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3 **1 Why mutual helping in most natural systems is neither conflict-free nor based on**  
4  
5 **2 maximal conflict**  
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26 12 Short title: Solving intermediate conflict levels  
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32 15 Keywords: cooperation, mutualism, by-product mutualism, prisoner's dilemma,  
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34 16 pseudoreciprocity, biological market  
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19 **Abstract:** Mutual helping for direct benefits can be explained by various game  
20 theoretical models, which differ mainly in terms of the underlying conflict of interest  
21 between two partners. Conflict is minimal if helping is self-serving and the partner  
22 benefits as a by-product. In contrast, conflict is maximal if partners are in a prisoner's  
23 dilemma with both having the payoff-dominant option of not returning the other's  
24 investment. Here, we provide evolutionary and ecological arguments for why these  
25 two extremes are often unstable under natural conditions and propose that interactions  
26 with intermediate levels of conflict are frequent evolutionary endpoints. We argue  
27 that by-product helping is prone to becoming an asymmetric investment game since  
28 even small variation in by-product benefits will lead to the evolution of partner  
29 choice, leading to investments and partner monitoring. Second, iterated prisoner's  
30 dilemmas tend to take place in stable social groups where the fitness of partners is  
31 interdependent, to the effect that a certain level of helping is self-serving. In sum,  
32 intermediate levels of mutual helping are expected in nature, while efficient partner  
33 control mechanisms may allow reaching higher levels.

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3 35 **Introduction**  
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5 36 Helping, defined as an act that increases the direct fitness of a recipient, has attracted  
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7 37 great interest as it is at odds with general Darwinian notions of competition and self-  
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10 38 interest. One solution has been Hamilton's (1964a,b) kin selection theory of altruism  
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12 39 where helping is directed at genetically related individuals. However, nature is full of  
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14 40 examples where helpers and recipients are unrelated, most obviously in interspecific  
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16 41 interactions, "...the basis of the world as we know it" (Bronstein 1994). Within the  
17  
18 42 same species, there are also countless examples of individuals helping unrelated  
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20 43 conspecifics, provided it yields overall direct fitness benefits. Given the great  
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22 44 confusion regarding terminology, the best we can do is to define each term when  
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24 45 using it for the first time. We follow Bshary & Bergmüller (2008) who put together  
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26 46 existing definitions in a coherent way. Based on Lehmann & Keller (2006) and  
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28 47 Bronstein (2001), mutual helping for direct fitness has been termed 'cooperation' if it  
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30 48 occurs between members of the same species and 'mutualism' if it occurs between  
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32 49 members of different species (see also Bronstein 2015).  
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38 51 Key topics in research on helping are to determine how population structure and life  
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40 52 history lead to unconditional helping and to identify the decision rules and partner  
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42 53 control mechanisms of conditional helping (Lehmann & Keller 2006). Partner control  
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44 54 occurs if a co-operator takes an action that lowers the pay-off of a defector, for  
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46 55 instance by defecting, punishing, or sanctioning the defector with premature  
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48 56 termination and refusal to interact again, or by switching to a new partner (Bshary &  
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50 57 Bergmüller 2008).  
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3 59 There is considerable confusion in the current literature regarding terminology for  
4 mutual helping for direct fitness. A key distinction for is between members of the  
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6 60 same species, which has been termed ‘cooperation’, and between members of  
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8 61 different species, which has been termed ‘mutualism’ (Lehmann & Keller 2006;  
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10 62 Bronstein 2001; 2015). In the following, we define each term separately, following  
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12 63 (Bshary & Bergmüller’s 2008) systematic review.  
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66 Although stable mutual helping can be explained by numerous models, the literature  
67 is dominated by two scenarios. Either helping is inherently self-serving, with no  
68 danger of defection, or it is an ‘investment’ (a payoff reduction irrespective of a  
69 partner’s action) that is compensated by future benefits, which creates a temptation to  
70 defect. We will first present both scenarios in detail before arguing that, in most  
71 biological systems, the assumptions upon which they are based are ecologically  
72 implausible. We will further argue that, in the real world, most cases of dyadic mutual  
73 helping are accompanied by some level of conflict, which in turn has selected for  
74 partner monitoring and control, both between related and unrelated individuals. We  
75 will present stylised games that capture what may well be the most common stable  
76 endpoint - intermediate levels of conflict - and propose ways in which these games  
77 could be explored in the future.

### 78 79 **Helping with minimal levels of conflict**

80 Arguably, the most straightforward condition for stable mutual helping is a situation  
81 in which each individual performs a self-serving act that benefits a partner as a by-  
82 product. We call this ‘by-product helping’ as it may occur within and between  
83 species. Brown (1983) has referred to the same condition as ‘by-product mutualism’,

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3 84 but this term clashes with the original use of the term ‘mutualism’, i.e. cooperation  
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5 85 between species (see Bronstein 2015)). A good example for ‘by-product helping’ is  
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7 86 the ‘selfish herd’ effect (Hamilton 1971). For example, seals reduce inter-individual  
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10 87 distances when swimming through zones with great white sharks, which is both self-  
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12 88 serving for the actor and beneficial for the partner, as it reduces the predation risk for  
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14 89 both (De Vos & O’Riain 2010). Another example is cooperative hunting, provided the  
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16 90 hunting success increases with group size (Lamprecht 1978, Boesch & Boesch 1989).  
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18 91 Cooperative hunting can also occur between species, as recently described in  
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20 92 interspecies interactions between groupers (a predatory fish) and other predatory  
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22 93 species (Bshary et al. 2006, Vail et al 2014). In these cases, the hunters position  
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24 94 themselves to maximize their own hunting success and immediately swallow any  
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26 95 captured prey, with no sharing (Bshary et al. 2006). Thus, the benefits accrue due to  
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28 96 self-serving coordination in time and space rather than through mutual investments.  
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34 98 A second form of stable helping without defection is positive **pseudo-reciprocity**  
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36 99 (Connor 1986). Positive pseudo-reciprocity involves an initial investment that enables  
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38 100 the recipient to perform a self-serving act that in turn benefits the investor as a by-  
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40 101 product. A prime example is the tri-trophic interaction between plants, insect  
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42 102 herbivores and parasitoid wasps (Turlings et al. 1990). When attacked by a herbivore,  
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44 103 the plant produces volatiles, which enables the wasp to detect the herbivore. The wasp  
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46 104 will then self-servingly lay her eggs into the herbivore, which will kill it and benefit  
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48 105 the plant **a by-product**.  Pseudo-reciprocity can also be mutual. For example, in  
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51 106 lichens, a composite organism of algae living in the filaments of a fungus, the fungus  
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53 107 invests by producing a shelter that enhances the efficiency of the algae’s  
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55 108 photosynthesis and nutrient production, which enables the fungus to grow more  
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3 109 rapidly and produce more shelter. As the fungus transfers the algae vertically to the  
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5 110 next generation of fungi, the fitness of both partners is interdependent, which prevents  
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7 111 defection from either side.  
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12 113 Due to the inherent stability of by-product helping and positive pseudo-reciprocity,  
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14 114 various authors have hypothesized that they should be abundant in nature (Clutton-  
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16 115 Brock 2009, Leimar & Hammerstein 2010, Bshary & Bronstein 2011). While many  
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18 116 well-documented examples are mutualisms, i.e. interactions between species, there  
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20 117 are also examples of cooperation, i.e. intraspecific interactions, such as the selfish  
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22 118 herd effect (Hamilton 1971).  
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## 26 27 120 **Helping with maximal levels of conflict**

