Y is successfully attacked by individuals having fitness X_1, \dots, X_k , resp., then it suffers a damage of $d(X_1, Y) + d(X_2, Y) + \dots + d(X_k, Y) = kdY$. The advantage of being a member of the envious group is that for them the number of potential harmful individuals is one less than for neutral people, because nobody attacks himself. Hence envy spreads if the sum of the cost of all envious attacks is smaller than the expected damage caused by an envious person. This statement of ours agrees with Hamilton's result (Hamilton, 1970, 1971), considering the fact that in our model envy causes damage to neutral and envious people with the same probability, provided they have the same fitness. We found that envy would spread in neutral groups without saturation if and only if

$$c < \frac{a_2}{n-1}d, \quad (3)$$

regardless the the number of envious people in the group.¹ This means that in the additive case there are two strict ESS: if condition (3) holds, then everyone is envious; and if condition (3) does not hold then everybody is neutral. Obviously, since envy is conditional spitefulness, there is more damage in a totally spiteful group than in a totally envious group, so envy reduces the total cost of spiteful competition (sum of the cost of damage and the degree of it).

Suppose now that the damage is *multiplicative*: assuming that the cumulative damage is independent of the order of attacks, the result of k simultaneous damages is a cumulative damage of proportion $1 - (1 - d)^k$. In this case envy has a positive relative advantage (1) so it spreads in neutral groups if the sum of the cost of all envious attacks plus the expected damage caused by $m - 1$ envious persons is less than the expected damage caused by m envious persons, formally

$$c < \left(1 - \frac{1}{2}(a_2 - a_1)^\alpha qd\right)^{k-1} \frac{da_2}{n-1}.$$

This condition depends on the number of envious players and now there is a mixed evolutionarily stable state. Table 1 contains the threshold values for the cost of envy for $a_1 = 1, a_2 = 2, n = 10, \alpha = 1, q = 0.1$ and $d = 0.2$. If the cost c is less than a threshold c_m , then envy spreads, since envy has positive relative advantage (1), otherwise neutrals come off better.

For instance, if $c_m = 0.04269$ then $m = 5$ is a mixed ESS, i.e. if the number of envious individuals is less than 5, then envy spreads but when there are more than 5 then the neutral strategy spreads. Just to make a comparison, in the additive model with the same parameters envy strategy is a strict ESS (envy is profitable for an arbitrary m), if $c < 0.04444$.

4. When Does Envy Outperform Spitefulness?

Let us assume that the damage is additive and consider a mixed population of neutral, envious and spiteful. We find that, when the cost is larger than the degree of damage, then neutral wins in Darwinian "struggle for existence". However, when the degree of damage is larger than the cost, then the spiteful strategist wins, since the unconditional damage can increase the relative advantage more than conditional damage. Consequently, in a well mixed

¹ For mathematical details, see Appendix A.

Table 1
Threshold values for the cost of envy.

k	1	2	3	4	5	6	7	8	9	10
c_k	0.04444	0.04400	0.04356	0.04312	0.04269	0.04226	0.04184	0.04142	0.04101	0.04060

population envious and spiteful pure strategists cannot coexist in our model.

We would like to point out that Hamilton’s kin-selection scenario is highly relevant to the above question. Following Hamilton’s kin-selection scenario we define a new type of behaviour, *envious-spiteful* strategy: envious within his/her family (brother or sister); and spiteful outside his/her family.² We emphasize that this strategist knows who is in its family and who is not and the behaviour of opponents depends on their relationship.³ We found that the envious-spiteful strategy outperforms neutral and spiteful ones in a well-mixed population, since the average amount of damages within a family is less than outside whenever envious-spiteful strategists can recognize their family with a non zero probability ($\lambda > 0$).

We note that in our model (when $\lambda = 1$), simultaneous observability of envious and spiteful behaviour depends on the size of group and the size of family. Firstly, if the ecologically determined group size (cf. Smith, 1985) is larger than the maximal size of a family, then an observer can see both behaviours at the same time. In the opposite case, an observer can see only envious behaviour, since at the end of evolution there is only one envious-spiteful family in each group. Clearly, a single envious-spiteful family is not evolutionary stable, since the mutant spiteful-spiteful family member (who is always spiteful) wins the competition within the family. So the evolutionary stability of envious-spiteful strategy needs further evolutionary factors. For instance, if different families compete with each other, then families having spiteful-spiteful members will probably be selected out by families without spiteful members, but this case needs further study (cf. Lehmann et al., 2007; Scheuring, 2010a).

Summing up, in this section we have pointed out that envious and spiteful may be observable at the same time. In a human experiment (Dawes et al., 2007), in 12% of costly taking, below average earners caused damage to a below average earner, which makes both of them poorer. From a Darwinian point of view, this behaviour is spiteful, which is clearly not an egalitarian motif.

