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# Nothing better to do? Environment quality and the evolution of cooperation by partner choice

Paul Ecoffet<sup>1,2</sup>

[paul.ecoffet@sorbonne-universite.fr](mailto:paul.ecoffet@sorbonne-universite.fr)

Nicolas Bredeche<sup>1,\*</sup>

Jean-Baptiste André<sup>2,\*</sup>

<sup>1</sup> Sorbonne Université, CNRS, ISIR, F-75005 Paris, France

<sup>2</sup> Institut Jean Nicod, Département d'études cognitives, ENS, EHESS, PSL Research University, CNRS, Paris France

\* Co-last authors

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## *Data availability*

All data and source code used for the making of this article is available at

<https://osf.io/p5whz>.

## *Keywords:*

Cooperation ; Partner Choice ; Agent-Based Model ; Resource availability ; Biological Market

# Nothing better to do? Environment quality and the evolution of cooperation by partner choice

## Summary Statement

Partner choice enables individuals to avoid defectors, but is seldomly observed in non-human animals. We show that the availability of opportunities, depending on both resources *and* partners, is critical.

## Abstract

The effects of partner choice have been documented in a large number of biological systems such as sexual markets, inter-specific mutualisms, or human cooperation. By contrast, this mechanism has never been demonstrated in a large number of intra-specific interactions in non-human animals such as collective hunts, although one would expect it to play a role as well. Here we use individual-based simulations to solve this apparent paradox. We show that the conditions for partner choice to operate are in fact restrictive. They entail that individuals can compare social opportunities and choose the best. The challenge is that social opportunities are often rare because they necessitate the co-occurrence of (i) at least one available partner, and (ii) a resource to exploit together with this partner. This has three consequences. Firstly, partner choice cannot lead to the evolution of cooperation when resources are scarce, which explains that this mechanism could never be observed in many cases of intra-specific cooperation in animals. On the other hand, partner choice can operate when partners constitute in themselves a resource, which is the case in sexual interactions and inter-specific mutualisms. Lastly, partner choice can lead to the evolution of cooperation when individuals are highly efficient at finding resources in their environment, which sheds light on the relationship between cognitive abilities and cooperation, in particular in the human species.

## 1. Introduction

Among the diversity of mechanisms put forward to explain the evolution of cooperation among non-kin, partner choice has been considered over the last twenty years as having probably played a particularly important role (Baumard, André, & Sperber, 2013; Bull & Rice, 1991; Eshel & Cavalli-Sforza, 1982; Noë & Hammerstein, 1994; Schino & Aureli, 2017;

27 West, Griffin, & Gardner, 2007). When individuals can choose among several different  
28 partners, which they can compare and compete against each other as in an economic  
29 market, this generates a selection pressure to cooperate more, in order to appear as a good  
30 partner, and attract others' cooperation (Noë & Hammerstein, 1994).

31 The effects of partner choice have been well described in a large number of biological  
32 systems. (Noë, Van Hooff, & Hammerstein, 2001). For example, in the interaction between  
33 cleaner fishes and their clients the law of supply and demand determines the way in which  
34 the added value of the interaction is shared, in accordance with market principles (Bshary  
35 & Grutter, 2006). When cleaners are rare, clients tolerate cheating on their part, while they  
36 become more picky when cleaners are numerous. The effects of partner choice have been  
37 documented in primate grooming, in meta-analyses showing that females groom  
38 preferentially those that groom them most and that a positive relation exists between  
39 grooming and agonistic support (Schino, 2007; Schino & Aureli, 2008). In vervet monkeys,  
40 experiments have shown that individuals groom others in exchange for access to food, and  
41 do so for longer periods when fewer partners are available (Fruteau, Voelkl, Van Damme, &  
42 Noë, 2009). The effects of partner choice have also been documented in humans where it  
43 has been shown that the need to attract social partners is a major driver of cooperation  
44 (Barclay, 2016; Barclay & Vugt, 2015; Barclay & Willer, 2007; Baumard et al., 2013;  
45 Stephane Debove et al., 2015). Besides, beyond cooperation partner choice also plays a  
46 decisive role in mating, leading to the evolution of secondary sexual characteristics, nuptial  
47 gifts, and/or to assortative matching (Andersson & Simmons, 2006; Hammerstein & Noë,  
48 2016; Zahavi, 1975).