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29 121 We define helping with maximal levels of conflict of interest as cases in which all  
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31 122 individuals would do best by fully defecting each other (i.e., in the absence of a  
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33 123 partner control) as the evolutionarily stable strategy. The exploitation aspect  
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35 124 distinguishes our **concepts of interest** from potentially stable lack of cooperation in  
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37 125 coordination games, in which non-coordinators do not exploit coordinators. In  
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39 126 interactions with maximal conflict, helping behaviour can only emerge if partners are  
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41 127 able to provide mutually conditional investments. We use the term ‘mutually  
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43 128 conditional investment’ as equivalent to Trivers’ (1974) ‘reciprocal altruism’, a term  
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45 129 we avoid as it clashes with Hamilton’s (1964) definition of ‘altruism’. i.e. helping  
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47 130 relatives due to kin selection. We avoid the term ‘reciprocity’ as a shortcut for  
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49 131 reciprocal altruism **as is the term** is currently used in many different ways. The  
50  
51 132 standard model for direct mutually conditional investments is the iterated prisoner’s  
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53 133 dilemma, a game in which two players repeatedly choose between cooperating and  
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3 134 defecting. The payoffs are such that mutual cooperating yields higher payoffs than  
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5 135 mutual defection, but in each single interaction defection maximises immediate  
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7 136 payoffs independently of the partner's action (Fig. 1). Thus, to cooperate is an  
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9 137 investment, where future return benefits can only be due to the partner providing  
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11 138 return investments. Due to the payoff structure, however, the temptation to defect is  
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13 139 continuously present.

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18 141 Despite a perpetual temptation to defect, a variety of partner control mechanisms can  
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20 142 nevertheless lead to stable mutual investments. In fact, economists have shown that  
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22 143 solutions with almost any frequency of investments are possible, provided mutual  
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24 144 helping creates a surplus in payoffs and a sufficient number of rounds are played  
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26 145 without a fixed known final round ('folk theorem': Binmore 2005). Large  unaware  
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28 146 of the economic literature, evolutionarily minded scientists **spent have expended**  
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30 147 considerable effort to identifying successful strategies that start cooperatively and  
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32 148 continue to cooperate as long as the partner also cooperates (reviewed by Dugatkin  
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34 149 1997). In the most famous strategy in an iterated prisoner's dilemma game, tit-for-tat,  
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36 150 one individual cooperates on the first iteration of the game and then does exactly what  
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38 151 the partner has done on the previous move, i.e., defect on a defector or cooperate with  
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40 152 a co-operator (Axelrod & Hamilton 1981). An alternative solution to achieve  
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42 153 mutually conditional investments in an iterated prisoner's dilemma type game is  
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44 154 'negative reciprocal investment' where a cooperative individual pays a cost to reduce  
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46 155 the payoff of a defecting partner ('punishment'; Clutton-Brock & Parker 1995).  
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48 156 Another particularly powerful partner control mechanism is to threaten with partner  
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50 157 switching, which promotes mutual investments, at least in well-mixed populations  
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52 158 (Izquierdo et al. 2010).