5. Evolution in Envious Group

In the following we are interested in Darwinian evolution in envious groups where damage is additive. We consider a game that contains three stages in a fixed order in time. In the beginning, each individual receives a random income (a_1 or a_2), in the second “giving stage” each envious-donor increases the fitness of every poorer individual by b (e.g. it gives a fixed quantity of food). In the

third “taking stage”, envious and envious-donor strategists use the same envy rule, thus decreasing the fitness of group members who proved to be more successful than themselves. At first glance, this fixed order of stages might seem a strict assumption, however, it is not the case. Now let us consider two types of donor strategies: the first donor strategist immediately gives after he wins a lot. The second type of donor does not give immediately, so there is a time period when there is a bigger fitness difference between players. Thus, the second donor is attacked by envious partners with a higher probability than the immediate donor, so that the immediate donor has an advantage over the waiting donor. This is the reason why we can assume that “giving stage” precedes the “taking stage”.

5.1. Clytemnestra’s Strategy

In the drama of Aeschylus, when Agamemnon arrives home, his wife Clytemnestra, who had been planning to kill her husband, tries to arise peoples’ envy against Agamemnon (Schoeck, 1966). Moreover, in a human experiment (Dawes et al., 2007), in 16.9% of costly giving, a below average earner gives score to an above average earner. We define *Clytemnestra’s strategy* as follows. When Clytemnestra has low fitness, she donates b to the most successful individuals, though she herself is neither spiteful nor envious. Clytemnestra’s strategy has other-regarding preference. However, from the point of view of egalitarian motives, Clytemnestra’s strategy cannot be explained, since it makes the rich richer and the poor poorer. Moreover, it is obvious that in neutral and spiteful groups Clytemnestra’s strategy is selected out. Contrarywise, in an envious group the recipient becomes the target of the envious group, consequently, envious individuals will decrease the recipient’s fitness. Clytemnestra’s strategy has two advantages by increasing the amount of damages in its group: Firstly, it takes advantage of envious group members damaging the most successful individuals, so radically decreases the advantage of the most successful individuals. Secondly, envious members have larger total cost of damage. We have shown that when

$$d < (n - 1)c \quad \text{and} \quad 2n < (k - 1)qd + (n - 2)qc,$$

Clytemnestra’s strategy wins the Darwinian competition against $(n - k - 1)$ neutral and k envious individuals. In other words, Clytemnestra’s strategy spreads in a group of $(n - k - 1)$ neutral and k envious individuals.

5.2. Charity as a Conditional Donation

Charity is costly giving which increases the below-average individuals’ income (e.g. food) and it is an altruistic behaviour, i.e. an individual increases the fitness of others at a price of its own fitness. Clearly, charity decreases the fitness difference between group members, since decrease is twice as much as the giving (donation). Obviously, in neutral and envious resident population, pure donation decreases the relative advantage of the donor, so it cannot invade. Therefore, we define *envious-donor* strategists who give to the poorest individuals a fixed amount of food and are also envious, so damage richer ones. Donation and damage additively increase and decrease the fitness of target individuals, respectively. We consider a size n group in which there are k envious-donor strategists and $n - k$ envious strategists, and we find that when the donation is

² The definition of family (or kin) is not simple. We use the strict one: family contains only the full siblings. The initiative background of this strict definition is that Jankowiak and Diderich (2000) found evidence for more solidarity between full siblings than between half siblings. Moreover, Segal and Hershberger (1999) found associations between zygosity and frequency of cooperation between twins. Humans help their family and close relatives first, while friends, neighbours, and strangers only come afterwards (Komter and Schuyt, 1993). Furthermore, parents and other family members receive more than twice as much help than do friends (Komter and Vollebergh, 2005).

These observations suggest that humans use a strategy depending on the degree of relationship. For simplicity, we do not consider this kind of strategy. Moreover, there is evidence that chimpanzees’ cooperative behaviour is mainly limited to kin and reciprocating partners (Silk et al., 2005).

³ We note that envious-spiteful strategy is similar to the “in-group love and out-group hate” behaviour (Yamagishi and Mifune, 2009).

relatively small compared to the difference between rich and poor, formally

$$nb < a_2 - a_1, \quad (4)$$

and the cost of damage is small, in the sense that for all k

$$n + \frac{n^2 - k(n-2)}{2}qc < \frac{n^2 + k(n-2)}{2}qd \quad (5)$$

holds, then the envious-donor strategy replaces the envious one (invades the resident envious group and becomes dominant). In general, there is an invader bound for charity; under this bound envy is an ESS, above this bound the envious-donor strategy is the ESS. The reason for this is that when there are m rich envious-donators each giving b to t poor envious individuals, then the fitness difference between donators and recipients decreases with $tb + mb$. Hence, when the number of donators increases then the fitness difference decreases, and so the probability of damage also decreases.

