



# Bet hedging based cooperation can limit kin selection and form a basis for mutualism

Joost C.M. Uitdehaag\*

Harnas 70, 5346 WR Oss, The Netherlands

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## ABSTRACT

Mutualism is a mechanism of cooperation in which partners that differ help each other. As such, mutualism opposes mechanisms of kin selection and tag-based selection (for example the green beard mechanism), which are based on giving exclusive help to partners that are related or carry the same tag. In contrast to kin selection, which is a basis for parochialism and intergroup warfare, mutualism can therefore be regarded as a mechanism that drives peaceful coexistence between different groups and individuals. Here the competition between mutualism and kin (tag) selection is studied. In a model where kin selection and tag-based selection are dominant, mutualism is promoted by introducing environmental fluctuations. These fluctuations cause reduction in reproductive success by the mechanism of variance discount. The best strategy to counter variance discount is to share with agents who experience the most anticorrelated fluctuations, a strategy called bet hedging. In this way, bet hedging stimulates cooperation with the most unrelated partners, which is a basis for mutualism. Analytic results and simulations reveal that, if this effect is large enough, mutualistic strategies can dominate kin selective strategies. In addition, mutants of these mutualistic strategies that experience fluctuations that are more anticorrelated to their partner, can outcompete wild type, which can lead to the evolution of specialization. In this way, the evolutionary success of mutualistic strategies can be explained by bet hedging-based cooperation.

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## 1. Introduction

A mechanism of cooperation based on the differences between two partners is called mutualism. This can take the form of interspecific mutualism, which is important e.g. in ecology, and intraspecific mutualism, which is important in e.g. the human economy (Trivers, 1971; Herre et al., 1999; Clutton-Brock, 2002; Bergstrom and Lachmann, 2003; Ferriere et al., 2002; Sachs et al., 2004; Foster and Wenseleers, 2006; Bronstein, 2009; Weyl et al., 2010). A general characteristic of mutualism is that the partners are mutually dependent because they are specialized. For instance, professional people or enterprises are specialists that have mutualistic interactions with customers and suppliers (Trivers, 1971; Boyd and Richerson, 1988). In the animal world, queen bees and fighter ants are specialists that have mutualistic interactions with their colonies (Sachs et al., 2004; Nowak et al., 2010; West, 2010). Specialists are defined as being able to do a few things well, in contrast to generalists, who can do many things poorly (Wilson and Yoshimura, 1994). Interestingly, in the evolution of the mutualism, specialists have increased their fitness in the context

of the group, at the cost of decreasing fitness in isolation. Most modern professionals or queen bees would not survive long without their group. Because mutualism causes partners to become increasingly dependent on each other, it is a basis for peaceful coexistence in societies (Clutton-Brock, 2002).

In promoting peaceful coexistence, mutualism is antagonized by kin selection (Zahavi, 1995; Clutton-Brock, 2002). Whereas mutualism is based on cooperation with non-related individuals, kin selection and the related inclusive fitness theory are based on cooperation with related partners (Hamilton, 1964). Associated with kin selection are so-called mechanisms of tag-selection. If a single gene or meme is considered, then all partners with a different allele can be called non-kin, and all partners with a similar allele kin. At the same time, if the allele is associated with a recognizable tag, preferential collaboration with kin amounts to preferential collaboration with tag-carriers. Important examples of tag selection mechanisms are the green beard, beard chromodynamics, and 'phenotypic similarity' (Dawkins, 1976; Riolo et al., 2001; Nowak and Sigmund, 2005; Nowak, 2006; Janssen and van Baalen, 2006; Antal et al., 2009). In short, both kin selection and tag-based selection oppose mutualistic strategies that promote cooperation with non-related and non-tagged partners. Consistently, it has been shown that kin and tag-based selection are a theoretical basis for parochialism, war and other attempts to

\* Tel.: 0031412624825.

E-mail address: [joostuitdehaag@zonnet.nl](mailto:joostuitdehaag@zonnet.nl)

damage non-kin, because those behaviours lead to enhanced survival of kin (Hamilton, 1964; Bernard et al., 2006; Choi and Bowles, 2007; Efferson et al., 2008).

Compared to hunter-gatherer societies, modern society is characterized by a relative absence of intergroup warfare, and by tolerance and non-violence to strangers (Sober and Wilson, 1998; Bowles, 2006). This behaviour is stimulated in many moral systems, where it has been summarized as the golden rule ('love your neighbour as yourself, Armstrong, 2007). Therefore, it appears as if, historically, mutualism has gained the upper hand over kin selection and parochialism (Choi and Bowles, 2007). However, this dominance of mutualism is not completely understood. It is known that mutualism can be modelled by a Prisoner's Dilemma (PD) (Trivers, 1971), and that tit-for-tat-like strategies can sustain mutualistic cooperation in presence of cheaters (Frank, 1994; Doebeli and Knowlton, 1998; Bergstrom and Lachmann, 2003; Yamamura et al., 2004). However, this does not explain how mutualism can outcompete kin selection (for reviews on cooperation see Fehr and Fischbacher, 2003; Nowak and Sigmund, 2005; Nowak, 2006).

Partner selection is an important factor in mutualism (Sachs et al., 2004; Foster and Wenseleers, 2006), and the boundary with kin selection can be understood in terms of selection of a non-related or a related partner. A related partner brings the inherent genetic advantages of kin selection, but a non-related partner can be preferred if she gives access to exclusive resources. Nevertheless, in simulations where, a tag-based strategy was introduced in a group of freely sharing tit-for-tat players (Uitdehaag, 2009), this resulted in tag-carriers exploiting the untagged players until the latter were extinct. This showed that, under equal payoffs, a strategy that selects related partners dominates more freely sharing and more mutualistic strategies. The central question of this work is therefore: which level of mutualistic advantages can beat kin selection. In other words: how can a player, if he has a choice, be triggered to cooperate with non-kin instead of kin?

The question is approached here by introducing an opportunity for mutualism in situations where kin selection and tag-based strategies are dominant. This is done by introducing a stochastically varying environment, which allows some individuals to obtain resources at a time when other individuals are lacking resources. Evolution in such a varying environment is the domain of bet hedging theory (Lewontin and Cohen, 1969; Philippi and Seger, 1989; Frank and Slatkin, 1990; Grafen, 2000; Kussell and Leibler, 2005; Roff, 2008; Ellner, 2009) and therefore relations from that field can be used to describe cooperation and mutualism. This gives new insight into how mutualism can stabilize groups, under which conditions it can outcompete kin selection, and how an initial mutualistic relation can evolve to generate specialized partners.

## Variance discount

First, the theory of evolution in a varying environment and bet hedging statistics need to be briefly introduced. It is well-known that if random variations in the environment lead to random variations in offspring, this leads to substantially fewer total offspring after  $t$  generations than without such variation. Suppose a species produces 2, 2, 2, 2, 2 and 2 offspring in successive years and another species produces 3, 1, 3, 1, 3 and 1 offspring. Then the first species ends up with  $2 \times 2 \times 2 \times 2 \times 2 \times 2 = 64$  members, and the second species with only  $3 \times 1 \times 3 \times 1 \times 3 \times 1 = 27$  members. Nevertheless, all individuals of species 1 and 2 have invested equal effort: the original founding members both have raised  $2+2+2+2+2+2=3+1+3+1+3+1=12$  young. Solely by spreading its offspring, species 1 has more successfully

proliferated itself. As the difference between 64 and 27 shows, the effects can be quite large.

More formally, suppose a player A exist for a  $t$  number of events  $i$ , where  $i$  is e.g. a generation or a season ( $i \in \mathbb{N}$ , all  $i$  span equal timeframes). In each event  $i$ , the player produces  $l_i$  offspring. If  $l_i$  fluctuates with a variation  $\delta_i$  around the arithmetic average  $\lambda$ , one can define  $l_i = \lambda + \delta_i$ , where  $\lambda = (1/t) \cdot \sum_{i=1}^t l_i$ . Because  $\delta_i$  is a variation:  $\sum_{i=1}^t \delta_i = 0$ . The total amount of descendants after  $t$  events, for player A, is then

$$N_{\text{total},t}^A = \prod_{i=1}^t l_i = \prod_{i=1}^t (\lambda + \delta_i) \quad (1)$$

Under the above restrictions,  $N_{\text{total},t}^A$  maximizes if  $(\lambda + \delta_1) = (\lambda + \delta_2) = (\lambda + \delta_3) = \dots = (\lambda + \delta_t)$ , which only occurs if  $\delta_i = 0$  for every  $i$ . We will call this the maximum offspring condition. Proofs for this can be found in the evolution literature (Yoshimura and Jansen, 1996), and in statistical mechanics.  $N_{\text{total},t}^A$  therefore maximizes with zero variation, and any variation will reduce the amount of offspring.

The exact reduction in total offspring, due to variations in offspring, can be quantified for the case of  $\delta_i \ll l_i$  (small variation) (Lewontin and Cohen, 1969; Yoshimura and Jansen, 1996). If the variance in the dataset  $\{l_1, \dots, l_t\}$  is defined as  $\sigma_A^2 = (1/t) \sum_{i=1}^t \delta_i^2$ , then

$$N_{\text{total},t}^A \approx \left( \lambda \left( 1 - \frac{\sigma_A^2}{2\lambda^2} \right) \right)^t \quad (2)$$

Eq. (2) is known as the variance discount equation, it states that the total offspring  $N_{\text{total},t}^A$  is always less than  $\lambda^t$ , because  $\lambda$  is reduced by the variance discount factor in the inner brackets.