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5 160 Various biologists have argued that, in contrast to by-product benefits and pseudo-  
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7 161 reciprocity, direct mutually reciprocal investment is rarely found in non-human  
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10 162 species, both in between- and within-species interactions (Bergstrom et al. 2003,  
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12 163 Hammerstein 2003, Stevens & Hauser 2004, Leimar & Hammerstein 2010, Raihani &  
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14 164 Bshary 2011, Raihani et al 2012), which is at odds with the theoretical literature.  
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16 165 There are a few convincing examples for mutually conditional investments, i.e.  
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18 166 experimental studies that demonstrate contingent helping: rats in a laboratory food  
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20 167 pulling task (Rutte & Taborsky 2008), flycatcher mobbing behaviour (Krams et al  
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22 168 2008), food provisioning in vampire bats (Carter & Wilkinson 2013 in combination  
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24 169 with Wilkinson 1984), apparent support for grooming in baboons (Cheney et al. 2010)  
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26 170 or tolerance and support for grooming in vervet monkeys (Borgeaud & Bshary 2015).  
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28 171 Despite these examples, there is still a general perception that there is a discrepancy  
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30 172 between the considerable efforts to find mutually reciprocal investments and the  
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32 173 empirical results.  
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38 175 The discrepancy between theoretical efforts and empirical evidence is understandable  
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40 176 but also surprising. It is understandable because theoreticians are not interested in  
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42 177 modelling conflict-free helping as the stability of helping in such cases is self-evident  
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44 178 and theoretically uninteresting, whereas the opposite is the case for helping resolving  
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46 179 maximal conflicts. What is currently debated, however, is why empiricists struggle to  
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48 180 find convincing examples of helping that involve mutually conditional investments  
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50 181 and what 'rare evidence' might actually mean. We therefore quickly summarise and  
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52 182 comment on some proposed explanations or opinions.  
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3 184 One argument for why evidence for mutually conditional investments is rare is that  
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5 185 such helping can only evolve if two mutations arise simultaneously in at least two  
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7 186 individuals that are potential partners of each other: to invest and the ability to invest  
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9 187 conditionally on the partner's return investment (André 2014). Such an admittedly  
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11 188 evolutionarily unlikely scenario has become known as the bootstrapping problem  
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13 189 (André 2014; see also André 2015 for some potential solutions). Alternatively, several  
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15 190 authors have pointed out that mutually conditional investments might be rare because  
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17 191 non-human species lack the necessary cognitive abilities to keep track of the outcome  
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19 192 of past social interactions, especially if this involves interactions with several partners  
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21 193 (Hammerstein 2003, Stevens & Hauser 2004).  
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28 195 While we acknowledge that evolvability and cognitive constraints  may prevent the  
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30 196 evolution of mutually conditional investments, in many **cases we** do not think that  
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32 197 these explanations suffice to explain the apparent rarity of mutually conditional  
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34 198 investments in nature. The evolvability argument seems to be based on assumptions  
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36 199 concerning gene-behaviour relations that do not apply to species with brains.  
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38 200 Vertebrates and invertebrates have been shown to learn appropriate behaviour via  
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40 201 classic and operant conditioning (Shettleworth 2010). In the latter, animals condition  
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42 202 their own behaviour as a function of the changes in the environment. It does not really  
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44 203 matter whether the environment is abiotic or an interaction partner and whether in the  
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46 204 latter case the situation is potentially cooperative or competitive. There are countless  
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48 205 examples in the optimal foraging literature showing that many species are capable of  
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50 206 efficiently fine-tuning their responses to payoff differences when moving between  
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52 207 food patches (Davies et al. 2012), and Kacelnik (2012) makes a strong case that such  
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54 208 foraging decisions can be most parsimoniously explained with the all-purpose tool  
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3 209 ‘operant conditioning’ rather than situation specific evolved rules-of-  
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5 210 thumbs/heuristics. A similar point has been made by Bshary & Oliveira (2015) who  
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7 211 argued that selection on brain functioning works mainly on higher functional circuits  
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9 212 involved in decision-making in a variety of different social situations. To our mind,  
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11 213 the same line of argument can be applied to explain situation-specific conditional  
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13 214 helping. All we need to explain is the evolution of learning rules (like strength of  
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15 215 reinforcement, weighing of past interactions, exploration of behavioural repertoire)  
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17 216 that allow individuals to adjust their behaviour during their lifetime. Dridi &  
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19 217 Lehmann (2014, 2015) give wonderful examples how exploratory trial-and-error  
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21 218 reinforcement learning rules evolve that allow individuals to solve an iterated  
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23 219 prisoner’s dilemma.  
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30 221 The argument made above puts the emphasis on the cognitive constraint hypothesis.  
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32 222 As we see it, this hypothesis is difficult to reconcile with the fact that individual  
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34 223 recognition is widespread in at least in various vertebrate clades like mammals, birds  
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36 224 and fishes (Griffiths & Ward 2011; Shettleworth 2010), and has even been shown in  
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38 225 social insects (Tibbets 2002). Lack of mobility allows ‘individual recognition’ based  
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40 226 on location, as is the case for ants interacting with their many partner species or for  
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42 227 pollinators interacting with flowering plants. Moreover, memory capacities are  
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44 228 apparently sufficient for learning through operant conditioning, with the evolution of  
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46 229 crucial learning rule parameters subject to natural selection (Dridi & Lehmann 2014,  
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48 230 2015). Indeed, it has repeatedly been argued that solving an iterated prisoner’s  
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50 231 dilemma game might not be as rare is often assumed because scientists were looking  
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52 232 for strategies proposed by theoreticians, like tit-for-tat, while animals make decisions  
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54 233 differently. For example, it has been argued that decisions about mutually conditional  
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3 234 investments may be based on a more general assessment of recent social interactions  
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5 235 ('attitudinal reciprocity', de Waal 2000), on the general quality of a relationship  
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7 236 ('emotional reciprocity', Schino & Aureli 2009), or on general past experience rather  
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9 237 than precise counting with each potential partner ('generalized reciprocity', Pfeiffer et  
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11 238 al. 2004) (see also Cheney 2011). All these proposed decision mechanisms could be  
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13 239 based on the dynamics of learning through operant conditioning (or on higher  
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15 240 cognitive processes if available). Two field experiments on baboons and on vervet  
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17 241 monkeys fit the idea of attitudinal or emotional mutually conditional investments  
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19 242 (Cheney et al. 2009, Borgeaud & Bshary 2015). Crucially, having recently groomed  
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21 243 another individual increases the probability of receiving his or her tolerance or  
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23 244 coalitionary support. This implies that the return investments are not 'all-or-nothing';  
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25 245 in fact, although effects that are conditional on recent grooming are present both in  
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27 246 related/bonded pairs and in unrelated/non-bonded pairs, they come on top of different  
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29 247 baseline levels for interactions without prior grooming. Various other experiments  
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31 248 (with both positive and negative results; Seyfarth & Cheney 1984; Hemelrijk 1994; de  
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33 249 Waal 1997, 2000; de Waal & Berger 2000; Koyama et al. 2006; Melis et al. 2008;  
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35 250 Brosnan et al. 2009; Brosnan & Beran 2009; Dufour et al. 2009; Pele et al. 2009;  
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37 251 Yamamoto & Tanaka 2009, 2010; Horner et al. 2011; Tiddi et al. 2011; Campenni et  
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39 252 al. 2015; Molesti & Majolo 2015) and a large number of correlational studies (Schino  
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41 253 2007) provide additional evidence for such graded mutually conditional investments  
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43 254 in primates. Based on this extensive experimental and correlational evidence, we  
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45 255 predict that graded mutually conditional investments are indeed common in primates  
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47 256 and will be found also in other taxa.  
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3 258 This statement applies not only to positive contingencies but also to negative ones, i.e.  
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5 259 punishment, where current correlational and experimental evidence is even rarer in  
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7 260 non-human animals (Raihani et al. 2012). While cognitive constraints may limit the  
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9 261 usefulness of punishment in various situations (Brosnan et al. 2010, Raihani et al  
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11 262 2012), the fact that aggressive responses to cheating can cause more cooperative  
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13 263 behaviour in fish in both inter and intra-specific interactions (Bshary & Grutter 2005;  
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15 264 Bshary & Bshary 2010; Raihani et al 2010) suggests that at least many vertebrate  
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17 265 species should have the cognitive requirements to use punishment.  
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23 267 This leads us to the issue of whether the phenomenon of strictly mutually conditional  
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25 268 investments solving an iterated prisoner's dilemma is truly rare, as we argued above.  
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27 269 To us it is a matter of perspective: if the game structure of every single case of  
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29 270 helping for direct benefits was known and total sums are made, we would expect  
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31 271 numerous cases of mutually conditional investments solving an iterated prisoner's  
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33 272 dilemma payoff matrix (i.e. in the 1000s, to put a rather preliminary estimate). To  
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35 273 place this in perspective, helping for direct benefits is ubiquitous, as shown by the  
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37 274 myriad of cases of pollination mutualism, plant-microbe interactions in the soil or  
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39 275 mutualisms involving ants protecting partner species. A group of mutualism  
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41 276 specialists proposed in 2003 that none of these cases is suspected to solve an iterated  
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43 277 prisoner's dilemma (Bergstrom et al. 2003), a view that has hardly changed since  
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45 278 (Bronstein 2015). We hope that these illustrations put our use of the term 'rare' into  
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47 279 perspective. Mutually conditional investments are so rare that we think that additional  
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49 280 arguments have to be explored in addition to (not instead of) arguments about  
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51 281 genetic/cognitive constraints.  
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3 283 **The ecology of helping for direct benefits**