In summary, charity can be considered as a “buy-off” strategy in the sense that a donator can decrease the damage of the envy of others, since the donation decreases the fitness difference, and thus the probability of damage also decreases.

6. Discussion

We introduced non-repetitive evolutionary games in which the basic income did not come from cooperative actions. We used a simple envy function (2) to describe the probability of damage done by envy.

We have found that envy outperforms the neutral strategy. We have also pointed out that when the cost is higher than the degree of the caused damage, then the neutral one wins in the Darwinian “struggle for existence”, but when the degree of damage is bigger than the cost, then the spiteful strategists win. Following Hamilton’s kin selection scenario we have shown that the envious-spiteful strategy wins against the spiteful one. We feel that other scenarios (introduced in the framework of prisoners dilemma (Nowak, 2006) which can guarantee that the cooperator strategy wins against the defector strategy) can also guarantee that envy wins against spitefulness. However, this needs further study since these scenarios consider repetitive games.

Finally, we assume that the “giving stage” precedes the “taking stage” in charity games. In the light of our results, other-regarding preference (envy, charity, Clytemnestra’s strategy) including egalitarianism motives (the first two) can be considered as consequences of Darwinian competition, i.e., individuals aim at increasing their own proportion rather than absolute contribution to the next generation, and other-regarding preference is a “method” for achieving that. Egalitarian motives decrease the fitness difference between group members and reduce the total cost of spiteful competition, which harmonizes with the general opinion that during human evolution the level of aggression (and so the cost of competition) decreases (Jones, 2008). Charity is a “buy-off” behaviour in the sense that the donator can decrease the damage caused by the envy of others. We do not state that only the defence against envy is the unique evolutionary reason for the emergence of charity, since there exist other Darwinian explanations of the origin of charity (e.g. food-sharing, Fruth and Hohmann, 2002 and reputation-building, Bereckei et al., 2007, namely, image scoring and indirect or direct reciprocity probably can explain the origin of charity (Nowak and Sigmund, 2005b) as well. A further possible Darwinian reasoning on the origin of human altruism is based on multilevel selection models, in which the survival probability of groups depends on the level of altruism within groups (Boza and Számadó, 2010; Bowles, 2006, 2009).

Envy and Clytemnestra’s strategy guarantee the positive relative advantage over the group while charity tries to preserve it. Further-

more, charity and Clytemnestra’s strategy do not spread in either purely neutral or spiteful groups, in this sense envy can guarantee the appearance and survival of these types of behaviour in our model.

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Appendix A.

In this section we present all background computations supporting our claims in full detail. In order to make switching between the main text and the calculations easier, here and in the main text we adopt the same structure of section numbering.

A.1. How Can Envy Spread in a Neutral Population?

Suppose there are n individuals, k of which are envious ($0 < k < n$). In the beginning each individual receives a random score; it can be thought as the measure of his/her fitness. These quantities are independent and identically distributed. Then envious individuals try to decrease someone else’s score. The probability of damage is $p(X, Y)$, where X and Y denote the scores of the attacker and of the victim, resp. The degree of damage is $d(X, Y)$, and a successful attack costs $c(X, Y)$.

A.1.1. Additive Damage

Suppose first that the damage is *additive*, that is, if Y is successfully attacked by X_1, \dots, X_ℓ , then it suffers a damage of $d(X_1, Y) + d(X_2, Y) + \dots + d(X_\ell, Y)$. Here and everywhere in the sequel we allow the scores to decrease below 0, though in practical situations the parameters of the model vary in such a way that negative scores have a negligibly small probability to occur.

The expected cost of envy is $(n-1)E[p(X, Y)c(X, Y)]$. The expected damage caused by an envious individual is $E[p(X, Y)d(X, Y)]$. The advantage of being a member of the envious group is that for them the number of potentially harmful competitors is one less than for neutral individuals, because no one attacks itself. Hence envy is advantageous if

$$(n-1)E[p(X, Y)c(X, Y)] < E[p(X, Y)d(X, Y)]. \quad (6)$$

Particularly, suppose that the initial scores only can take on two different values, $a_1 < a_2$, with equal probabilities, the cost is constant: $c(X, Y) = c$, and the damage is a fixed proportion of the victim’s score: $d(X, Y) = dY$. Finally, let the probability of a successful attack be

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

Here c, d, q, α are nonnegative parameters; the first three are typically small, compared to the initial scores. Taking $\alpha = 0$ implies that the probability of damage does not depend on the relative or absolute difference of the scores, it is always the same whenever a competitor of higher score is in sight. By increasing α one can make the damaging mechanism more and more sensitive to bigger differences.

We have then

$$E[c(X, Y)p(X, Y)] = \frac{1}{4}\Delta^\alpha qc, \quad E[d(X, Y)p(X, Y)] = \frac{1}{4}\Delta^\alpha qda_2,$$

where $\Delta = a_2 - a_1$.