49 On the other hand, there are a number of other biological situations in which one would  
50 typically expect partner choice to also play an important role, but where no such effect has  
51 ever been demonstrated. These include most intraspecific collective actions in non-human  
52 animals. This is particularly salient in collective hunts such as collobus hunting in  
53 chimpanzees, or pack hunting in carnivores. No empirical evidence in these species  
54 suggests that individuals cooperate for reasons related to partner choice, either to attract  
55 partners or to be accepted by them in their hunts. On the contrary, the majority of available  
56 data are consistent with the more parsimonious explanation that individuals are simply

57 doing what is in their immediate best interest at any given time (Melis, Hare, & Tomasello,  
58 2008; Melis, Schneider, & Tomasello, 2011; Packer, 1986; Packer & Ruttan, 1988). In  
59 particular, if cooperation in collective hunts was driven in part by the need to appear as a  
60 good partner, individuals would be expected to willingly share the product of their hunts in  
61 a way that depends on everyone's actual engagement, to encourage participation in other  
62 hunts in the future. However, such voluntary and conditional sharing has never been  
63 documented in animal collective hunts (Melis et al., 2011). In evolutionary terms, therefore,  
64 collective hunting in these species is most likely an instance of *by-product* cooperation,  
65 rather than an instance of reciprocal cooperation based on partner choice. This lack of  
66 observation is all the more surprising given that, in similar collective actions, human  
67 behaviours are demonstrably driven by the need to appear as a good partner (Alvard &  
68 Nolin, 2002; Baumard et al., 2013). One may therefore wonder why the same effects did not  
69 produce the same consequences in other species.

70 Such a lack of observation could always be the consequence of methodological difficulty in  
71 empirically proving the existence of partner choice, and more generally of conditional  
72 cooperation, outside humans (McElreath et al., 2003; Raihani & Bshary, 2011). However, we  
73 would like to suggest an alternative here, namely that there is in fact a strong constraint  
74 impeding partner choice in a large number of situations.

75 Partner choice requires that individuals can compare and choose among several  
76 opportunities for cooperation. In some cases, *partners* themselves constitute opportunities  
77 for cooperation and partner choice then only requires that partners are many and  
78 accessible. This is the case, for instance, in mating markets, or in most instances of  
79 interspecific mutualism.

80 In other cases, however, finding an opportunity for cooperation requires more than just  
81 finding a partner. This is what happens when cooperation consists of several individuals  
82 working together to exploit environmental resources. In this case, a cooperation  
83 opportunity requires both a partner(s) and a resource, which imposes an additional  
84 constraint limiting the scope of partner choice. When resources are scarce, there are always  
85 few options to compare, and partner choice cannot operate. This could explain the lack of

86 cooperation, beyond by-product cooperation, in many instances of collective actions in the  
87 wild despite the availability of potential partners.

88 To our knowledge, all models published so far on the evolution of cooperation by partner  
89 choice focus on situations where finding a partner is sufficient to create an opportunity to  
90 cooperate. In this case, they show that partner choice is able to drive the evolution of  
91 cooperation in a relatively wide range of circumstances (Aktipis, 2004, 2011; J.-B. André &  
92 Baumard, 2011; André & Baumard, 2011; Barclay, 2011; Campenni & Schino, 2014;  
93 Stéphane Debove et al., 2015; Debove, Baumard, & André, 2017; Geoffroy, Baumard, &  
94 Andre, 2019; Johnstone & Bshary, 2008; McNamara, Barta, Fromhage, & Houston, 2008;  
95 Noë & Hammerstein, 1994). In this paper, we wish to examine what happens on the  
96 contrary when resource availability constitutes a constraint on the operation of partner  
97 choice. To do so, we simulate the evolution of agents placed in an environment containing  
98 resources that can be exploited collectively. We show that, in a low-resource environment,  
99 and even if there are plenty of partners, partner choice is not able to drive the evolution of  
100 cooperation as individuals cannot pit the few cooperation opportunities against each other.  
101 What is more, we also show that the number of potential partners actually has a negative  
102 effect on the evolution of cooperation when patches are scarce. When potential partners are  
103 numerous relative to the number of patches available, there are always too many  
104 individuals on any given resource as individuals have nothing else to do anyway. Hence,  
105 there is no point in trying to attract partners but on the contrary there are benefits in trying  
106 to limit their number. Partner choice is thus only effective when the number of available  
107 partners lies within a precise range of values, all the narrower as the availability of patches  
108 is low.