## 2. Bet hedging based sharing is an evolutionarily stable strategy

If variation reduces proliferative success, reducing variation is a way of increasing fitness. Such a strategy is known as bet hedging (Philippi and Seger, 1989; Ellner, 2009). Its role in cooperation has remained unexplored, although there is interest in variation as cooperation-enhancing mechanism (Wagner, 2003; McNamara et al., 2004; Helbing and Yu, 2009; Santos et al., 2008).

In the human setting many variations occur that can be alleviated through cooperation. For instance, when a successful hunter has caught more than she can eat, this is a positive variation. If she has no success, this is a negative variation. If a group of hunters with varying success are sharing meat, they are in fact bet hedging. Other examples are: care for the sick and mending damage on capital goods. Interestingly these situations were also mentioned in relation to Prisoner's Dilemma (PD) payoff structures (Trivers, 1971, 2006; Boyd and Richerson, 1988; Frean, 1991; Nowak and Sigmund, 1994). Bet hedging is therefore an elegant underlying mechanism to explain the payoffs in the PD, on of the most intensely studied cooperative settings. Otherwise, these payoffs are merely assumed (Boyd and Richerson, 1988).

To further show that bet hedging is a basis for cooperation, a previously published computational model was adapted (Uitdehaag, 2009), in which a population plays an alternate repeated PD game (Trivers, 1971). In this model, the cooperative tit-for-tat strategy (Axelrod and Hamilton, 1981) is evolutionarily stable if players are allowed to remember, and preferentially share with, players who previously shared with them. It is known that memory is important for cooperation (Milinski and Wedekind, 1998). Furthermore, it is a fixed population model, in which a certain fraction of players dies,

and is replaced by offspring of more successful strategies (for model details see Appendix A). This is a difference with the analytical result Eq. (2) that assumes a growing population. The simulations therefore test if bet hedging can also be a basis for cooperation in a fixed population.

The simulations were first run in the absence of reciprocal sharing, with players experiencing variation in offspring levels. In this setting, it is confirmed that a mutant with decreased levels of variation is able to dominate the wild type population, even from a small starting population (not shown). In a next step, reciprocal sharing was introduced, and the cooperative tit-for-tat strategy was allowed, which quickly outcompetes the non-sharing strategy (Fig. 1A). This confirms the dominance of tit-for-tat in a PD game (Axelrod and Hamilton, 1981). More interestingly, however, through sharing the invading strategy manages to reduce the effective level of variation (Fig. 1B). The tit-for-tat strategy therefore behaves as a bet-hedging strategy.

### 3. The fluctuations of optimal sharing partners need to be anticorrelated

As a next step, the optimal partners for sharing are investigated. Bet hedging based sharing requires a donor with a surplus and a receiver in need. Moreover, two players can only develop a cooperative relationship if their status of donor and receiver alternates in time (Nowak and Sigmund, 1994). Therefore, only partners who experience fluctuations that are out of phase can productively share.

Let us define player B as partner to player A. At event  $i$ , B has offspring  $m_i$  which varies with  $\varepsilon_i$  around the arithmetic average  $\eta$ :

$$\eta = \frac{1}{t} \sum_{i=1}^t m_i \text{ and } \sum_{i=1}^t \varepsilon_i = 0$$

Let A and B engage in a sharing relationship in which they share an amount that allows  $s_i$  offspring. In order not to confound the argument, it is assumed that sharing is cost-free, and that the value of the share is absolute (meaning that it varies not with player perspective:  $(\delta l_i / \delta s_i) = (\delta m_i / \delta s_i)$ ). In this way, the effects of the timing of sharing can best be illustrated. The offspring of A

and B can be expressed as

$$l_i = \lambda + \delta_i - s_i \text{ and } m_i = \eta + \varepsilon_i + s_i \quad (3)$$

If the share  $s_i$  has a positive value, player A donates a share to B. If  $s_i$  has a negative value, B donates a share to A. Both players will not want to be net payers after  $t$  events, so

$$\sum_{i=1}^t s_i = 0, \text{ which leads to } \sum_{i=1}^t (\delta_i - s_i) = 0, \text{ and also } \sum_{i=1}^t (\varepsilon_i + s_i) = 0$$

The total offspring after  $t$  events is:

$$N_{\text{total}, t}^A = \prod_{i=1}^t (\lambda + \delta_i - s_i) \text{ and } N_{\text{total}, t}^B = \prod_{i=1}^t (\eta + \varepsilon_i + s_i) \quad (4)$$

When the maximum offspring condition is imposed, then  $N_{\text{total}, t}^A$  and  $N_{\text{total}, t}^B$  maximize, respectively, if  $\delta_i - s_i = 0$  and  $\varepsilon_i + s_i = 0$ , for every  $i$ . Therefore

$$s_i = \delta_i = -\varepsilon_i \quad (5)$$

Eq. (5) states that bet-hedging based sharing works optimally if the offspring fluctuations of A and B are perfectly anticorrelated, and both sides hand out all surplus above their average  $\lambda$  or  $\eta$ . This assumes that A and B can perfectly assess the value of the surplus  $\delta_i$  or  $\varepsilon_i$  (see below). However, the conclusion is general: whenever A has a good time, B has to have a bad time.

In order to realize the condition of Eq. (5), A and B can follow the most simple, but also the most complete, sharing arrangement: both pool their surpluses, and both take half of the pool. This leads to the following expression for their offspring production,

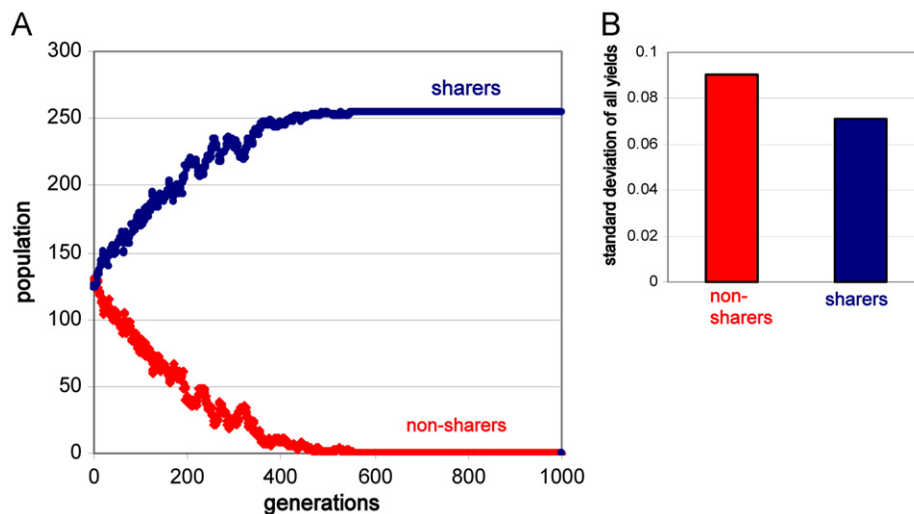
$$l_i = \lambda + \frac{1}{2}(\delta_i + \varepsilon_i) \quad (6)$$

$$m_i = \eta + \frac{1}{2}(\delta_i + \varepsilon_i) \quad (7)$$

The new variation  $1/2(\delta_i + \varepsilon_i)$  can be substituted for  $\delta_i$  in the variance discount Eq. (2), and it can be investigated under which conditions A and B, through sharing, are better off (see Appendix B.1). This leads to the following condition:

$$\frac{\sigma_{AB}}{\sigma^2} < 1 \quad (8)$$

Here,  $\sigma_{AB}$  is the covariance between the fluctuations of A and B,  $\sigma_{AB} = (1/t) \sum_{i=1}^t \delta_i \varepsilon_i$ . In addition, the simple sharing



**Fig. 1. Sharers dominate non-sharers in a game with varying individual yields.** (A) Sharers follow the strategy of giving surpluses to players that they received from before ('friends') or, if there is no friend available, a random player. This strategy resembles generous tit-for-tat (Nowak, 2006). Non-sharers follow the strategy of never sharing. (B) The result of sharing is a lower average standard deviation which results in better survival. Standard deviations were calculated over the yields of all players per strategy over the first 400 rounds.

arrangement between A and B works only if their variances are equal (see Appendix B.1). Therefore:  $\sigma^2 \equiv \sigma_A^2 = \sigma_B^2$  where  $\sigma_B^2 = (1/t) \sum_{i=1}^t e_i^2$ .

Eq. (8) says that A and B can only productively share if the covariance of the fluctuations they experience is smaller than their variance. Eq. (8) is nothing more than a Pearson correlation coefficient  $\rho_{AB}$ , and Eq (8) can therefore also be written as  $\rho_{AB} < 1$ . The smaller the covariance term (the more anticorrelation), the more the variance discount is dampened, and the more productive the collaboration is. Eq. (8) is a general condition for bet-hedging induced cooperation between A and B.