Thus, envy is profitable if and only if

$$c < \frac{da_2}{n-1},$$

regardless how many envious individuals are there are in the population. In this case envy will completely spread without saturation: it is always worth switching from neutral to envious strategy.

A.1.2. Multiplicative Damage

Another possibility for multiple damage is the case where the effects of successive attacks are calculated from the actual, reduced score. In order that the cumulative damage be independent of the order of attacks we have to require that

$$d(X_2, Y - d(X_1, Y)) = d(X_1, Y - d(X_2, Y)).$$

This condition is fulfilled when $d(X, Y)$ does not depend on X , e.g., for $d(X, Y) = dY$. This leads to the model of *multiplicative damage*. In that case the result of ℓ simultaneous damages is a cumulative damage of proportion $1 - (1 - d)^\ell$.

Consider an individual with score y . Suppose there are ℓ envious strategists hanging around. Introduce $f(y) = E[p(X, y)]$ and let I_j be the indicator of the event that attacker j damages. The expected loss caused by all those malevolent individuals is

$$\begin{aligned} E \left[y \left(1 - \prod_{j=1}^{\ell} (1 - d^{I_j}) \right) \right] &= E \left[y \left(1 - \prod_{j=1}^{\ell} (1 - dI_j) \right) \right] \\ &= y(1 - (1 - df(y))^\ell). \end{aligned} \tag{6}$$

For envious individuals $\ell = k - 1$, while for neutral ones $\ell = k$. Hence, envy is profitable on average if

$$(n - 1)cE[f(Y)] + E[Y(1 - (1 - df(Y))^{k-1})] < E[Y(1 - (1 - df(Y))^k)],$$

that is, if

$$c < \frac{E[Yf(Y)(1 - df(Y))^{k-1}]}{E[f(Y)]} \cdot \frac{d}{n-1}.$$

The right hand side is a decreasing function of k , thus c and d can be chosen in such a way that a saturation level of envy should emerge: when the number of envious individuals reaches a certain threshold, it is no more profitable to switch from neutral to envious strategy. Thus polymorphism can be observed.

Particularly, with our choice of $p(X, Y)$ we have

$$f(a_1) = 0, \quad f(a_2) = \frac{1}{2} \Delta^\alpha q, \quad E[f(Y)] = E[p(X, Y)] = \frac{1}{4} \Delta^\alpha q,$$

hence the condition is

$$c < \left(1 - \frac{1}{2} \Delta^\alpha qd \right)^{k-1} \cdot \frac{da_2}{n-1}.$$

A.2. When Does Envy Outperform Spitefulness?

In the following calculations we adopt the terminology of human society, so we will speak about property, poor and rich people, instead of individuals with lower or higher fitness. Our only reason to do so is to make explanation simpler and clearer by using everyday terms. However, let us emphasize that our model is primarily of biological and not economical character.

Generalizing the model of the previous section we consider a population of size n , where there are k envious, m spiteful and $n - k - m$ neutral individuals, $0 \leq m \leq n - k$, that is, either the spiteful or the neutral type can be missing. Both the spiteful and the envious types want to damage other people's property at their own cost, but the envious one only attacks richer people, with success

probability depending on the difference of their score, while the spiteful one attacks everybody else without consideration. Neutral people do not cause any damage.

For the sake of simplicity, we assume again that the initial score only can take on two different values, $a_1 < a_2$, with equal probabilities. Let the amount of damage be fixed at d , and the cost of damaging at c . We suppose that damage is additive. We also suppose that a spiteful attacker succeeds with probability p_s , while an envious one succeeds with probability $q(Y - X)$, where X and Y denote the score of the attacker and of the victim, resp., and X must be less than Y . In our case it means that an envious poor individual attacks a rich one with probability $q(a_2 - a_1)$.

Let us compute and compare the expected loss for the three types.

Consider two arbitrary people. The probability that the first one makes a successful attack on the second one is $p_e = (1/4)q(a_2 - a_1)$, p_s , or zero, according that he/she is envious, spiteful, or neutral. Hence the expected loss of an envious person is $L_e = (n - 1)p_e c + (k - 1)p_e d + mp_s d$. Similarly, the expected loss of a spiteful person is $L_s = (n - 1)p_s c + kp_e d + (m - 1)p_s d$, while a neutral person's loss is $L_n = kp_e d + mp_s d$ on average. Comparing L_e , L_s , and L_n we can see that if $p_e < p_s$, which is plausible to presume, then $d < (n - 1)c$ (i.e., relatively high cost of damaging) implies $L_n < L_e < L_s$, and in the case when $d > (n - 1)c$ (low cost of damaging) the order is reversed.