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5 284 Here, we follow up on the possibility that prisoner's dilemma-type payoff structures  
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7 285 are rarely found in nature due to ecological reasons (Bshary & Bronstein 2011). We  
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10 286 do so not in mathematical terms but by developing socio-ecologically relevant  
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12 287 scenarios. As all three of us are empiricists, we apologize for the realistic possibility  
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14 288 ~~that as the number of references to the theoretical literature is relatively low,~~ we might  
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16 289 miss out on relevant models that would have made our points already in a more  
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18 290 elegant (i.e. mathematical) way. Also, while we think that models that allow for  
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21 291 continuous investments are biologically more realistic, we illustrate our points with  
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23 292 stylised games with discrete behavioural options. We do so because we think that the  
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25 293 logic is easier to grasp and because we are interested in different classes of models,  
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27 294 i.e. models that predict no conflict, intermediate conflict and maximal conflict (Fig.  
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29 295 1). This classification holds for both continuous and discrete behavioural options (see  
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31 296 Doebeli et al 2004 or Bshary et al. 2008 for continuous options in snowdrift and  
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33 297 prisoner's dilemma games). Before we challenge the ecological validity of prisoner's  
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35 298 dilemma-type payoff matrices, we will challenge the notion that conflict-free  
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37 299 cooperation/mutualism is a stable endpoint of mutual helping in nature. Both  
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39 300 scenarios (starting out with by-product benefits or with prisoner's dilemma payoff  
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41 301 structure) have in common that the resulting levels of conflict are intermediate, i.e.  
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43 302 cooperative behaviour would persist to some extent even in the absence of partner  
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45 303 control mechanisms. Furthermore, both scenarios have in common that selection leads  
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47 304 to changes in individual strategy spaces, which in turn leads to changes in game  
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49 305 structure and corresponding payoff matrix.  
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3 307 A specific example is provided by Friedman & Hammerstein (1991) in their analysis  
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5 308 of egg trading in the simultaneously hermaphroditic hamlet fish (see Akçay &  
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7 309 Roughgarden 2011; Steward & Plotkin 2014 for other models). Hamlets form pairs in  
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9 310 the late afternoon. Partners alternate several times between releasing eggs and  
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11 311 fertilising eggs (Fischer 1988). This seems to be rather inefficient compared to each  
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13 312 partner releasing all eggs in one bout. However, such a release pattern would be  
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15 313 vulnerable to cheaters: as eggs are more costly to produce the individual that releases  
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17 314 its eggs first would face the risk that the partner fertilises the eggs and then leaves to  
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19 315 find a new partner that still has eggs. Releasing all eggs in one bout would correspond  
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21 316 to a sequential one-shot prisoner's dilemma game, where defection is the only stable  
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23 317 outcome. The evolution of a parcelling strategy, combined with waiting till late  
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25 318 afternoon, overcomes the problem of defection. Parcels are so small that the best  
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27 319 response to receiving a parcel for fertilisation is to give a parcel, to which the best  
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29 320 response is to provide the next parcel, until all eggs are fertilised. This is because the  
30  
31 321 benefits of staying are larger than the benefits of leaving: leaving involves search  
32  
33 322 costs and the risk of not finding another partner in the little time before sunset  
34  
35 323 (Friedman & Hammerstein 1991). Thus, the evolution of a parcelling strategy has  
36  
37 324 transformed the payoff matrix for each decision from a prisoner's dilemma game to a  
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39 325 pseudoreciprocity game (Friedman & Hammerstein 1991).  
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### 327 **Why most cases of helping are likely to involve intermediate levels of conflict**

#### 328 **a) Shifts from chance by-product benefits to coordination to conditional** 329 **helping in an asymmetric game**

330 As discussed earlier, by-product mutualism and positive pseudoreciprocity are based  
331 on the notion that helping is free of conflict, which provides ideal starting points for

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3 332 the evolution of helping, as often argued for mutualisms (Bergstrom et al. 2003,  
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5 333 Barbu et al. 2011). However, we argue that this game structure is often not stable.  
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7 334 Where by-product benefits occur, there would inevitably be selection on increased  
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9 335 association rates that cause coordination costs as well as selection on partner choice  
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11 336 (cf. Noë et al. 1991; Noë & Hammerstein 1995). We illustrate these points with an  
12  
13 337 example of collaborative hunting between groupers and partner species, such as  
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15 338 moray eels. While the benefits are entirely due to by-products of self-serving  
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17 339 behaviour, the magnitude of these benefits is likely to vary between individuals.  
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19 340 Empirically, it has been described that the willingness to participate in cooperative  
20  
21 341 hunting is variable in both partners (Bshary et al. 2006). Furthermore, there seems to  
22  
23 342 be individual variation in the ability to coordinate movements, perseverance, and the  
24  
25 343 frequency with which prey is flushed towards the partner. Such variation can be due  
26  
27 344 to ontogenetic effects, with evidence for individuals changing their behaviour  
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29 345 drastically between subsequent years (Redouan Bshary, unpublished data). In  
30  
31 346 addition, it seems likely that partners of different sizes have different prey preferences  
32  
33 347 and differential effects on prey escape behaviours. As a result, individuals have the  
34  
35 348 choice between more or less suitable (profitable) partners, and laboratory experiments  
36  
37 349 have demonstrated that groupers readily do choose better collaborators (Vail et al.  
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39 350 2014), something demonstrated first in chimpanzees (Melis et al 2006).  
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351  
352 The key point here is that these interspecific hunting associations form a biological  
353 market with individuals having the choice between different partners, sometimes  
354 belonging to different species, e.g. groupers may choose from moray eels, Napoleon  
355 wrasses and octopuses (Vail et al. 2014). As soon as there is exchange of goods or  
356 services, the market forces of supply and demand are expected to start operating (Noë