A few expansions of Eq (8) are worthwhile mentioning. First, under the simplified conditions above, a mutant A' has more fitness than A if its covariance with B is smaller (see Appendix B.2)

$$\sigma_{A'B} < \sigma_{AB} \quad (9)$$

Secondly, if A and B are allowed to only to share a portion  $s_i$  of their surpluses, instead of pooling them fully, a stable cooperative relationship can also be formed if  $\sigma_A^2 \neq \sigma_B^2$ , for which the conditions are somewhat more complex (see Appendix B.3)

Thirdly, if cooperation is considered in a group of more than two players, the fluctuations can be reformulated as a cooperation matrix. This leads to the result that for a stable group of sharers, the trace of the matrix of shares and variations is ideally zero. This has interesting implications for group diversity (see Appendix C).

#### 4. Bet hedging based sharing is a basis for mutualism

The source of environmental fluctuations is partly stochastic, for instance the weather could influence offspring levels. However, another part results from the response of the individual to these fluctuations. For instance, the impact of a period of food-shortage will be less for individuals with a low metabolism than for individuals with a high metabolism. In this manner, the offspring fluctuations are related to an individual's geno- or memotype, and in this way Eq. (8) can be applied to mutualism.

It needs to be noted that, if some genotype would be better adapted than average to a particular fluctuation in the environment, this would simply be a competitive advantage, and not a basis for mutualism. What is also needed, is that the same genotype does worse at other events, so it needs help in those conditions. For mutualism requiring help is just as essential as contributing meaningfully. Therefore, particularly geno- or memotypes that are a specialization are suitable to engage in mutualistic interactions.

As illustration, assume that under the metabolism phenotype above lies a gene for muscle development. One allele  $M$  codes for increased muscularity, which does well in times of abundant wildlife, because it leads to increased hunting success. However, the allele concomitantly increases metabolism of the carrier, because of the energy requirement of the muscle. Now, another allele  $S$  of the same gene codes for decreased muscularity, and thus less hunting success, but also decreased energy use. The advantage of this allele is that it increases stamina in times of food shortage. Because both alleles have pros and cons, carrier  $A^M$  of allele  $M$  would do well to collaborate with a carrier  $B^S$  of allele  $S$ . In times of abundant game,  $A^M$  would catch so much there would be enough to share with  $B^S$ . In times of food shortage, the sickly  $A^M$  could be cared for by  $B^S$ . Both would benefit more than if  $A^M$  would collaborate with another carrier of  $M$  (M-type), or if  $B^S$  would collaborate with another carrier of  $S$  (S-type), and thus  $A^M$  and  $B^S$  have a mutualistic relation.

#### 5. Mutualism can dominate kin selection

Next, the antagonism between mutualism and kin selection is studied (Clutton-Brock, 2002). In kin selection, the fitness effects of helping others are proportional to the relatedness to the partner (Hamilton, 1964). In mutualism, fitness is expected to be inversely proportional to relatedness. As pointed out above, it would be extremely interesting to see if (and when) mutualism can prevail over kin selection.

The mathematical treatment of kin selection is terms of inclusive fitness explicitly lists the relatedness  $R$  (Hamilton, 1964; Grafen, 2006; van Veelen, 2007; Fletcher and Doebeli, 2009; Nowak, 2010). Starting from this equation, it is possible to incorporate the impact of variance discount on inclusive fitness (see Appendix D.1). The variance, in turn, can be split into stochastic and genetic components, and for this latter component, the variance discount penalty minimizes if there is cooperation with dissimilar partners (Appendix D.2). If the specific example of mutualism between the  $S$  and  $M$  alleles is then taken (Appendix D.3), this leads to the following condition under which the benefits of variance reduction outweigh the cost of missed inclusive fitness

$$\sigma_{\alpha\beta} < \sigma^2 - \sigma_p^2 \frac{\Delta R}{R_M} \quad (10)$$

Here  $\sigma_{\alpha\beta}$  is the covariance between the genetically encoded offspring fluctuations of  $A^M$  and  $B^S$ .  $\sigma^2$  is the genetically encoded variance of an individual player, and  $\sigma_p^2$  is the stochastic variance that can be dampened even when collaborating with kin (see Appendixes D.2 and D.3).  $\Delta R$  is the difference in relatedness between  $A^M$  and  $B^S$ , and  $R_M$  is the relatedness between  $A^M$  and another M-type player.

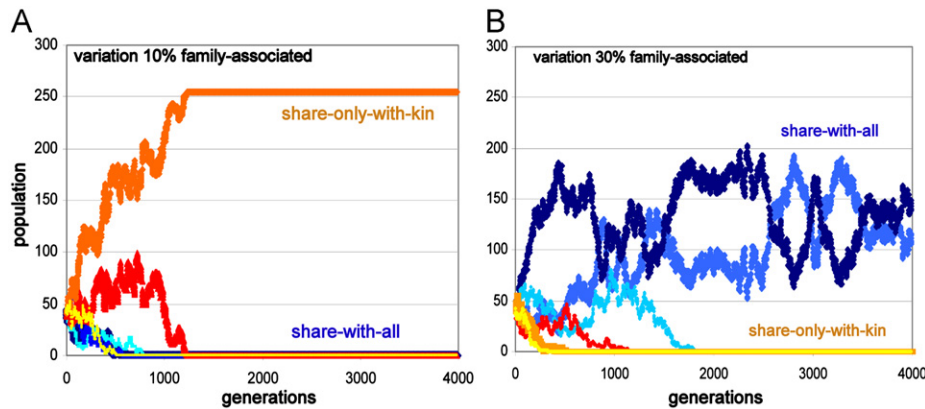
Basically, Eq. (10) is an extension of Eq. (8). If S- and M-types are equally related, then  $\Delta R=0$ , and Eq. (10) reverts to Eq. (8). If  $\Delta R > 0$ , the inequality of Eq. (10) is harder to satisfy, and this is the inclusive fitness penalty of cooperating with non-related partners. However, if the variance  $\sigma^2$  is sufficiently large, and the covariance  $\sigma_{\alpha\beta}$  sufficiently low, then Eq. (10) can be satisfied, and mutualism can overcome inclusive fitness.

In addition to this theoretical result, the dominance of mutualism over kin selection can be shown in the computational model. Let us return to the example of  $S$  and  $M$  alleles. It is well-known that, if some players in a group carry an altruistic gene that allows alternate sharing with a tit-for-tat strategy, this gene will spread until the whole group consists of sharers (Nowak, 2006). Such a group is present in the simulation of Fig. 1. Although in the evolutionarily stable situation, all members of the group carry the altruistic gene, they can be otherwise genetically diverse. For example population members can be a mixture of lean and muscular people.

Now let us show how kin selection can dominate in the above population (see also Uitdehaag, 2009). Suppose that a mutant altruistic gene arises in a carrier of the muscularity allele  $M$ . This mutant is more self-selecting and induces players to share only with other muscular people (carriers of  $M$ ). Within a few generations, this will result in the whole population being dominated by M-types that follow the self-selecting strategy. This resembles a green beard mechanism (Dawkins, 1976; Riolo et al., 2001; Jansen and van Baalen, 2006). Because all muscular people are kin, with respect to gene  $M$ , it is also a kin-selection mechanism. Here, the stable population consists solely of muscular people.

In the simulations, this mechanism is modelled by allowing a new mutant strategy *share-only-with-kin*, which follows the rule that it shares exclusively with players with a *share-only-with-kin* strategy, but accepts shares from any player (see Fig. 2 for exact strategy definitions). From Fig. 2A and earlier work (Uitdehaag,





**Fig. 2. Kin selection is outcompeted by neutral sharers when variation has a large genetic contribution.** Players were divided into six different families. Three families (red/orange/yellow) followed a *share-only-with-kin* strategy, in which they donate shares to friendly players, but only if they are from their own family, otherwise they decline to share (they accept shares from anyone). This earlier defined strategy (Uitdehaag, 2009) is a form of kin-selection. Three other families (shades of blue) followed a *share-with-all* strategy, in which they share with anyone, as outlined in Fig. 1A. (A) Outcome when variation is for 90% related to player number, and 10% related to family number ( $gencontr=0.1$ , see Appendix A). (B) Outcome when variation is for 70% related to player number, and for 30% related to family number ( $gencontr=0.3$ ). In this case the *share-with-kin* strategy dies out because it cannot reduce variation optimally, as it is committed to sharing with players that have the same family number. Now two *share-with-all* families develop a mutualistic relationship. As control, these simulations were also performed including families that follow a non-sharing strategy, as defined in Fig. 1. This leads to quick extermination of the non-sharing strategy in all cases, because of its higher variation (not shown). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2009), it is evident that this strategy evolutionarily dominates more freely sharing strategies (*share-with-all*), confirming the dominance of kin selection.

In the example, the tag is not an arbitrary marker (such as beard colour), but muscularity because the next step in the analysis requires a functional marker. Suppose carriers of allele  $S$ , who are more lean, are also present in the population. Now sustained collaboration between muscular people would be at a disadvantage compared to sustained collaboration between muscular and lean people, because of variance discount. Suppose a new mutant altruistic gene appears, that induces collaboration between lean and muscular players, then this allele will now evolutionarily dominate the self-selecting mutant. The population, after equilibrium has been established, will be a mix of muscular and lean people.