Thus, envy outperforms spitefulness if the cost of damaging is relatively high. However, in that case the neutral strategy (do no harm) is even more profitable. Neutrals drop behind when the cost of damaging is low, but in that case spitefulness wins. How can the envious strategy spread after all? The answer may reside in family preference. Suppose there are n individuals, k of which form a family. Towards a family member they behave enviously with probability λ , and spitefully with probability $1 - \lambda$. All the other people are purely spiteful. All other parameters of the model coincide with those above. Then the average loss is

$$[(k - 1)\lambda p_e + (k - 1)(1 - \lambda)p_s + (n - k)p_s](c + d)$$

within the family, and $(n - 1)p_s(c + d)$ outside. The latter is always greater if only $p_e < p_s$ and $k > 1$.

Finally, let us emphasize that the total cost of competition decreases if the envy spreads at the expense of spitefulness, and this is even true without assuming family preference or the relatively high cost of damaging. The total loss in a population consisting of k envious, m spiteful, and $n - k - m$ neutral people is equal to $(n - 1)(c + d)(kp_e + mp_s)$, which increases if k grows and m decreases in such a way that $m + k$ remains fixed.

A.3. Clytemnestra's Strategy

In a mixed population of envious and neutral individuals Clytemnestra's strategy is to donate to "richer" individuals so as to inflict envious attacks on them, though she herself is neither spiteful, nor envious.

Suppose there are n individuals, k of which are envious, the others are neutral, except one, who follows Clytemnestra's strategy. We consider the same model as in the previous parts, that is, in the beginning everyone receives an initial score of a_1 or a_2 , at random, independently of each other. In this way there will be "poor" and "rich" individuals in the population. Then, if Clytemnestra is poor, she donates b to each wealthier competitor. Finally, envious individuals try to do harm to richer ones. As before, the cost and the amount of damage are constant c and d , resp. The probability of a successful attack is equal to q times the difference of the scores.

We will show that if $d < (n-1)c$, and $2n < (k-1)qd + (n-2)qc$, then the expected loss of Clytemnestra is less than that of other neutral or envious strategists, so thus she wins the competition.

The loss of a neutral individual comes from the damage by envious competitors. If Clytemnestra is rich, the expected damage is $(1/4)k\Delta qd$, and if she is poor, it is $(1/4)k(\Delta + b)qd$ (Δ still stands for the difference $a_2 - a_1$). Do not forget about Clytemnestra's gift, which is equal to b with probability $1/4$. Thus the average loss is

$$L_n = \frac{1}{4} \left[-b + \left(\Delta + \frac{b}{2} \right) kqd \right].$$

Clytemnestra's loss comes from the cost of donation and from the damage by envious individuals. The former is $(1/4)(n-1)b$, and the latter is $(1/4)k\Delta qd$ on the average. In the aggregate this is

$$L_c = \frac{1}{4} [(n-1)b + k\Delta qd].$$

Finally, consider an envious individual. It can get a donation of b with probability $1/4$. If Clytemnestra is poor, it damages everybody else (except her) with probability $(1/4)(\Delta + b)q$, and it suffers damage from other envious individuals with the same probability. If Clytemnestra is rich, it attacks her with probability $(1/2)\Delta q$, and damages everybody else with probability $(1/4)\Delta q$. It also suffers damage from other envious individuals with the same probability per capita. Altogether this makes an average loss of

$$L_e = \frac{1}{4} \left[-b + (n-1)\Delta qc + \frac{n-2}{2} bqc + (k-1)\Delta qd + \frac{k-1}{2} bqd \right].$$

From this $L_c < L_n$ immediately follows. On the other hand, one can transform inequality $L_c < L_e$ into the following equivalent form

$$\Delta q[(n-1)c - d] + \frac{b}{2} [(k-1)qd + (n-2)qc - 2n] > 0,$$

thus completing the proof.

A.4. When Is Charity Profitable?

Consider a population of n individuals. They all are envious, and k of them are charitable, $1 \leq k \leq n-1$. In the beginning each individual receives a random score, then charitable individuals donate: they give every poorer one a certain amount. Finally all individuals act according to the rules of envy; they try to damage wealthier competitors' fitness.

We assume again that the initial score only can take on two different values, $a_1 < a_2$, with equal probabilities. Introduce the notations $m = n - k$, and $\Delta = a_2 - a_1$. Let the donation be equal to b , the damage to d , and the cost of damaging to c , where b , c , and d are suitable positive constants. It is reasonable to suppose that b is relatively small compared to Δ , so that charity would not change fitness order in the population, i.e., $\Delta > nb$. We suppose again that the probability of successful damaging is proportional to the difference of scores, that is, if X and Y denote the fitness of the attacker and of the victim, respectively, $X < Y$, then the probability of damage is $q(Y-X)$.

We still do not care if someone's score decreases below zero. This cannot happen if the initial fitness is large enough: $a_1 > (n-1) \max\{c, d\}$. We remark that in real-world circumstances c is usually smaller than d .

Our aim is to find conditions under which charity is profitable in an envious environment.