109 We believe that this constraint plays a central role in explaining that, in many species,  
110 although individuals do participate in collective actions, sometimes finely coordinating  
111 their behaviour with that of others, they do not actually seek to cooperate beyond what is in  
112 their immediate personal interest. In contrast, in the case of the human species, thanks to  
113 extensive cognitive skills individuals are able to extract resources from a greater variety of  
114 situations. As a result, humans actually live in an environment that is much richer in  
115 resources than other species. Hence they can compare and compete over a greater diversity

116 of opportunities for cooperation against one another, and are thus forced to cooperate more  
117 intensively to attract partners.

## 118 2. Methods

119 We consider a population of  $N_e$  individuals living in an environment consisting of  $\omega$   
120 different patches on which resources are located. Every generation of the simulations is  
121 constituted of  $T$  time steps during which individuals gather payoff units. At the end of these  
122  $T$  time steps, individuals reproduce in proportion to their total payoff, and die. During a  
123 time step, every individual is considered one by one in a random order. When her turn  
124 comes, an individual evaluates each of the  $\omega$  patches of the environment, including the  
125 patch where she is currently located, assigns each a score (details in section 2.1), and then  
126 moves toward the patch with the highest score, or stays on her current patch if that's the  
127 one with the highest score. Once every individual has taken this decision, individuals  
128 express their cooperation strategy on their local patch, and they collect a payoff that  
129 depends on their own and their partners' cooperation strategy. Patches can disappear every  
130 time step, with a probability  $d$ , and are then immediately replaced by an empty patch.

131 In our analyses, we will vary  $N_e$ , which represents the number of individuals present  
132 together in the environment (i.e. the social population size). However, we want to keep  
133 constant the genetic population size ( $N \geq N_e$ ) so as not to alter the relative strength of drift  
134 and selection. To do so, we create  $\lceil N_e/N \rceil$  parallel environments. The  $N$  individuals of the  
135 genetic population are then randomly assigned, so that each environment has exactly  $N_e$   
136 individuals. For the last environment to be completed, randomly chosen genetic individuals  
137 are duplicated, but their payoff in this environment is then not considered for the  
138 calculation of their fitnesses.

### 139 2.1. The decision-making mechanisms

140 The individuals' strategy in this environment consists of two separate decisions.



141 On the one hand, the individual must evaluate the different patches available and assign a  
142 score to each. This decision is made by an artificial neural network, called the “patch  
143 ranking” network. For each patch, this neural network has the following input information:  
144 (i) the number of other individuals already present on the patch, (ii) the average level of  
145 cooperation expressed by these individuals in the last time step, (iii) the level of  
146 cooperation that the focal individual would express should she join this patch, and (iv) a  
147 binary that indicates whether or not the individual would have to move in space in order to  
148 join this patch (i.e. this binary distinguishes the patch where the individual is currently  
149 located from all other patches). For (i), (ii) and (iii), their values are partitioned into a  
150 number of decimals and a number of units, each projected to a distinct input of the neural  
151 net. This allows the controller to easily distinguish small variations.

152 On the other hand, the individual must decide on a level of cooperation once she is on a  
153 patch. This decision is made by another artificial neuron network called the “cooperation”  
154 network (plus some phenotypic variability, see below). As an input, this neural network  
155 only has the number of other individuals present on the same patch as the focal. This entails  
156 that we assume that the agent cannot modulate her cooperation level in function of others’  
157 cooperation level. This assumption is meant to exclude the possibility that partner control  
158 strategies may evolve, and allows us to focus only on the effect of partner choice (Schino &  
159 Aureli, 2017).

160 The connection weights of both networks constitute the genome of each agent. They evolve  
161 by natural selection as exposed in the section 2.3.

### 162 **2.1.1. Phenotypic variability of cooperation**

163 Each individual  $i$  present on a patch invests a given amount  $x_i$  into cooperation –where  $x_i$  is  
164 decided by the individual’s cooperation network. However, as is now well established in the  
165 literature, selective pressures in favour of any form of conditional cooperation, and  
166 therefore in particular in favour of partner choice, stem from the presence of some  
167 variability in partners’ cooperative behaviour (see (McNamara & Leimar, 2010) for a  
168 review of this idea). In order to capture the effect of variability in the simplest possible way,  
169 here we consider the effect of phenotypic variance in the expression of individuals’ genes.