In the simulations, this case was modelled by splitting the fluctuations in two components: an individual random component *varind*, and a tag-associated random component *vargenet* (here the tag is a family number). This means that all players with the same family number, on top of individual variation *varind*, will experience a joint variation *vargenet*. The relative proportions of the *varind* and *vargenet* terms are tuned by a factor *gencontr* (see Appendix A for details). Fig. 2A shows that with a small contribution of *vargenet*, the *share-only-with-kin* strategy is dominant, but if the *vargenet* contribution is increased, the *share-with-all* strategy emerges again as evolutionarily most successful. The final result is that two families survive, who are locked in a mutualistic relationship (Fig. 2B). This proves that, once environmental fluctuations are considered, sharing with and protecting 'others' can indeed be rational behaviour.

## 6. The evolution of bet hedging based cooperation can lead to specialization

Once a bet-hedging based relation has formed, its evolution can go two ways. First an individual can adapt in such a way that its own offspring variation is reduced, leading to more fitness, and also a reduced dependence on collaboration to dampen fluctuations. The second, and more interesting way, is that an individual can increase its level of collaboration, in which case it could even

bear increased individual variance, as long as it is dampened by collaboration. This is a path of specialization.

Let us illustrate specialization in the model example. Suppose that the gene variant  $S$  can evolve to  $S'$ , yielding even less muscle, at the benefit of even lower metabolism. Now an  $S'$ -type will never be able to catch game. However, it is conceivable that the collaboration between  $S'$  and  $M$  is more productive than between  $S$  and  $M$ . For instance, the lower food intake of  $S'$  could mean that more is left for  $M$  in times of food shortage. In this case, as long as  $M$  and  $S$ -types remain cooperative, evolution will lead to formation of  $S'$ .

The mutation of  $S$  into  $S'$  is a case of specialization, since an  $S'$ -type is even more fit than  $S$  in times of food shortage, and even less fit in times of abundant game. The  $S'$ -type can do one thing (surviving scarcity) even more well (Wilson and Yoshimura, 1994). Paradoxically, the  $S'$ -type has decreased overall fitness in isolation. This can be measured by its increased variance discount. The pair of  $S'$  and  $M$ -types is therefore only more fit than  $S$  and  $M$ , if  $S'$  and  $M$  can buffer their increased variation by sharing. This can be measured by a lower fluctuation covariance of the mutant pair (Eq. (9)). The bet hedging context therefore allows a logical description of the evolution towards the specialized  $S'$  and  $M$  pair.

As an illustration, consider a very simple case in which there are only two events possible, 1 (hunting season) and 2 (scarcity) which generate genotype-dependent responses of  $\alpha_1$  and  $\alpha_2$ , for player A, and  $\beta_1$  and  $\beta_2$  for player B. These variables fluctuate around an average of 0 and assume the following values:

$$\text{Before sharing A : } \alpha_1 = -2 \quad \alpha_2 = 2$$

$$\text{B : } \beta_1 = 4 \quad \beta_2 = -4$$

$$\sigma_\alpha^2 = \frac{1}{2}((-2)^2 + 2^2) = 4, \quad k\sigma_\beta^2 = \frac{1}{2}(4^2 + (-4)^2) = 16,$$

$$\sigma_{\alpha\beta} = \frac{1}{2}(-2 \times 4 + (2 \times -4)) = -8$$

$$\text{After sharing A : } \alpha_1 = 1 \quad \alpha_2 = -1$$

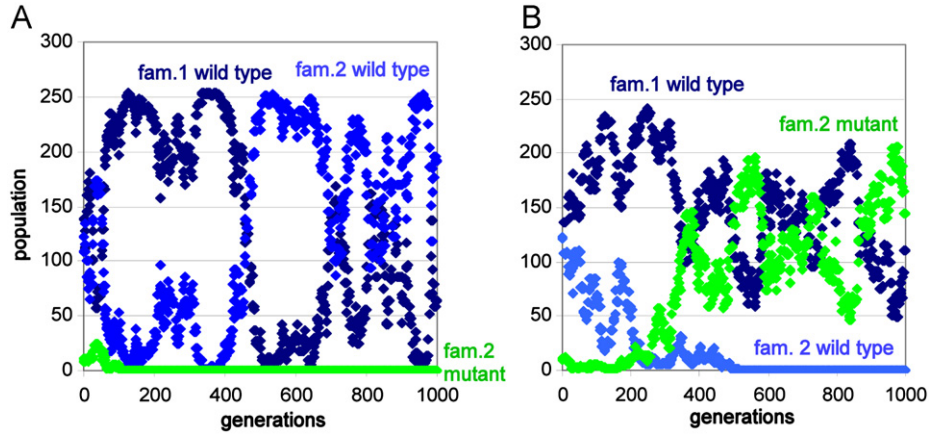
$$\text{B : } \beta_1 = 1 \quad \beta_2 = -1$$

$$s_1 = -3 \quad s_2 = 3$$

$$\sigma_\alpha^2 = \frac{1}{2}(1^2 + (-1)^2) = 1, \quad \sigma_\beta^2 = \frac{1}{2}(1^2 + (-1)^2) = 1,$$

$$\sigma_{\alpha\beta} = \frac{1}{2}(1 \times 1 + (-1 \times -1)) = 1$$

(Note that A and B both profit from the cooperation, even though both have different fitness, which relates to the discussion in Appendix C).



**Fig. 3. A mutant that experiences increased fluctuation covariance to a third partner can replace its mother family.** Two families (blue) that follow a *share-with-all* strategy (the two surviving families in Fig. 2B, see caption there for strategy definition) are locked in a bet hedging relation. Family 1 experiences gene-related variation (through variable *vargenet*)  $\alpha_i$ , and family 2 variation  $\beta_i$ . They are invaded by a mutant of family 2 (green) with variation  $\beta'_i$  that experiences different covariance  $\sigma_{\alpha\beta'}$  with family 1. (A) If the  $\alpha\beta'$  covariance is not improved, the mutant cannot replace wild type family 2. The statistics before sharing are:  $\sigma_{\alpha}^2=0.083$ ,  $\sigma_{\beta}^2=0.083$ ,  $\sigma_{\beta'}^2=0.083$ ,  $\sigma_{\alpha\beta}=-0.007$ ,  $\sigma_{\alpha\beta'}=-0.007$ ,  $\sigma_{\beta\beta'}=0.083$ , showing that  $\sigma_{\alpha\beta'}=\sigma_{\alpha\beta}$ . (B) If the  $\alpha\beta'$  covariance is improved, the mutant can take over from wild type family 2. Statistics here are:  $\sigma_{\alpha}^2=0.055$ ,  $\sigma_{\beta}^2=0.057$ ,  $\sigma_{\beta'}^2=0.057$ ,  $\sigma_{\alpha\beta}=-0.0005$ ,  $\sigma_{\alpha\beta'}=-0.05$ ,  $\sigma_{\beta\beta'}=0.0047$ , so now  $\sigma_{\alpha\beta'} < \sigma_{\alpha\beta}$ . Simulations were similar to those outlined in Fig. 2B and Appendix A, with the following changes: a constant value of 0.5 was added to the average yield  $l_i$  (this stabilizes the game by reducing total variance) and this value was also added to the threshold for death to make it 0.6. Factor *gencontr*=0.7. In order to have all families experience similar variances before sharing, and therefore to exclude general variance discount effects, the factor *vargenet* is a more complex expression: *vargenet*( $\alpha$ )=*fract*·*rand1*+(1−*fract*)·*rand2*, *vargenet*( $\beta$ )=*fract*·*rand3*+(1−*fract*)·*rand4*, *vargenet*( $\beta'$ )=*fract*·*rand3*+(1−*fract*)·(1−*rand2*), where *rand1*...*rand4* are random numbers between 0 and 1, and where *fract* assumes values 1.0 and 0.2 in panels A and B, respectively. Initial population sizes: fam.1: 122, fam. 2: 122, fam. 2 mutant: 11. In panel A, repeated simulations not all result in the same outcome: in 20% of cases, due to chance, the initial mutualism between family 1 and 2 collapses, resulting in the dominance of wild type family 1 or 2.

Now suppose a specialized mutant player A' takes the place of A. Player A' has improved fitness at event 2, at expense of fitness at event 1. For instance A' has an allele for muscle growth that is twice as efficient. Now the following values are measured:

$$\begin{aligned} \text{Before sharing} \quad A: \alpha'_1 = -4 \quad \alpha'_2 = 4 \\ B: \beta_1 = 4 \quad \beta_2 = -4 \\ \sigma_{\alpha'}^2 = \frac{1}{2}((-4)^2 + 4^2) = 16, \quad \sigma_{\beta}^2 = \frac{1}{2}(4^2 + (-4)^2) = 16, \\ \sigma_{\alpha\beta} = \frac{1}{2}(-4 \times 4 + (4 \times -4)) = -16, \\ \text{After sharing} \quad A: \alpha'_1 = 0 \quad \alpha'_2 = 0 \\ B: \beta_1 = 0 \quad \beta_2 = 0 \\ s_1 = -4 \quad s_2 = 4 \\ \sigma_{\alpha'}^2 = 0, \quad \sigma_{\beta}^2 = 0, \quad \sigma_{\alpha\beta} = 0 \end{aligned}$$

If player A' is considered before sharing, the mutation has clearly been harmful, as A' suffers from increased variance compared to player A:  $\sigma_{\alpha'}^2 > \sigma_{\alpha}^2$  ( $16 > 4$ ). However, after sharing the mutation turns out to be beneficial:  $\sigma_{\alpha'}^2 < \sigma_{\alpha}^2$  ( $0 < 1$ ). Note that also player B, after sharing, profits from the mutation. Because of these properties, this is a case of a specialization.