We refer to the charitable group as group A , all the other individuals are referred to as group B . Let U and V denote the number of rich individuals in groups A and B , resp. They are independent random variables with binomial distribution of parameter $1/2$ and order k and m , resp.

Let us review the possible sources of loss in both groups:

- (i) Donation from A to B .
- (ii) Attacks within group A .
- (iii) Attacks within group B .
- (iv) Attacks made by the poor of A on the rich of B .
- (v) Attacks made by the rich of A on the rich of B .
- (vi) Attacks made by the poor of B on the rich of A .

The expected number of events in the above cases can be computed in the following way:

- (i) $N_1 = E[U(m-V)] = \frac{km}{4}$.
- (ii) $N_2 = E[U(k-U)q(\Delta - (n-V)b)]$
 $= \frac{k(k-1)}{4} \left(\Delta - \left(n - \frac{m}{2} \right) b \right) q$.
- (iii) $N_3 = E[V(m-V)q(\Delta - Ub)] = \frac{m(m-1)}{4} \left(\Delta - \frac{k}{2} b \right) q$.
- (iv) $N_4 = E[(k-U)Vq(\Delta - Ub)] = \frac{km}{4} \left(\Delta - \frac{k-1}{2} b \right) q$.
- (v) $N_5 = E[UVq(n-U-V)b] = E[UV(k-U)]bq + E[UV(m-V)]bq$
 $= \frac{km}{4} \cdot \frac{n-2}{2} bq$.
- (vi) $N_6 = E[U(m-V)q(\Delta - (n-V)b)]$
 $= E[U(m-V)](\Delta - kb)q - E[U(m-V)^2]bq$
 $= \frac{km}{4} (\Delta - kb)q - \frac{m(m+1)}{4} \cdot \frac{k}{2} bq$
 $= \frac{km}{4} \left(\Delta - \left(n - \frac{m-1}{2} \right) b \right) q$.

Hence the total expected loss of group A is equal to $T_A = N_1b + N_2(c+d) + N_4c + N_5c + N_6d$, while that of group B is equal to $T_B = -N_1b + N_3(c+d) + N_4d + N_5d + N_6c$. From this the average loss of a charitable individual is

$$L_A = \frac{T_A}{k} = \frac{1}{4} \left[(n-1)\Delta q(c+d) - \left(\frac{n^2 + k(n-2)}{2} q(c+d) - m(1+nqc) \right) b \right],$$

and the average loss of other individuals is

$$L_B = \frac{T_B}{m} = \frac{1}{4} [(n-1)\Delta q(c+d) - k(1+nqc)b].$$

Therefore, charity is profitable, if

$$n + \frac{n^2 - k(n-2)}{2} qc < \frac{n^2 + k(n-2)}{2} qd. \quad (7)$$

It is quite surprising that this condition does not contain b at all. If (7) holds, charity increases the expectation of the average result in both groups, and the bigger is the donation b , the greater is the gain. One may think it cannot be true for large values of b , since it is obviously not worth giving a poor individual more than the damage it would otherwise do. That is, b should definitely be less than $q\Delta d$. That is true, and is not in contradiction with (7), because our computation above is only valid when $0 \leq b \leq \Delta/n$. If b grows beyond Δ/n , more and more correction terms appear in L_A and L_B , and finally it turns out that further increase in the gift is no more useful. In fact, from condition (7) it follows that $b < q\Delta d$. Indeed, $q\Delta d > qdnb$ by supposition, and (7) implies that

$$qdn > \frac{2n^2 + (n^2 - k(n-2))nqc}{n^2 + k(n-2)} \geq \frac{2n^2 + (n^2 - n(n-2))nqc}{n^2 + n(n-2)} = \frac{n+qc}{n-1} > 1.$$

From (7) we obtain a lower bound for the size of the charitable group:

$$k > \frac{n}{n-2} \cdot \frac{2+nq(c-d)}{q(c+d)}.$$

Condition (7) is satisfied by every $k = 1, 2, \dots, n-1$, if

$$n + \frac{n^2 - (n-2)}{2} qc < \frac{n^2 + (n-2)}{2} qd.$$

Interestingly, this can hold even in the case when the cost of an attack is slightly bigger than the damage it can cause.

Let us add that the total loss of the whole population is

$$\begin{aligned} T_A + T_B &= (N_2 + N_3 + N_4 + N_5 + N_6)(c+d) \\ &= \frac{1}{4} \left[n(n-1)\Delta - \frac{k(n^2 + (n-2)k)}{2} b \right] q(c+d), \end{aligned}$$

which is a decreasing function of the size k of the charitable group. Thus, charity decreases the total cost of competition.