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3 357 et al. 1991, Noë & Hammerstein 1995). In particular, groupers should preferentially  
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5 358 associate with partner species or individuals that provide the best by-product benefits  
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7 359 and partners should prefer groupers that provide the best by-product benefits for them  
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9  
10 360 in turn. As the hunting associations are mutually beneficial, being involved in more of  
11  
12 361 them means increased foraging success, which should translate into an increased  
13  
14 362 fitness. Therefore, individuals are under selection to choose good partners and to be  
15  
16 363 chosen frequently. Competition within a class of traders over access to partners is  
17  
18 364 predicted to lead to outbidding (Noë et al. 1991). In the cooperative hunting example,  
19  
20 365 there is some observational evidence for outbidding at the partner recruitment stage.  
21  
22 366 First, it seems clear that groupers preferentially seek moray eels rather than Napoleon  
23  
24 367 wrasses to initiate a joint hunt in order to search for suitable prey (Bshary et al. 2006):  
25  
26 368 groupers associate above chance levels with moray eels but not with Napoleon  
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28 369 wrasse. The preference breaks down in areas where there are few partners available  
29  
30 370 (Vail et al. submitted). In contrast, in areas where partners are more abundant than at  
31  
32 371 the initial study site (Bshary et al. 2006), groupers alter their behaviour in an  
33  
34 372 important aspect: they rarely initiate joint hunting but instead join moray eels that  
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36 373 already started to move through the reef (Vail et al. submitted). Thus, the coordination  
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38 374 costs to start a hunting association are paid flexibly by different partner species  
39  
40 375 depending on partner availability. Arguably, most by-product mutualisms are likely to  
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42 376 involve such coordination costs. For example, mixed species associations in primates  
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44 377 yield by-product benefits due to the reduction in predation risk but the coordination  
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46 378 requires deviation from optimal foraging routes. The presence of this trade-off  
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48 379 explains why associations do not occur 100% of the time (Noë & Bshary 1997).  
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3 381 The conflict is well illustrated with the battle-of-the-sexes game in which two players  
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5 382 want to be together but differ in their spatial preferences, which create a conflict about  
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7 383 who is paying the cost for being together. Biological market theory can make  
8  
9 384 predictions about which class of traders is winning the battle and which one is losing  
10  
11 385 it (Noë & Hammerstein 1995). In the absence of markets, differences in needs may  
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13 386 result in ‘leaders’ and ‘followers’ (Lamprecht 1996; Harcourt et al. 2009; see  
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15 387 Bergstron & Lachmann 2003 for an evolutionary scenario for mutualisms) and, it is  
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17 388 also possible that individuals alternate in paying the coordination cost. Note that this  
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19 389 would lead to an alternating helping pattern without involving an iterated prisoner’s  
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21 390 dilemma payoff matrix.  
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27 392 In the grouper example, there is currently only evidence for shifts in which a partner  
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29 393 pays the coordination costs. However, it is easy to imagine that the biological market  
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31 394 would select newly arising strategies that go beyond the provisioning of by-product  
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33 395 benefits. For example, while successful individuals immediately stopped the  
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35 396 collaboration in all observed cases of successful hunts, an individual that would  
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37 397 continue the collaboration under such conditions might well benefit from such  
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39 398 investments if this increases the chance that partners more readily accept invitations  
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41 399 by this individual and/or choose this individual with increased probability.  
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47 401 In sum, we propose that any interaction that starts out as by-product benefits or as  
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49 402 pseudoreciprocity has the potential to evolve into a system that involves specific  
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51 403 investments with the sole purpose to be chosen as a partner, as soon as the system  
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53 404 involves a biological market. Under such circumstances, stable investments can be  
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55 405 achieved through the threat of partner switching, a form of negative pseudoreciprocity  
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3 406 (Bshary & Bergmüller 2008): individuals invest because it would otherwise be in the  
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5 407 self-interest of the partner to stop the interaction and switch to a different individual.  
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7 408 In conclusion, any form of by-product benefit may lead to partner choice whenever  
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9 409 partners differ in the magnitude of by-product benefits they provide. This in turn leads  
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11 410 to competition through outbidding and the evolution of investments, which are  
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13 411 monitored and insured through the threat of partner switching.  
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19 413 Fig 2 summarises the important steps from chance meetings to an asymmetric game in  
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21 414 a biological market. The amount of extra investment will be a function of the relative  
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23 415 abundance of the two classes of partners (Johnstone & Bshary 2008). If conditional  
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25 416 choices by the choosing class have a minor cost (denoted  $\epsilon$  in Fig. 2), negative  
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27 417 frequency dependent selection leads to the coexistence of bidding individuals  
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29 418 ('cooperators') and non-bidding individuals ('defectors') and partner switching as the  
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31 419 partner control mechanism employed by members of the choosing class. This scenario  
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33 420 corresponds in various important features to arguments put forward recently by André  
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35 421 (2015), who argued that the initial presence of helping may facilitate the evolution of  
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37 422 conditionals **strategies as** such a scenario resolves the bootstrapping problem.  
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43 424 **b) Shifts from maximal mutual levels of conflict to intermediate mutual levels of**  
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45 425 **conflict**