The specialist mutation, however, can already be identified from the statistics *before* sharing. Appendix B.2 shows that the relevant condition is  $\sigma_{\alpha'}^2 + 2\sigma_{\alpha'\beta} < \sigma_{\alpha}^2 + 2\sigma_{\alpha\beta}$  which translates in the above example to  $16 - 2 \cdot 16 < 4 - 2 \cdot 8$ , or  $-16 < -12$ , which indicates that the mutation is favourable. Fluctuation statistics can therefore predict partnership suitability of a set of players. In this light, the process of specialization can be defined as one that increases individual variances, but improves covariance between partners.

To illustrate this process further, simulations were conducted with two cooperating families in a randomly fluctuating environment (similar to the situation in Fig. 2B) to which a mutant of the second family was introduced. This mutant experiences fluctuations that are more correlated with family 1 (Fig. 3). The mechanism behind this is not specified, but it could be any mechanism in which something rare to the partner is increasingly formed, at the expense of reduced production of something not rare; for instance, the mutant for surviving scarcity described

above. The total variance experienced by mutant and wild type before sharing was kept constant. Indeed, when the mutant experiences sufficiently correlated fluctuations, it can dominate family 2, from which it originated (Fig. 3B). This is also described by Eq. (9). The mutant has adapted itself to family 1. In short, evolutionary pressure on variance reduction, in combination with a stable sharing relationship, can lead to adaptation to partners and the evolution of a specialization.

## 7. Discussion

In this work, bet hedging in a variable environment is presented as a model for cooperation, and a basis for mutualism. The model is based on partners who reduce offspring variations in time (fluctuations) by alternate sharing of surpluses. Interestingly, the model can also be transferred to other mutualistic arrangements, for instance the case in which partners simultaneously share exclusive resources (Sachs et al., 2004; Foster and Wenseleers, 2006). The basis of such a mutualism is that both organisms need a spectrum of nutrients in order to grow (e.g. a plant needs phosphate, nitrate, water, sunlight, etc.), of which some resources are provided by the partner, in return for a donation of excess resources of another type (for a review see Bronstein, 2009). Whereas the alternate sharing in the bet hedging model can be modelled by the alternate PD (Nowak and Sigmund, 1994), this new situation is now based on the simultaneous sharing of different resources, and can be modelled by the simultaneous PD (Axelrod and Hamilton, 1981). Both forms of PD have been shown to favour similar strategies (Freen, 1991; Nowak and Sigmund, 1994; Uitdehaag, 2009). For the 'simultaneous' mutualism, any deviations from the ideal nutrient spectrum could be captured in a variance, which would be a measure for the growth-retarding effects of a suboptimal nutrient supply. In other words, also here a variance discount would apply. The most productive mutualisms would then involve partners with the lowest covariance between their nutrient spectra. In this analysis, the time axis would be replaced by a nutrient-type axis. In short,

it is likely that many of the results of this work would also be valid for the mutualism that simultaneously shares resources, which would show that bet hedging can be a general concept in mutualism.

In general, the bet hedging view of mutualism gives interesting insights in group stability and cooperation. Eq. (8) suggests that variations in the response to living conditions of two organisms could be measured, and a correlation coefficient  $\rho_{AB}$  calculated. This predicts if these organisms are theoretically able to have a mutualistic relationship. Moreover, Eq. (9) predicts which mutants will be able to invade that mutualism. In addition, if it is assumed that players have to guess their surpluses before sharing with their partner, then their guessing error might explain supercooperation, a hitherto enigmatic experimental phenomenon (Appendix C; Guth et al., 1982; Forsythe et al., 1994; Nowak, 2006).

An important reason to develop the bet hedging model for mutualism, was to investigate if a mutualistic strategy could beat parochial strategies such as kin selection and tag-based selection, which remained unbeaten in theoretical work (Fehr and Fischbacher, 2003; Nowak and Sigmund, 2005; Nowak, 2006; Fletcher and Doebeli, 2009). Here it is confirmed that, whereas kin selection and inclusive fitness benefits increase with relatedness to a partner, bet hedging benefits decrease with relatedness (Eq. 10). The reason for this is that more distantly related partners experience more dissimilar fluctuations (if fluctuations are coupled to genotypes). In general, mutualism dominates kin selection if the covariance of the partner fluctuations is smaller than the individual partner variances (Eq. (10)).

The dominance of mutualism is supported by simulations, which show that more mutualistic strategies dominate kin selective strategies if fluctuations are sufficiently high (Fig. 2). In contrast to the analytical results, the simulations assume a fixed population. Therefore, it would be interesting to also analytically study the impact of bet hedging in a fixed population. For this, it is necessary to replace the reproductive rate in Eq. (1) as fitness measure by the expected-lifetime-production-of-offspring, which combines reproductive rate with the individual death rate (Mylius and Diekman, 1995). In this measure, bet hedging will both affect reproductive and death rates (see also Appendix A), and a new relation for variance discount effects on fitness will have to be derived. Another interesting extension will be evaluating the competition between mutualism and kin selection in other well-characterized numerical models such as the Moran process (Nowak et al., 2004), which is also based on the PD, but is more parameter-free. In all these cases, it is predicted that in a varying environment, there is a clear limit to kin selection as a successful strategy.

As shown, mutualism can also dominate tag-based selection. If tags are associated with an occasionally advantageous phenotype, such as in the example of a gene for muscularity, it pays to cooperate with dissimilar tags, rather than similar tags. Importantly, this reasoning requires functional tags (see above). This is a more narrow range of possibilities than for mechanisms of tag-based selection, which generally can use arbitrary tags (Riolo et al., 2001; Jansen and van Baalen, 2006; Antal et al., 2009). However, in practice, group formation is much promoted if tags are associated with functionality (McElreath et al., 2003; Efferson et al., 2008), making it reasonable to assume a role for functional tags.

Another important reason to develop the bet hedging model for mutualism, is to study specialization. Specialization differs from an evolutionary track that increases fitness by reducing an individual's variance discount, which leads to less need for cooperation. In contrast, specialization increases fitness by increased cooperation, which compensates increased individual variance discount. Bet hedging analysis gives a quantitative

condition under which specialization can be evolutionary successful: the covariance of a mutant with its partner, added to the increased variance of the mutant, needs to be lower than the similar sum for wild type (above and Appendix B.2). In this way, evolution can follow a track that leads to increased mutual dependency.

Continuing specialization can lead to ever increasing mutual dependency to the point where survival alone is impossible. Because the group as a collective gets more evolutionarily fit, but the individuals *in isolation* less fit, this generates the appearance as if individuals sacrifice fitness in favour of group fitness. In other words, as if group evolution is taking place (Sober and Wilson, 1998; Nowak, 2006; Bowles, 2006; Wild et al., 2009; Salomonsson, 2010). However, what happens is that the individuals adapt to the microcosmos of the group.

If the bet hedging model is extended to a group of cooperators, Eq. (C.4) shows that a stable group is defined by a maximally dampened collective fluctuation (Appendix C). Such a group is more stable than a group that splits wealth evenly, because no group members are net payers, and such a group can also accept members that contribute relatively little (Appendix C). The group has a natural group size, determined by the number of individuals needed to dampen out the entire collective fluctuation (Eq. (C.4), see also van Veelen et al., 2010 on cooperative level and group size). Moreover, if variance discount is the only fitness factor, such a 'perfect' group of diverse mutualistic individuals has a higher collective reproductive rate than any other collective. From the viewpoint of a group selection process (Nowak, 2006; Salomonsson, 2010; van Veelen et al., 2010), the diverse, mutualistic group will be able to dominate a group of related individuals (kin) that behaves equally altruistic. Therefore, also from a multilevel selection perspective, mutualism can dominate kin selection.

In short, bet-hedging based cooperation provides a natural setting in which mutualism can evolutionary dominate parochial strategies such as kin selection and tag-based selection. Furthermore, it can be shown that the evolution of a mutualism can lead to specialization. Such insights lead to increased understanding of human behaviour, ecological diversity and the organization of labour. Bet hedging based sharing is therefore a very useful concept in the study of cooperation.

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## Appendix A. Model

The simulations are extensions of an earlier model (Uitdehaag, 2009). In short: in a Microsoft Excel worksheet, 255 players are divided into families. Within a family, all players follow the same strategy. Players of the same family are 100% kin, as they are genetically and behaviourally indistinguishable. Each round a player harvests an amount  $l_i = \lambda + \delta_i$ , where  $\lambda = 0$  and  $\delta_i = (1 - \text{gencontr}) \cdot \text{varind} + (\text{gencontr}) \cdot \text{vargenet}$ . The variable *varind* is an individual random amount between 0 and 1, and *vargenet* is a random amount between 0 and 1 that is similar for all individuals sharing the same family number. The variable *gencontr* serves to weigh these two sources of individual and family-associated variation.

Players have the option to share with other players. An evolutionarily stable tit-for-tat like setup is used (Axelrod and Hamilton, 1981; Nowak, 2006) (Fig. 2) in which players can remember a limited list of players from whom they received shares before. The longer this list, the more robustly cooperative players can distinguish defecting players, but also the less flexibly they can outcast players that have switched strategy. The optimum memory for cooperative strategies to dominate in the described setup is 4 (Uitdehaag, 2009), which is the value used in all simulations.