170 At each generation of our simulations, each individual is subject to the effect of a *phenotypic*  
 171 *noise* that modifies her cooperation level. If  $x_i^g$  is the cooperation level decided by the  
 172 cooperation network of individual  $i$ , then the actual cooperation level player by the  
 173 individual is  $x_i = x_i^g + \epsilon$ , where  $\epsilon$  is drawn randomly as follows. The interval  $[-1, 1]$  is  
 174 uniformly split in  $N_e$  values, and every individual gets one value of  $\epsilon$  chosen among these  $N_e$   
 175 values without replacement.

## 176 2.2. The payoff function

177 Individuals present on the same patch play a modified version of the n-player prisoner's  
 178 dilemma. Consider a focal individual  $i$  playing  $x_i$ , in a patch on which there are  $n - 1$  other  
 179 individuals whose average level of cooperation is  $\bar{x}_{-i}$ . The payoff of individual  $i$  is given by

$$180 \quad P(x_i, \bar{x}_{-i}, n) = F(n) \times \left[ ax_i + b\bar{x}_{-i} - \frac{1}{2}x_i^2 \right]$$

181 where  $a$  represents the immediate, self-interested, benefit of cooperation, and  $b$  represents  
 182 the social benefit of cooperation for others. The function  $F(n)$  is meant to capture the fact  
 183 that there is an optimal number of individuals exploiting a patch and is given by

$$184 \quad F(n) = e^{-\frac{(n - \hat{n})^2}{2\sigma^2}}$$

185 where  $\hat{n}$  is the optimal number of individuals per patch and  $\sigma$  measures the tolerance to  
 186 variations in the number of individuals per patch (i.e.,  $\sigma^{-1}$  measures the strength of the  
 187 penalty that stem from being a suboptimal number of individuals on the same patch).

188 This payoff function has been chosen in such a way that, in the absence of partner choice,  
 189 the evolutionarily stable strategy is always to invest the individually optimal investment  
 190 (i.e.  $x_{ESS} = a$ ), whereas the "socially optimal" cooperation, that is the level of cooperation  
 191 that would maximise the average payoff of individuals on the patch, is to invest  $\hat{x} = a + b$ .

## 192 2.3. The evolutionary algorithm

193 Each individual has a genome composed of the weights of its two neural networks, which  
 194 makes a total of 84 genes  $g = (g_1, \dots, g_{84})$  with  $g_i \in ] - 10, 10[$ . We consider a population of

195 fixed size  $N$ . The first generation is composed of  $N$  individuals with random genes for the  
 196 neural network weights, drawn uniformly in  $] - 1,1[$ . We then use a fitness proportionate  
 197 evolutionary algorithm to simulate evolution. After the  $T$  time steps of a generation have  
 198 taken place, individuals all reproduce and die. A new population of  $N$  individuals is built out  
 199 of the previous generation by sampling randomly among the  $N$  parents in proportion to  
 200 their cumulated payoff, according to a Wright-Fisher process.

201 A mutation operator is applied on each offspring. Every gene of every offspring has a  
 202 probability  $\mu$  to mutate and a probability  $1 - \mu$  to stay unchanged. If a gene  $g_i$ , with value  $v_i$ ,  
 203 mutates, it has a probability 0.9 to mutate according a normal distribution and thus reach a  
 204 new value sampled in  $\mathcal{N}(v_i, 0.1)$  and a probability 0.1 to mutate according to a uniform  
 205 distribution and thus reach a new value sampled in  $\mathcal{U}(] - 10, 10[)$ .