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47 426 An assumption of the standard iterated prisoner's dilemma game is that current  
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49 427 interaction partners have an independent past and an independent future once the  
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51 428 game is over. As a consequence the fitness of individuals is independent of the one of  
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53 429 their partner, apart from the link that is created through the payoff consequences of  
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55 430 their decisions during interactions. However, these assumptions are frequently not  
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3 431 met in nature, especially in animals that are most likely to have iterated interactions:  
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5 432 animals that live in stable social groups characterised by kinship, long-term  
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7 433 relationships, and social bonds. Under such conditions, the fitness of the social  
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10 434 animals can be strongly determined by interdependencies. The best-known and most-  
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12 435 studied interdependency is based on genetic relatedness and the resulting biological  
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14 436 altruism (kin selection, Hamilton 1964ab). Interestingly, however, long-term social  
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16 437 bonds between genetically unrelated individuals or even just being a member of the  
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18 438 same group are likely to have similar effects (Kokko et al. 1999; Eshel & Shaked  
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20 439 2001; Roberts 2005). As Roberts (2005) proposed, the logic of 'r' in Hamilton's rule  
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22 440 can in principle be applied to any form of interdependence and denoted the coefficient  
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24 441 's' for stake. Note though the functioning is quite different: the value of r is fixed for  
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26 442 related individuals, while a coefficient of interdependence between genetically  
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28 443 unrelated individuals can change with time and directly affects the values of b and c.  
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30 444 As an example of interdependence between unrelated individuals, in a slave-making  
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32 445 ant species, several unrelated queens team up and rapidly produce a sufficient number  
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34 446 of workers that can defend the common nest. For individual queens, there is no  
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36 447 temptation to cheat because any failure to contribute will automatically lead to the  
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38 448 failure of all queens (Bernasconi & Strassmann 1999). Once enough workers exist,  
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40 449 the interdependence between queens drops below a critical threshold and the queens  
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42 450 fight each other to the death until a single victor remains (Bernasconi & Strassmann  
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44 451 1999). The principle of interdependence applies more generally to social animals as  
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46 452 any helping that generates benefits from repeated interactions over a long time period  
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48 453 is likely to cause interdependence between partners. The higher the interdependence,  
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50 454 the more often social situations become such that it is a self-serving strategy to  
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52 455 support partners when they need it. Long-term partners become social assets that need  
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3 456 to be cherished and are costly to lose: helping is under positive selection as long as  
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5 457 the benefits for the recipient times the degree of interdependency outweighs the cost  
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7 458 of helping (Roberts 2005). Remember that this rule does not predict that individuals  
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9 459 always help, but that helping is contingent on the act yielding net benefits  
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11 460 *independently* of any reciprocal investment. Hence, we do not necessarily expect the  
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13 461 strict contingency postulated by the model of mutually conditional investments.  
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21 463 So what cases of helping between unrelated individuals may involve important levels  
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23 464 of interdependency? We propose that, as a general rule, interdependency is correlated  
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25 465 with the stability of partner availability. Stable relationships are most likely to occur  
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27 466 in stable groups. For example, in bi-parental bird species with life-long monogamy,  
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29 467 the death of the partner causes a decrease in the fitness of the surviving individual  
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31 468 (Black et al. 1996; Ens et al. 1996). Similar effects seem also to be present in primates  
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33 469 (Engh et al 2006). In many primates, individuals of one sex (typically females) remain  
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35 470 **all their life within their natal group** (Wrangham 1980). Evidence is accumulating that  
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37 471 under such circumstances, a stable core social network has a positive effect on  
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39 472 individual fitness (Silk et al 2009, 2010).  
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43 474 Interdependence is by no means restricted to group living species. Mutualisms in the  
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45 475 form of symbioses provide many good additional examples. Here, genetic  
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47 476 interdependence is absent but interdependence might still be strong if partners live  
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49 477 intimately together over extended time periods; it is maximal in case of joint vertical  
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51 478 transmission to the next generation. Well known cases of such symbioses include gut  
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53 479 bacteria, lichens, corals and some ant mutualisms (Bronstein 1994, 2001). For such  
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3 480 cases, it has been argued that interests are rather aligned and conflicts small  
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5 481 (Bronstein 1994, 2001, Leimar & Hammerstein 2010).

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9 483 **Interdependency versus mutually conditional investments based on an iterated**  
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11 484 **prisoner's dilemma**

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14 485 Despite the various critical reviews and the well-established role of mutual  
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16 486 dependency on helping, there is a considerable literature that seeks to explain helping  
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18 487 behaviour as forms of mutually conditional investments within an iterated prisoner's  
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20 488 dilemma framework, often based on observational data. Various recent highly  
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22 489 interesting studies on alternated helping with respect to vigilance in rabbitfish pairs  
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24 490 (Hughes & Bellwood 2015), coordinated hunting in lionfish (Lönstedt et al 2014)  
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26 491 and leading during migration flights in geese (Voelkl et al. 2015) yield great examples  
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28 492 for coordination but not for mutually conditional investments solving an iterated  
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30 493 prisoner's dilemma, at least not until it is demonstrated that investments are  
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32 494 contingent and a prisoner's dilemma payoff matrix is the most parsimonious  
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34 495 assumption. We argue that the latter is the more challenging part because of the  
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36 496 frequent occurrence of genetic and social interdependencies. We illustrate this  
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38 497 concern in Fig. 3, in which we show how interdependencies can transform a payoff  
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40 498 matrix that looks like a prisoner's dilemma into other games once the effects of  
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42 499 interdependency are included (see Dugatkin 1997 ; Peña et al 2015 for theoretical  
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44 500 papers).

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51 502 The best-known among the games emerging from interdependencies is the snowdrift  
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53 503 game, which is also called the hawk-dove game (when emphasising the competitive  
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55 504 rather than cooperative nature of an interaction; Maynard-Smith 1982). In this game,  
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3 505 an individual's best option depends on what the partner is doing. If the partner  
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5 506 cooperates the best option is to defect, if the partner defects the best option is to  
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7 507 cooperate. This is because mutual defection yields the lowest payoff for both players.  
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10 508 As a consequence, the success of cooperating and defecting displays negative  
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12 509 frequency dependence (Maynard-Smith & Price 1973). One possible solution is to  
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14 510 cooperate and to defect with probabilities that generate stable frequency dependence  
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16 511 (Maynard-Smith & Price 1973). However, this will lead to cases in which both  
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18 512 partners defect and hence both lose out, and hence various mechanisms may lead to  
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20 513 the emergence of co-operators and defectors (Doebeli et al. 2004, Dridi & Lehmann  
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22 514 2014). An even better solution would be that the two partners cooperate. How  
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24 515 partners would achieve this solution is not obvious, however, as an individual that  
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26 516 knows that the partner always defects should always cooperate to maximize its own  
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28 517 payoff. Mutually conditional helping that is contingent on the partner's behaviour  
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30 518 would provide a solution. The option to switch partners in a biological market might  
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32 519 offer an alternative control mechanism to achieve high levels of mutual help as co-  
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34 520 operators could leave defectors. As the baseline level of helping is not zero like in a  
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36 521 prisoner's dilemma payoff matrix but b/c, resulting high levels of helping would be  
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38 522 partially self-serving and partially mutually conditional investments (Fig. 4).  
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## 526 **General discussion**

527 Our general goal has been to understand the evolution of dyadic cooperation and  
528 mutualism. The theoretical literature is heavily biased towards the iterated prisoner's  
529 dilemma game, but there is little evidence for this game in natural systems. A