The most recent partner from the memory list is given a share if three conditions are met: (1) it fits in a player's strategy, (2) a surplus is harvested this round (defined as  $l_i - 0.5$ ) and (3) this surplus exceeds the surplus of the sharing partner. A share consists of half the difference in surpluses (this is equivalent to the partners pooling  $l_i$  and each taking half). After harvesting and sharing a net share of  $s_i$ , a new yield is determined  $l'_i = l_i + s_i$ .

In the simulation, a fixed cutoff is used for players who had poor harvests and did not get enough shares: they die if  $l'_i < 0.1$  in all simulations. Thus about 10% of the population is refreshed each generation. Increasing this number will lead to more rapid strategy changes. Decreasing will lead to longer times before the competing strategies are in equilibrium (Uitdehaag, 2009). The empty places that result from the deaths are filled with offspring from successful players. The production of offspring is random, with a chance proportional to a player's total yield  $l'_i$  that round. This cycle is iterated over 1000–4000 rounds  $i$  (generations or events). At the start of any simulation, all families have equal starting populations, unless otherwise indicated. Family numbers are randomly assigned to players, as are initial lists of friends. All simulations were repeated over ten times, and in all cases the same strategies went extinct or survived, unless otherwise indicated (Fig. 3A). The simulations differ from the mathematical model in the text in that it has a fixed population. Therefore in the simulation evolutionary success is not only dependent on the amount of offspring, but also on the avoidance of death.

## Appendix B

### Appendix B.1. Correlation statistics between collaborators

The main text defines that if A and B share fully each round, then A and B dampen their yields to

$$l_i = \lambda + \frac{1}{2}(\delta_i + \varepsilon_i) \quad (\text{B.1})$$

$$m_i = \eta + \frac{1}{2}(\delta_i + \varepsilon_i) \quad (\text{B.2})$$

Now player A improves his offspring if

$$N_{\text{total,new},t}^A > N_{\text{total},t}^A \quad (\text{B.3})$$

Using the approximation for variance discount Eqs. (2) and (B.3) can be rewritten as

$$\begin{aligned} 1 - \frac{\frac{1}{4} \sum_{i=1}^t (\delta_i + \varepsilon_i)^2}{2\lambda^2} &> 1 - \frac{\sum_{i=1}^t \delta_i^2}{2\lambda^2} \\ \Leftrightarrow \sum_{i=1}^t (\delta_i + \varepsilon_i)^2 &< 4 \sum_{i=1}^t \delta_i^2 \\ \Leftrightarrow \sum_{i=1}^t (\delta_i^2 + \varepsilon_i^2 + 2\delta_i \varepsilon_i) &< 4 \sum_{i=1}^t \delta_i^2 \\ \Leftrightarrow \sum_{i=1}^t (\varepsilon_i^2 + 2\delta_i \varepsilon_i) &< 3 \sum_{i=1}^t \delta_i^2 \end{aligned} \quad (\text{B.4})$$

If the following variances and covariances are defined

$$\frac{1}{t} \sum_{i=1}^t \varepsilon_i^2 = \sigma_B^2, \quad \frac{1}{t} \sum_{i=1}^t \delta_i^2 = \sigma_A^2, \quad \frac{1}{t} \sum_{i=1}^t \delta_i \varepsilon_i = \sigma_{AB}$$

then Eq. (B.4) can be transformed into

$$\Leftrightarrow \sigma_B^2 + 2\sigma_{AB} < 3\sigma_A^2 \Leftrightarrow \sigma_B^2 + 2\sigma_{AB} - 3\sigma_A^2 < 0 \quad (\text{B.5})$$

For player B, the same analysis applies, because B also needs to benefit from the sharing. This leads to an additional requirement of

$$\Leftrightarrow \sigma_A^2 + 2\sigma_{AB} < 3\sigma_B^2 \Leftrightarrow \sigma_A^2 + 2\sigma_{AB} - 3\sigma_B^2 < 0 \quad (\text{B.6})$$

If (B.5) and (B.6) are solved for the case that their left hand side equals 0, this leads to

$$\sigma_A^2 = \sigma_B^2 = \sigma^2 \text{ and } \frac{\sigma_{AB}}{\sigma^2} = 1 \quad (\text{B.7})$$

Throughout this work, it is assumed that all variances are greater than zero. Combining Eq. (B.7) with inequalities (B.5) and (B.6) leads to

$$\frac{\sigma_{AB}}{\sigma^2} < 1 \quad (\text{B.8})$$

### Appendix B.2. Evolutionary success conditions for a mutant player A'

Suppose players A and B are cooperating on a bet-hedging basis, as in the situation outlined above. Now suppose a mutant player A' arises with variation  $\delta'_i$ , which has an equal ability to cooperate with B. This mutant then has more fitness, compared to player A, if

$$N_{\text{total},t}^{A'} > N_{\text{total},t}^A \quad (\text{B.9})$$

$$\sum_{i=1}^t (\delta'_i + \varepsilon_i)^2 < \sum_{i=1}^t (\delta_i + \varepsilon_i)^2 \quad (\text{B.10})$$

$$\begin{aligned} \Leftrightarrow \sum_{i=1}^t \delta_i^2 + 2\delta'_i \varepsilon_i &< \sum_{i=1}^t \delta_i^2 + 2\delta_i \varepsilon_i \\ \Leftrightarrow \sigma_{A'}^2 + 2\sigma_{A'B} &< \sigma_A^2 + 2\sigma_{AB} \end{aligned} \quad (\text{B.11})$$

In the case outlined above,  $\sigma_A^2 = \sigma_{A'}^2 = \sigma_B^2 = \sigma^2$

$$\Leftrightarrow \sigma_{A'B} < \sigma_{AB} \quad (\text{B.12})$$

### Appendix B.3. Correlation statistics when there is partial sharing

Suppose that A and B no longer pool and divide their entire surpluses, but that they exchange a share  $s_i$  which is a portion of their surplus. Their offspring yields are then formulated as

$$\begin{aligned} A : l_i &= \lambda + (\delta_i + s_i) \\ B : m_i &= \eta + (\varepsilon_i - s_i) \end{aligned} \quad (\text{B.13})$$

The variance for player A in the new situation (when there is sharing) is defined as

$$\begin{aligned} \sigma_{A,\text{new}}^2 &= \frac{1}{t} \sum_{i=1}^t (\delta_i + s_i)^2 = \frac{1}{t} \sum_{i=1}^t (\delta_i^2 + 2\delta_i s_i + s_i^2) \text{ and} \\ \sigma_{A,\text{old}}^2 &= \frac{1}{t} \sum_{i=1}^t \delta_i^2 \end{aligned} \quad (\text{B.14})$$



Sharing is evolutionarily advantageous if it reduces variance discount, therefore

$$\sigma_{A,\text{new}}^2 < \sigma_{A,\text{old}}^2 \Leftrightarrow \sum_{i=1}^t (\delta_i^2 + 2\delta_i s_i + 2s_i^2) < \sum_{i=1}^t \delta_i^2 \Leftrightarrow \sum_{i=1}^t (2\delta_i s_i + 2s_i^2) < 0 \quad (\text{B.15})$$

Repeating this analysis for player B results in

$$\sum_{i=1}^t (-2\delta_i s_i + 2s_i^2) < 0 \quad (\text{B.16})$$

Redefining  $\sigma_{\text{sh}}^2 = (1/t) \sum_{i=1}^t s_i$  and  $\sigma_{\text{shA}} = (1/t) \sum_{i=1}^t s_i \delta_i$  and  $\sigma_{\text{shB}} = (1/t) \sum_{i=1}^t s_i \delta_i$ , and combining this with Eqs. (B.15) and (B.16) leads to new conditions for bet-hedging based sharing

$$-\sigma_{\text{shA}} > \sigma_{\text{sh}}^2 \text{ and } \sigma_{\text{shB}} > \sigma_{\text{sh}}^2 \quad (\text{B.17})$$

In the case of Appendix B.1, in which players A and B pool their fluctuations, and each take half of the pool, then  $s_i = 1/2(\delta_i - \delta_i)$ . When this is substituted in Eq. (B.17), it reverts to Eq. (B.8). Therefore Eq. (B.8) is a special case of Eq. (B.17).

### Appendix C. Correlation between sharer fluctuations in larger groups

Here the analytical treatment is expanded to a group of more than two cooperators. Even without resorting to the variance discount approximation, some interesting results can be obtained. First it is convenient to introduce matrix notation. Suppose a group  $G$  of collaborating players  $j$ . Here  $j$  can assume a character value such as A, B, etc. Let the offspring of player  $j$  at event  $i$  (previously  $l_i$ ) now be denoted as  $l(i)^j$ , which is shortened to  $l^j$ . The average offspring for  $j$  is  $\lambda_j$ . A share received by player  $j$  from player  $k$  is labelled  $s(i)_{jk}$ , which is shortened to  $s_{jk}$ . If  $k=j$ , then  $s_{jj}$  denotes the individual variation that is called  $\delta_i$  above. After sharing, the total yield at event  $i$  then becomes

$$l^j = \lambda_j + \sum_{k \in G} s_{jk} \quad (\text{C.1})$$

The maximum offspring condition states that in the optimal case, variations are zero for each player every round:

$$l^j - \lambda_j = \sum_{k \in G} s_{jk} = 0 \quad (\text{for every } j) \quad (\text{C.2})$$

If Eq. (C.2) is valid for every  $j$ , then the summation over all players  $j$  must also be equal to zero

$$\sum_{j \in G} \sum_{k \in G} s_{jk} = 0 \quad (\text{C.3})$$

The amount that player  $j$  gives to  $k$ , must be equal to the amount that  $k$  receives from  $j$ , therefore  $s_{jk} = -s_{kj}$ . In Eq. (C.3), this cancels out all diagonal terms, leading to

$$\sum_{j \in G} s_{jj} = 0 \quad (\text{C.4})$$

Eq. (C.4) states that within group  $G$ , participants can most successfully collaborate if their added fluctuations negate each other every round  $i$ . In other words, if the trace of their sharing matrix is zero. This is a generalization of the result  $\delta_i = -\varepsilon_i$  (Eq. (5)) derived for two players.