206 The evolutionary algorithm is run for  $G$  generations.

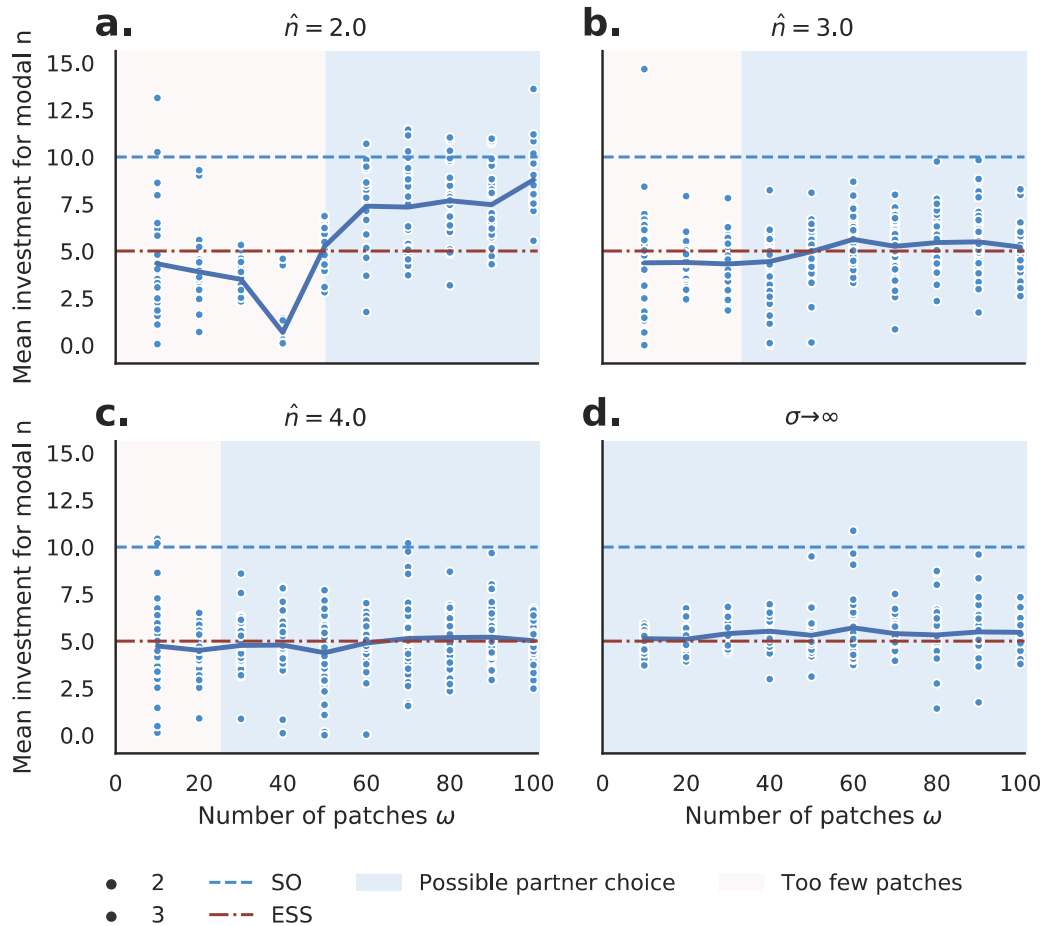
| Parameter          | Description  | Value    |
|--------------------|--|----------|
| <b>Environment</b> |  |          |
| $N$                | Population size  | 100      |
| $d$                | Probability of disappearance of patches, per time step         | 1/1 000  |
| $T$                | Number of timesteps per generation                             | 1 000    |
| $c_m$              | Cost of moving to another patch                                | 0        |
| $N_e$              | Number of individuals in the local environment                 | variable |
| <b>Payoff</b>      |  |          |
| $a$                | Immediate personal benefit of cooperation                      | 5        |
| $b$                | Social benefit of cooperation                                  | 5        |
| $\hat{n}$          | Optimal number of individuals per patch                        | variable |
| $\sigma$           | Tolerance to variations in the number of individuals per patch | variable |
| <b>Evolution</b>   |  |          |
| $G$                | Number of generations  | 1 500    |

$\mu$  Probability of mutation per gene per generation 0.01

## 207 3. Results

### 208 3.1. Cooperation cannot evolve when patches are scarce

209 We simulated the evolution of a population of  $N_e = 100$  individuals for  $G = 1500$   
210 generations, for different values of the number of resource patches  $\omega$ , but always in a  
211 situation where the optimal number of individuals per patch was  $\hat{n} = 2$ . Cooperation only  
212 evolved when patches were more abundant than a threshold (Fig. 1, a). This can be  
213 understood as follows. When resource patches are few, precisely when  $\omega < \frac{N_e}{\hat{n}}$ , individuals  
214 have little cooperation opportunities and there are therefore always more individuals per  
215 patch than what would be optimal (in this case, the optimal number of individuals per patch  
216 is  $\hat{n} = 2$ ). As a result, additional individuals joining a patch are more of a nuisance than a  
217 benefit, and there is therefore no benefit in trying to attract partners by appearing  
218 cooperative.