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3 530 currently popular alternative explanation is pseudo-reciprocity (Clutton-Brock 2009,  
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5 531 Leimar & Hammerstein 2010), a situation in which partners have come to rely on  
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7 532 each other with a stake in other's success, and so both benefit from helping. While  
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10 533 pseudoreciprocity is thus rather conflict-free, we have made verbal arguments why  
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12 534 ecology and evolution may often alter individual strategy space such that asymmetric  
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14 535 games emerge in which conflicts of interest between partners are of intermediate level  
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16 536 rather than minimal or maximal. Conversely, we argued for games of maximal  
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18 537 conflict, i.e. in the form of iterated prisoner's dilemmas, that ecology and evolution  
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20 538 may often drive individual strategy space such that interdependency leads to games  
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22 539 with intermediate conflict levels, as exemplified by the snowdrift game.  
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27 541 The take home message is that some level of conflict is bound to be widespread in  
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29 542 both cooperation and mutualism. On the other hand, maximal conflict based on a  
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31 543 prisoner's dilemma payoff matrix is most likely rare. Even the primate examples  
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33 544 presented earlier that provided convincing evidence for mutually conditional  
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35 545 investments between non-bonded group members (Cheney et al 2010; Borgeaud &  
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37 546 Bshary 2015) might still be built on top of a low level of unconditional helping due to  
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39 547 interdependence (group augmentation, Kokko et al. 1999). The temptation to fully  
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41 548 defect is most likely to be found in some mutualisms characterised by short  
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43 549 interactions where the fitness of a behavioural phenotype of an individual is hardly  
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45 550 affected by the partner's survival. However, we do not know of cases based on mutual  
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47 551 temptation to defect as assumed by the iterated prisoner's dilemma game. Instead,  
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49 552 mutualisms often represent games with asymmetric strategic options. Marine cleaning  
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51 553 mutualisms involving cleaner wrasses of the genus *Labroides* provide a case in point.  
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53 554 These cleaners have inherent preference for the clients' mucus over their  
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3 555 ectoparasites, so that feeding on the latter can be interpreted as an investment (Grutter  
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5 556 & Bshary 2003). More importantly, cleaners that follow their inherent preferences  
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7 557 (i.e. cheat by feeding on mucus) may slightly reduce client survival but will otherwise  
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10 558 not suffer any further r<sup>o</sup>ussions, mainly because they interact with many different  
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12 559 clients (Côté 2000) and typically live shorter than them (data available on  
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14 560 fishbase.org). In contrast, the vast majority of client species has no means to defect on  
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16 561 a cleaner, i.e. to perform a behaviour that increases own payoff at the expense of a  
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18 562 cooperating cleaner. Possibly because the conflict does not involve interdependencies,  
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20 563 the system has yielded experimental evidence for a variety of partner control  
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22 564 mechanisms, including punishment, partner switching and social prestige (Bshary &  
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24 565 Grutter 2005, Pinto et al. 2011). Asymmetric cheating options are highly abundant in  
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26 566 mutualisms, with experimental evidence that contingent helping may occur even in  
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28 567 plants and insects (Pellmyr & Huth 1994; Kiers et al. 2003; Brandenburg et al. 2012).  
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30 568 For within-species cooperation, evidence for pay-to-stay in cooperatively breeding  
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32 569 systems (Bergüller & Taborsky 2005) provides a class of examples if one classifies  
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34 570 reduced conflict as cooperation. Hamilton & Taborsky (2005) made the point that in  
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36 571 the absence of additional incentives pay-to-stay only leads to minimal exploitation of  
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38 572 breeders by helpers.  
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45 574 In conclusion, we see great scope for both theoreticians and empiricists to consider  
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47 575 games with intermediate levels of conflict, and to explore how selection on changes in  
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49 576 individual strategy spaces lead to changes in game structure and payoff matrices.  
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51 577 Mutual or alternating, conditional helping does not in itself provide evidence for an  
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53 578 iterated prisoner's dilemma, as the same patterns may emerge in an iterated snowdrift  
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55 579 game or an iterated battle-of-the-sexes game. Furthermore, as we have suggested  
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3 580 repeatedly in this paper, the market conditions in each study system have to be  
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5 581 understood and incorporated. While free markets favour both conflict and the easy  
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7 582 solution of partner switching, more restricted markets reduce conflict but potentially  
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10 583 offer no solution to the remaining conflict level.

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14 585 Finally, it will be interesting to investigate in how far the payoff structure is linked to  
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16 586 various features of social interactions in stable groups; i.e. features that have been  
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18 587 traditionally introduced by primatologists to the study of animal behaviour: gradual  
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20 588 build-up of relationships (bonds; Silk 2003), reconciliation and other repair or  
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22 589 servicing mechanisms (Aureli & Waal 2000), including negotiation (van de Waal et  
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24 590 al. 2013) or inequity aversion (Brosnan & de Waal 2003). Linked to this issue, one  
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26 591 can ask questions about the cognition underlying these features. Stake-based  
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28 592 cooperation is predominantly described in long-lived animals with long-term social  
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30 593 bonds, individual recognition, and good memory capacities (Seyfarth & Cheney  
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32 594 2012) but stakes exist also in other systems. The monitoring of partner behaviour  
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34 595 within a broader social context and corresponding high degrees of freedom with  
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36 596 respect to own behavior may well make social relationships cognitively demanding  
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38 597 and hence a key aspect of the Social brain hypothesis (Dunbar & Schultz 2007). Of  
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40 598 overarching importance is that we understand the ecology of our study species.  
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42 599 Differences in life-history, social systems, genetic relatedness and cognitive abilities  
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44 600 are likely to have a major influence on levels of helping and underlying decision  
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46 601 rules. Only if we know the diversity of social interactions and helping patterns  
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48 602 observable in our study species in nature can we conduct meaningful field or lab  
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50 603 experiments.  
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3 605 **Acknowledgements**  
4

5 606 We thank the editors for the invitation to write this paper. Furthermore, we are  
6  
7 607 grateful to Michael Taborsky, Jean-Baptiste André and an anonymous referee for  
8  
9 608 constructive comments. All authors are funded by individual grants from the Swiss  
10  
11 609 Science Foundation.  
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16 611 **Competing interests**  
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18 612 The authors declare no competing interest  
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23 614 **Authors' contributions**  
24