An interesting implication of Eq. (C.4) is that it provides an answer to the question: What kind of new members should be accepted into a group? Eq. (C.4) states that any new group member should be accepted who further brings the total group offspring fluctuation closer to zero, because this benefits the whole group. The absolute contribution of a new member is less important than the diversity she brings into the group.

If within the group there is a subgroup that also satisfies Eq. (C.4), then this subgroup could split off without further variance discount penalty. So a stable group must also be the minimally possible group within its participants. This leads to an additional condition for stability,

$$\sum_{j \in G'} s_{jj} \neq 0 \quad (\text{C.5})$$

Here  $G'$  is any subgroup of  $G$ . Eq. (C.4) says that in an ideally stable group, all participants must make a unique contribution.

It is not unlikely that matrix theory or group theory would allow further exploration of Eqs. (C.4) and (C.5) but this falls outside the scope of the current work. However, some further interpretation can be done. From the perspective of an individual A in a group, it is important to remain in the group, as leaving will hugely increase fluctuations. In order for A to assure group membership, it is best to make a unique contribution that maximally reduces the matrix trace. Player A would fear that her contribution to the group is no longer unique or useful. Player A would also fear the emergence of group members that are less dependent on shares from the others. Therefore, diversity is a main parameter that binds a bet hedging group.

The Eq. (C.4) also provides a definition of fairness in a group. What can each member expect to get from a communal effort? It might seem fair to divide the total yield every round between all  $n$  members (let us call this a 'full' share), so everyone is able to generate an average  $(1/n) \sum_{j \in G} \lambda_j$  offspring. As a result, members with a high average yield consistently donate resources to members with low average, and the high-average earners could be better off leaving the group. However, Eq. (C.4) suggests another principle. Each group member can expect to get her environmental fluctuations cancelled (let us call this a 'fair' share). In other words: she can expect protection from the group from natural setbacks. Within such a group, all members retain their individual average offspring yields  $\lambda_j$ . This leads to a more stable group, and is therefore an optimal way of organizing solidarity.

In a bet hedging group, members will have to estimate their expected average offspring ( $\lambda_j$ ), and the surplus they can deal out. If the estimate is too high: not enough favours are built up for meagre times. If estimated too low, too much wealth is dealt away. Therefore a player with a positive outlook on the future (a feeling that  $l_{\text{current}}$  is above  $\lambda$ ) will share more than one with a more negative outlook (a feeling that  $l_{\text{current}}$  is below  $\lambda$ ). If participants in sharing games think they are in wealthy times, they might donate therefore relatively large portions of wealth to build up favours for meagre times. This could be the basis of experimentally observed supercooperation (Guth et al., 1982; Forsythe et al., 1994; Nowak, 2006).

### Appendix D

#### Appendix D.1. Bet hedging combined with inclusive fitness

In the main text it was shown how bet-hedging based sharing can counteract kin selection. Below, it is shown how this effect can be incorporated in Hamilton's equation for inclusive fitness (kin selection) (Hamilton, 1964; Grafen, 2006; van Veelen, 2007; Nowak et al., 2010). This relation was chosen because it is well-known, although variance discount effects will play a role in any mechanism of self selection. The inclusive fitness  $W_{IF}$  can be expressed as (Nowak et al., 2010)

$$W_{IF} = \sum_j \frac{\partial}{\partial \delta_{\text{sel}}} \frac{\partial w_j}{\partial s} \Big|_{\delta_{\text{sel}} = 0} R_j \quad (\text{D.1})$$

The summation is over all individual players  $j$ .  $R_j$  is the relatedness between the focal individual and  $j$ . The right differential describes how the strategy  $s_*$  of the focal player influences the fitness  $w_j$  of individual  $j$ . The increment  $\delta_{sel}$  in the left differential is the intensity of selection, and can be seen as the fraction of  $s_*$  which is implemented in order to get only weak selection. (note that  $\delta_{sel}$  and  $s_*$  have no relation to  $\delta_i$  and  $s_i$  used above).

The fitness effect in Eq. (D.1) is originally calculated for a certain timeframe of  $t$  steps, in which the environment is constant. If now environmental fluctuations are introduced over this timeframe, variance discount can be applied if  $\delta_i \ll l_i$  (see above). This imposes that bet hedging is a weak force in selection, which fits well with the weak selection assumption in inclusive fitness. First the fitness effects of variance discount are expressed as the geometric average of  $N_{total,t}$

$$w_{j,discount} = (N_{total,t})^{1/t} = N_{total,i}/N_{total,i-1} \approx 1 - \left(1 - \frac{\sigma^2}{2\lambda_j^2}\right) \quad (D.2)$$

This can be combined with the fitness effects in absence of variation ( $w_j$ )

$$w_{j,var} = w_{j,discount} w_j \approx \lambda_j \left(1 - \frac{\sigma_j^2}{2\lambda_j^2}\right) w_j \quad (D.3)$$

If  $\delta_{sel}$  can be interpreted as the (minimal) fraction with which  $s_*$  is implemented (Nowak et al., 2010), then the double differential can be approximated by

$$\frac{\partial}{\partial \delta_{sel}} \frac{\partial w_{j,var}}{\partial s_*} \approx \frac{\partial[(\delta_{sel} w_{j,var}(s_*) + (1 - \delta_{sel}) w_{j,var}(0))]}{\partial \delta_{sel}} \approx w_{j,var}(s_*) - w_{j,var}(0) \quad (D.4)$$

In Eq. (D.4)  $w_{j,var}(s_*)$  is the fitness after the focal player's strategy  $s_*$  is applied, and  $w_{j,var}(0)$  the fitness before. For simplicity let  $s_*$  be the bet hedging component of a total strategy of the focal individual, and  $w_j$  be independent of  $s_*$ :  $w_j(s_*) = w_j(0) = w_j$ . If  $\sigma_{j,s_*}^2$  is the variance of individual  $j$  after  $s_*$  is applied, and  $\sigma_{j,0}^2$  the variance before, then Eq. (D.4) can be combined with Eq. (D.3) into:

$$\Leftrightarrow \lambda_j \left(1 - \frac{\sigma_{j,s_*}^2}{2\lambda_j^2}\right) w_j - \lambda_j \left(1 - \frac{\sigma_{j,0}^2}{2\lambda_j^2}\right) w_j = \frac{1}{2\lambda_j} (\sigma_{j,0}^2 - \sigma_{j,s_*}^2) w_j \quad (D.5)$$

Now the inclusive fitness equation results from combining Eqs. (D.1) and (D.5).

$$W_{IF,var} = \sum_j \frac{1}{2\lambda_j} (\sigma_{j,0}^2 - \sigma_{j,s_*}^2) \cdot w_j R_j \quad (D.6)$$

Eq. (D.6) is a general expression for inclusive fitness effects of variance discount. If strategy  $s_*$  reduces variance, then the term in brackets is positive, and contributes positively to  $W_{IF,var}$  for related partners.

#### Appendix D.2. Bet hedging-based sharing with fluctuations that associate with genotype

Next it is proven, using Eq. (D.6), that bet hedging can stimulate cooperation between less related partners. For that a more detailed model is needed. Assume a freely interacting society with S-type and M-type players, who differ only in their alleles for the muscularity gene. Offspring at event  $i$  can be written as

For an S-type:  $l_i = \lambda + \delta_i$

For an M-type:  $m_i = \eta + \varepsilon_i$

Now assume that the variations  $\delta_i$  and  $\varepsilon_i$  are more complex than assumed earlier, and consist of three additive components: a

response due to carrying  $S$  (called  $\alpha_i$ ) or  $M$  (called  $\beta_i$ ), a response due to other genes ( $\phi_i$ ), and a response due to an individual stochastic factor  $p_i(j)$ , which is related to player number  $j$ . Let us assume that all  $p_i(j)$  are independently drawn from the same distribution, and that all components, except  $\alpha_i$  and  $\beta_i$ , are independent. Because fluctuations are considered, not fitness advantages, the net sum of all variations must be zero:

$$\sum_{i=1}^t \alpha_i = \sum_{i=1}^t \beta_i = \sum_{i=1}^t \phi_i = \sum_{i=1}^t p_i(j) = 0 \quad (D.7)$$

Now the fluctuations of types  $S$  and  $M$  can be written as:

$$\begin{aligned} \delta_{ij} &= \alpha_i + \phi_i + p_i(j) \\ \varepsilon_{ij} &= \beta_i + \phi_i + p_i(j) \end{aligned} \quad (D.8)$$