References

- Berecki, T., Birkas, B., Kerekes, Zs., 2007. Public charity offer as a proximate factor of evolved reputation-building strategy: an experimental analysis of a real-life situation. *Evol. Hum. Behav.* 28, 277–284.
- Bowles, S., 2006. Group competition, reproductive leveling, and the evolution of human altruism. *Science* 314, 1569–1572.
- Bowles, S., 2009. Did warfare among ancestral hunter–gatherers affect the evolution of human social behaviors? *Science* 324, 1293–1298.
- Boza, G., Számadó, S., 2010. Beneficial laggards: multilevel selection, cooperative polymorphism and division of labour in threshold public good game. *BMC Evol. Biol.* 10, 336.
- Brosnan, S.F., de Wall, F.B.M., 2003. Monkeys reject unequal pay. *Nature* 425, 297–299.
- Brosnan, S.F., Schiff, H.C., de Wall, F.B.M., 2005. Tolerance for inequity may increase with social closeness in chimpanzees. *Proc. Roy. Soc. B* 272, 253–258.
- Burkart, J.M., Fehr, E., Efferson, C., van Schaik, C.P., 2007. Other-regarding preferences in a non-human primate: common marmosets provision food altruistically. *PNAS* 104, 19762–19766.
- Dawes, C.T., Fower, J.H., Johnson, T., McElreath, R., Smirnov, O., 2007. Egalitarian motives in human. *Nature* 446, 794–796.
- Dobson, F.S., Chesser, R.K., Zinner, B., 2000. The evolution of infanticide: genetic benefits of extreme nepotism and spite. *Ethol. Ecol.* 12, 131–148.
- Dutton, D.G., Boyanowsky, E.O., Bond, M.H., 2005. Extreme mass homicide: from military massacre to genocide. *Aggress. Viol. Behav.* 10, 437–473.
- Fehr, E., Bernhard, H., Rockenbach, B., 2008. Egalitarianism in young children. *Nature* 454, 1079–1084.
- Fehr, E., Fischbacher, U., 2003. The nature of human altruism. *Nature* 425, 785–791.
- Fehr, E., Schmidt, K., 1999. A theory of fairness, competition, and cooperation. *Q. J. Econ.* 114, 817–868.
- FitzGerald, G.J., 1992. Egg cannibalism in sticklebacks: spite or selfishness. *Behav. Ecol. Sociobiol.* 30, 201–206.
- Foster, G.M., 1967. *Tzintzuntzan: Mexican Peasant in a Changing World*. The Little, Brown and Company, Boston.
- Fruth, B., Hohmann, G., 2002. How bonobos handle hunts and harvests: why share food? In: Boesch, C., Hohmann, G., Marchant, L. (Eds.), *Behavioural Diversity in Chimpanzees and Bonobos*. Cambridge University Press, pp. 231–243.
- Garay, J., 2009. Cooperation in defence against a predator. *J. Theor. Biol.* 257, 45–51.
- Garay, J., Varga, Z., 2005. Evolutionary dynamics for economic behaviour: competitor versus optimization. *PU.M.A* 16, 399–409.
- Garay, J., 2007. Relative advantage and fundamental theorems of natural selection. In: Deutsch (Ed.), *Mathematical Modelling of Biological Systems*, vol. II. Birkhauser, Boston, Basel, Berlin, pp. 63–74.
- Goel, A.M., Thakor, A.V., 2005. Green with envy: implications for cooperate investment distortions. *J. Business* 78, 2255–2287.
- Guth, W., Peleg, B., 2001. Are the profit-maximisers the best survivors? *J. Econ. Behav. Org.* 11, 479–499.
- Hamilton, W.D., 1970. Selfish and spiteful behaviour in an evolutionary model. *Nature* 228, 1218–1220.
- Hamilton, W.D., 1971. Selection of selfish and altruistic behaviour in some extreme model. In: Eisenberg, J.F., Dillon, W.S. (Eds.), *Man and beast: comparative social behavior*. Smithsonian Institution, Washington, DC, pp. 57–91.
- Hansen, R.G., Samuelson, W.F., 1988. Evolution in economic game. *J. Econ. Behav. Org.* 10, 315–338.
- Hill, S.E., Buss, D.M., 2006. Envy and positional bias in the evolutionary psychology of management. *Manage. Decis. Econ.* 27, 131–143.
- Hofbauer, J., Sigmund, K., 1998. *Evolutionary Games and Population Dynamics*. Cambridge Univ. Press.
- Jankowiak, W., Diderich, M., 2000. Sibling solidarity in a polygamous community in the USA: unpacking inclusive fitness. *Evol. Hum. Behav.* 21, 125–139.
- Johnson, T., Dawes, C., Fower, J.H., McElreath, R., Smirnov, O., 2009. The role of egalitarian motives in altruistic punishment. *Econ. Lett.* 102, 192–194.