25 615 All three authors were involved in the initial discussion of the topic. RB drafted a first  
26  
27 616 version that was then edited by KZ mainly for clarity and by CvS for conceptual  
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29 617 issues.  
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3 883 **Figure legends**  
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5 884 Fig. 1: relative payoff matrices for 4 different stylised games. In each game two  
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7 885 players have the choice of either invest (cooperate) or defect. The payoffs in the  
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10 886 matrix are those for player 1. As the prisoner's dilemma is typically illustrated with  
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12 887 the numbers 3,0,5,1 we kept these numbers for the other games. Note that in the  
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14 888 battle-of-the-sexes game, mutual investment would mean that each player goes to  
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16 889 where the partner would prefer to go, meaning that each one ends up alone at the own  
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18 890 less preferred place, which leads to the lowest possible payoff.  
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21 891  
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23 892 Fig. 2: Changes of payoffs as a consequence of selection leading to changes of  
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25 893 individual strategies. Payoffs in each matrix are ranked relative to each other and not  
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27 894 comparable between payoff matrices. The first payoff matrix represents a game prior  
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29 895 to evolution, where players meet by chance and increase their payoffs as a  
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31 896 consequence of by-product benefits. Due to resulting selection on increased  
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33 897 associations, coordination costs arise that could be shared paid by one partner.  
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35 898 Asymmetric partner choice options will to members of the chosen class trying to  
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37 899 outbid each other by evolving extra investments for the sole benefit of partners in  
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39 900 order to be chosen. If conditional choices by the choosing class has a minor cost  $\epsilon$ ,  
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41 901 negative frequency dependent selection leads to the coexistence of bidding  
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43 902 individuals ('cooperators') and non-bidding individuals ('defectors'). As members of  
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45 903 the chosen class need to pay the coordination costs in any case, they invariably gain  
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47 904 less than members of the choosing class.  
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54 906 Fig. 3: Examples how payoff matrices that fulfil the criteria for a prisoner's dilemma  
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56 907 ( $T > R > P > S$  and  $2R > T + S$ ) transform into qualitatively different payoff matrices if  
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3 908 there is either genetic relatedness or social interdependency between partners. In all  
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5 909 cases, Hamilton's relatedness coefficient  $r =$  the interdependency coefficient  $s = 0.5$ .  
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7 910 The first payoff matrix transforms to a snowdrift game, the second to a game in which  
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9 911 investing is dominant over defecting, and the third into a game we are not aware it has  
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11 912 a name. Crucially, all the resulting payoff matrices do not feature always defect as an  
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13 913 ESS but instead intermediate or full levels of cooperation.  
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19 915 Fig. 4: On the left: ESS 'default' levels of cooperating in different games: 100% for  
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21 916 by-product benefits and positive pseudoreciprocity, b/c for a snowdrift game and 0%  
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23 917 for a prisoner's dilemma game. For the latter games, iterated interactions may allow  
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25 918 the evolution of full cooperation based on mutually conditional investments. Given  
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27 919 that snowdrift games yield intermediate levels of cooperating by default, the  
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29 920 challenge for researchers will be to identify the additional partially reciprocal  
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31 921 investments on top of those intermediate levels. 

Prisoner's dilemma

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		player 2	
		invest	defect
player 1	invest	3 / 3	1 / 4
	defect	4 / 1	2 / 2

By-product helping

		player 2	
		help	no help
player 1	help	4 / 4	2 / 3
	no help	3 / 2	1 / 1

Battle-of-the-sexes

option1  
player 1  
option2

		player 2	
		option1	option2
player 1	option1	4 / 3	2 / 2
	option2	1 / 1	3 / 4

Snowdrift game

help  
player 1  
no help

		player 2	
		help	no help
player 1	help	3 / 3	2 / 4
	no help	4 / 2	1 / 1

Fig.1



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Prisoner's dilemma matrices

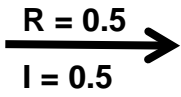
resulting matrices

**player 2**

	invest	defect
<b>invest</b>	R = 3	S = 0
<b>defect</b>	T = 5	P = 1

**player 2**

	invest	defect
R = 4.5	S = 2.5	
T = 5	P = 1.5	



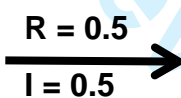
Snowdrift game

**player 2**

	invest	defect
<b>invest</b>	R = 3	S = 0
<b>defect</b>	T = 4	P = 1

**player 2**

	invest	defect
R = 4.5	S = 2.5	
T = 4	P = 1.5	



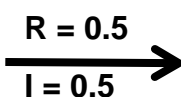
'Prisoner's delight'

**player 2**

	invest	defect
<b>invest</b>	R = 2	S = 0
<b>defect</b>	T = 3	P = 1

**player 2**

	invest	defect
R = 3	S = 1.5	
T = 3	P = 1.5	



?equal opportunities?

Fig.3

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ESS levels of cooperating

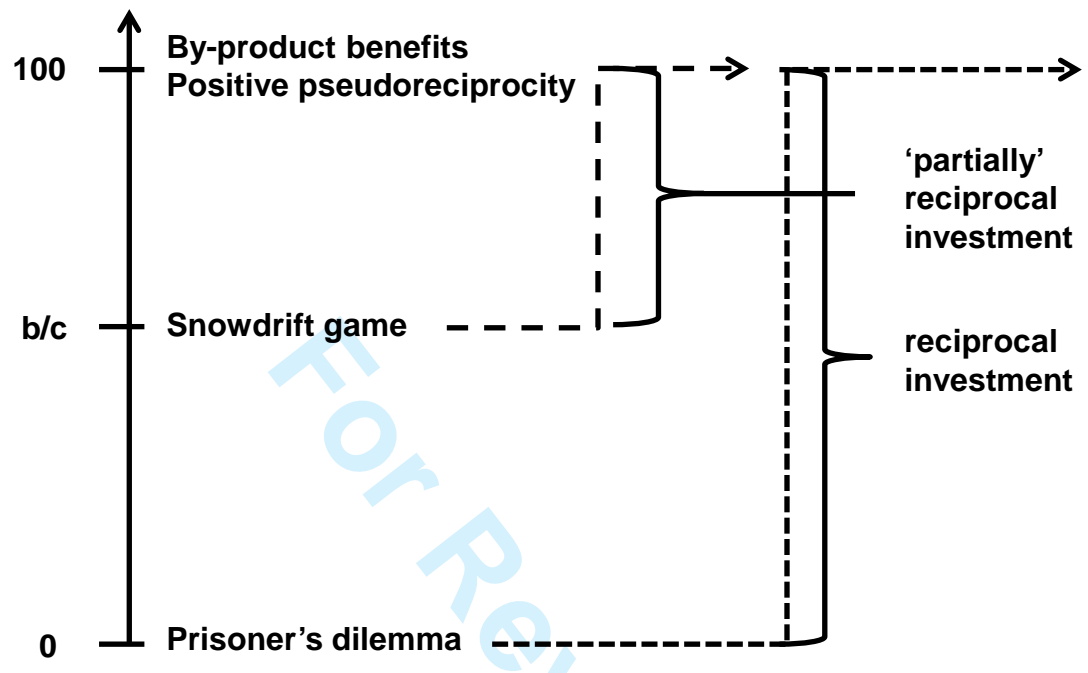


Fig.4

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Fig. 2: Shifts from chance by-product benefits to coordination to conditional helping in an asymmetric game