Suppose again that players simply share by pooling their surpluses, and splitting 50:50. This leads to the following common fluctuations for two partners A and B, if

$$\text{both are S-types: } \frac{1}{2} (\delta_{iA} + \delta_{iB}) = \frac{1}{2} (2\alpha_i + 2\phi_i + p_i(A) + p_i(B)) \quad (D.9)$$

$$\text{one is S, the other M: } \frac{1}{2} (\delta_{iA} + \varepsilon_{iB}) = \frac{1}{2} (\alpha_i + \beta_i + 2\phi_i + p_i(A) + p_i(B)) \quad (D.10)$$

$$\text{both are M-types: } \frac{1}{2} (\varepsilon_{iA} + \varepsilon_{iB}) = \frac{1}{2} (2\beta_i + 2\phi_i + p_i(A) + p_i(B)) \quad (D.11)$$

Eq. (D.6) can be combined with Eqs. (D.9–D.11). Without loss of generality, it can be assumed that the focal individual is A, and an S-type. First, the variances are evaluated before and after sharing with partner B, when she is the same S-type as the focal individual

$$\sigma_{S,0}^2 = \frac{1}{t} \sum_{i=1}^t \delta_{iA}^2 = \frac{1}{t} \sum_{i=1}^t (\alpha_i + \phi_i + p_i(B))^2 \quad (D.12)$$

$$\sigma_{S,s_*}^2 = \frac{1}{t} \sum_{i=1}^t \left(\frac{1}{2} (\delta_{iA} + \delta_{iB})\right)^2 = \frac{1}{4t} \sum_{i=1}^t (2\alpha_i + 2\phi_i + p_i(A) + p_i(B))^2 \quad (D.13)$$

The covariances of all terms equal zero, and the  $p_i(A)$  and  $p_i(B)$  have the same variance  $\sigma_p^2$  leading to

$$(\sigma_{S,0}^2 - \sigma_{S,s_*}^2) = \frac{1}{t} \sum_{i=1}^t p_i(B)^2 - \frac{1}{4} p_i(A)^2 - \frac{1}{4} p_i(B)^2 = \frac{1}{2} \sigma_p^2 \quad (D.14)$$

Eq. (D.14) is simple but interesting. If it is combined with Eq. (D.6), it states that also sharing between partners with the same genotype generates fitness advantages from variance discount. This is because the individual stochastic fluctuations are dampened.

If partner B is an M-type

$$\sigma_{M,0}^2 = \frac{1}{t} \sum_{i=1}^t \varepsilon_{iA}^2 = \frac{1}{t} \sum_{i=1}^t (\beta_i + \phi_i + p_i(B))^2 \quad (D.15)$$

$$\begin{aligned} \sigma_{M,s_*}^2 &= \frac{1}{t} \sum_{i=1}^t \left(\frac{1}{2} (\delta_{iA} + \varepsilon_{iB})\right)^2 \\ &= \frac{1}{4t} \sum_{i=1}^t (\alpha_i + \beta_i + 2\phi_i + p_i(A) + p_i(B))^2 \end{aligned} \quad (D.16)$$

Because  $\alpha_i$  and  $\beta_i$  are not independent, this leads to

$$\begin{aligned} (\sigma_{M,0}^2 - \sigma_{M,s_*}^2) &= \left(\frac{1}{4t} \sum_{i=1}^t 4\beta_i^2 - \alpha_i^2 - \beta_i^2 - 2\alpha_i\beta_i\right) \\ &+ \frac{1}{2} \sigma_p^2 = \left(\frac{1}{4t} \sum_{i=1}^t 3\beta_i^2 - \alpha_i^2 - 2\alpha_i\beta_i\right) + \frac{1}{2} \sigma_p^2 \end{aligned} \quad (D.17)$$

Eq. (D.17) needs to be positive, otherwise it would be better not to share at all.

$$\frac{1}{4t} \sum_{i=1}^t 3\beta_i^2 - \alpha_i^2 - 2\alpha_i\beta_i > -\frac{1}{2}\sigma_p^2 \quad (\text{D.18})$$

In addition, a variant of Eq. (D.17) can be constructed from the perspective of partner B (by switching  $\alpha$  and  $\beta$ ). Because both partners need to profit from the sharing relationship, also this variant needs to be positive, leading to

$$\frac{1}{4t} \sum_{i=1}^t 3\alpha_i^2 - \beta_i^2 - 2\alpha_i\beta_i > -\frac{1}{2}\sigma_p^2 \quad (\text{D.19})$$

If  $1/t \sum_{i=1}^t \alpha_i^2 = \sigma_\alpha^2$  and  $(1/t) \sum_{i=1}^t \beta_i^2 = \sigma_\beta^2$  then the solution of the set of Eqs (D.18) and (D.19) requires  $\sigma_\alpha^2 = \sigma_\beta^2 \equiv \sigma^2$ . This particular condition arises because A and B follow a complete sharing arrangement, as pointed out above. If this solution is combined with Eq. (D.17)

$$(\sigma_{M,0}^2 - \sigma_{M,s}^2) = \frac{1}{2}(\sigma^2 - \sigma_{\alpha\beta} + \sigma_p^2) \quad (\text{D.20})$$

The use of Eq. (D.20) in Eq (D.6) gives a fitness condition for heterotypic sharing. It has an extra term  $\sigma^2 - \sigma_{\alpha\beta}$  compared to homotypic sharing in Eq. (D.14). If  $\sigma^2 = \sigma_{\alpha\beta}$  then the fluctuations experienced by A and B have a similar phase and Eqs. (D.14) and (D.20) are identical. The term of Eq. (D.20) is greater than that of Eq. (D.14) if  $\sigma_{\alpha\beta} < \sigma^2$ . In other words: when the fluctuations mediated by  $\alpha$  and  $\beta$  are less than perfectly correlated, there is a fitness advantage for an S-type to collaborate with an M-type, rather than a more related S-type.

#### Appendix D.3. Bet hedging and kin selection inversely depend on relatedness

Next, fitness is studied in more detail by combining Eqs. (D.14) and (D.20) with Eq. (D.6). Assume that the society consist of  $N_S$  players of type S, and  $N_M$  players of type M. S and M-types are all related by descent, but in such a way that S-types are more related to the S-type focal player:  $R_S = R_M + \Delta R$  ( $\Delta R > 0$ ). In addition,  $N_O$  players of type O are present, who are not available for sharing, and who are not related by descent ( $R_O = 0$ ). If  $R_j$  is defined as a normalized identity by descent, which can be negative (Grafen, 2006), the pool of O-types serves to ensure that  $R_S > 0$  and  $R_M > 0$ .

Now let the focal player implement her strategy by choosing a sharing relation with an S-type for  $f_S$  part of her time, and with an M-type for an  $f_M$  part, with  $f_S + f_M = 1$ . This generates the following fitness for the focal player from Eqs. (D.6, D.14 and D.20),

$$W_{IF} = \frac{w_S N_S}{4\lambda_S} f_S \sigma_p^2 R_S + \frac{w_M N_M}{4\lambda_M} f_M (\sigma^2 - \sigma_{\alpha\beta} + \sigma_p^2) R_M \quad (\text{D.21})$$

$$\text{Let us define } \frac{w_S N_S}{4\lambda_S} = w'_S \text{ and } \frac{w_M N_M}{4\lambda_M} = w'_M$$

In Eq. (D.21), for an indiscriminate strategy  $f_S = f_M$ , for a self selective strategy  $f_S = 1$ , and for a purely heteroselective strategy  $f_M = 1$ .

If  $\sigma_{\alpha\beta} \geq \sigma^2$  then Eq. (D.21) maximizes for a self selective strategy. Kin selection is then dominant. The focal player will aim for a population that contains only S-types. How does Eq. (D.21) maximize if  $\sigma_{\alpha\beta} < \sigma^2$ ? Interestingly, the outcome of Eq. (D.21) for  $f_M = 1$  can be larger than for  $f_S = 1$  if

$$w'_M (\sigma^2 - \sigma_{\alpha\beta} + \sigma_p^2) R_M > w'_S \sigma_p^2 R_S \Leftrightarrow \sigma_{\alpha\beta} < \sigma^2 - \sigma_p^2 \left( \frac{w'_S R_S}{w'_M R_M} - 1 \right) \quad (\text{D.22})$$

If only fitness differences between S and M are considered that arise from variance discount and relatedness, all other factors can

be set equal by assuming  $w'_M = w'_S$ . Then Eq. (D.22) further simplifies to

$$\Leftrightarrow \sigma_{\alpha\beta} < \sigma^2 - \sigma_p^2 \frac{\Delta R}{R_M} \quad (\text{D.23})$$

If the inequality in Eq. (D.23) is satisfied, then a heteroselective strategy beats a self selective strategy. If S and M are equally related, then  $\Delta R = 0$ , and Eq. (D.23) reverts to Eq. (8) in the main text. If  $\Delta R > 0$ , Eq. (D.23) is harder to satisfy, because of inclusive fitness. However, heterotypic cooperation can still be fruitful if  $\sigma_{\alpha\beta}$  is low enough. Thus, if the anticorrelation between the fluctuations experienced by an M-type or S-type is sufficiently negative, then the concomitant  $\Delta R$  between S and M is surmountable. In this way, collaborating with less related partners can be more advantageous than collaborating with more related partners. Due to variance discount, an S-type focal player now has an incentive to cooperate with M-types.

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