- Jones, D., 2008. Human behaviour: killer instincts. *Nature* 451, 512–515.
- Kasper, C., Voelkl, B., Huber, L., 2008. Tolerant mouth-to-mouth food transfers in common marmosets. *Primates* 49, 153–156.
- Knowlton, N., Parker, G.A., 1979. An evolutionary stable strategy approach to indiscriminate spite. *Nature* 279, 419–421.
- Komter, A., 2010. The evolutionary origin of human generosity. *Int. Sociol.* 25, 443–464.
- Komter, A., Schuyt, K., 1993. Gechsenken en relaties [gift and relationships]. *Beleid en Maatschappij*, XX, 277–285.
- Komter, A., Vollebbergh, W.A.M., 2005. Solidarity in dutch families: Family ties and strain? *J. Fam. Issues* 23, 171–188.
- Lehmann, D.R., 2001. The impact of altruism and envy on competitive behaviour and satisfaction. *Int. J. Res. Mark.* 18, 5–7.
- Lehmann, L., Keller, L., West, S., Roze, D., 2007. Group selection and kin selection: two concepts but one process. *PNAS* 104, 6736–6739.
- Leimar, O., Hammerstein, P., 2001. Evolution of cooperation throughout indirect reciprocity. *Proc. Roy. Soc. B* 264, 745–753.
- Li, Y., Jin, X., Su, X., Kong, Peng, C., 2010. Cooperation and charity in spatial public goods game under different strategy update rules. *Physica A* 389, 1090–1098.
- Maynard Smith, J., Price, G.R., 1973. The logic of animal conflict. *Nature* 246, 15–18.
- Nowak, M.A., Sigmund, K., 2005a. Evolution of indirect reciprocity. *Nature* 437, 1291–1298.
- Nowak, M.A., Sigmund, K., 2005b. Evolution of indirect reciprocity. *Nature* 437, 1291–1298.
- Nowak, M.A., 2006. Five rules for the evolution of cooperation. *Science* 314, 1560–1563.
- Ohtsuki, H., Iwasa, Y., 2006. The leading eight: social norms that can maintain cooperation by indirect reciprocity. *J. Theor. Biol.* 239, 435–444.
- Pusey, A., Murray, C., Wallauer, W., Wilson, M., Wroblewski, E., Goodall, J., 2008. Severe aggression among female *Pan troglodytes schweinfuthii* at gombe national park, tanzania. *Int. J. Primatol.* 29, 949–973.
- Range, F., Horn, L., Viranyi, Zs., Huber, L., 2009. The absence of reward induces inequity aversion in dog. *PNAS* 106, 340–345.
- Schaffer, M.E., 1989. Are the profit-maximiser the best survivors? *J. Econ. Behav. Org.* 12, 29–45.
- Scheuring, I., 2010a. Coevolution of honest signaling and cooperative norms by cultural group selection. *BioSystems* 101, 79–87.
- Scheuring, I., 2010b. Egalitarian motive in punishing defectors. *J. Theor. Biol.* 264, 1293.
- Schoeck, H., 1966. *Der Neid. Eine Theorie der Gesellschaft*. Verlag Karl Albert, Freinburg im Breisgau, München.
- Segal, N.L., Hershberger, S.L., 1999. Cooperation and competition between twins: findings from prisoner's dilemma game. *Evol. Hum. Behav.* 20, 29–51.
- Silk, J.B., Brosnan, S.F., Vonk, J., Henrich, J., Povinelli, D.J., Richardson, A.S., Lambeth, S.P., Mascaró, J., Schapiro, S.J., 2005. Chimpanzees are indifferent to the welfare of unrelated group members. *Nature* 437, 1357–1359.
- Smith, E.A., 1985. Inuit foraging groups: some simple models incorporating conflicts of interest, relatedness and central-place sharing. *Ethol. Sociobiol.* 6, 27–47.
- Smith, R.H., Kim, S.H., 2007. Comprehending envy. *Psych. Bull.* 133, 46–64.
- Takimoto, A., Hika Kuroshima, H., Fujita, K., 2009. Capuchin monkeys (*cebus apella*) are sensitive to others' reward: an experimental analysis of food-choice for conspecifics. *Anim. Cogn.* 13, 161–249.
- Taylor, C., Chen, J., Iwasa, Y., 2007. Cooperation maintained by fitness adjustment. *Ecol. Evol. Res.* 9, 1023–1041.
- Townsend, S.W., Slocombe, K.E., Thompson, M.E., Zuberbohler, K., 2007. Female-led infanticide in wild chimpanzees. *Curr. Biol.* 17, 335–356.
- Vickery, W.L., Brown, J.S., FitzGerald, G.J., 2003. Spite: altruism's evil twin. *Oikos* 102, 413–416.
- Yamagishi, T., Mifune, N., 2009. Social exchange and solidarity: in-group love or out-group hate. *Evol. Hum. Behav.* 30, 229–237.
- Zizzo, D.J., 2003. Money burning and rank egalitarianism with random dictator. *Econ. Lett.* 81, 263–266.