219

220 *Fig 1: Mean investment in simulation for different number of opportunities  $\omega$  and a fixed*  
 221 *population of  $N_e = 100$  individuals. Results after 1 500 generations. **a.** When  $\hat{n} = 2, \sigma = 1$*   
 222 *Cooperation evolves when  $\omega \geq 50$ . **b-c.** For  $\hat{n} \geq 3, \sigma = 1$ , cooperative behaviours never evolve.*  
 223 ***d.** When  $\sigma \rightarrow \infty$ , there is no pressure for agent to attract partners and cooperative behaviours*  
 224 *never evolve.*

225 We then simulated the evolution of cooperation in situations where the optimal number of  
 226 individuals per patch,  $\hat{n}$ , was larger (Fig. 1, b-c). Overall, the outcome was even less  
 227 favourable to cooperation. This may seem paradoxical but can be understood as a  
 228 consequence of the law of large numbers. When the number of individuals per patch is  
 229 large, whether it is greater or less than  $\hat{n}$ , the effect of each individual on the average quality  
 230 of her patch is very small anyway. There is therefore little value for an individual to invest  
 231 in cooperation to try and attract partners.

232 We performed the same simulations in the case where the number of individuals per patch  
233 is neutral ( $\sigma \rightarrow \infty$ , Fig. 1, d). Cooperation did not evolve either and this can be understood  
234 also because there cannot be any benefit in attracting partners when the number of  
235 individuals per patch does not matter.

236 Finally, we run simulations where we vary the coefficient of friction  $\sigma$  and find that the  
237 lower the friction (ie. the higher the  $\sigma$ ), the less cooperative the agents are. The results are  
238 available in the supplementary materials (Fig. S1). We also varied the cost of moving for the  
239 agents and find that the higher the cost, the less cooperative the agents are, as expected  
240 from the literature on partner choice. These results are available in the supplementary  
241 materials (Fig. S2).

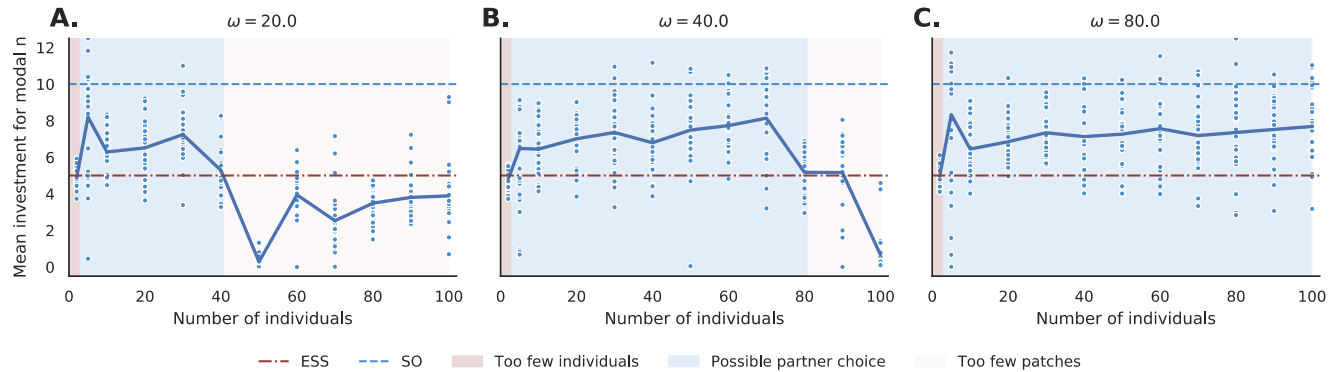
242 Overall, the evolution of cooperation by partner choice can only take place in the restricted  
243 conditions where (i) there is an optimal number of individuals per resource patch, (ii) this  
244 optimal number is low, and (iii) the number of resource patches in the environment is large.

### 245 **3.2. Cooperation cannot evolve when there are too many partners** 246 **around**

247 In a second step, we simulated again the evolution of a population of  $N = 100$  individuals  
248 for  $G = 1500$  generations in a situation where the optimal number of individuals per patch  
249 was  $\hat{n} = 2$ , but this time we held the number of patches constant,  $\omega = 20$ , while varying the  
250 actual number of individuals,  $N_e$ , present together in the environment.

251 In this case, cooperation only evolved when the number of individuals in the environment  
252 was intermediate. This can be understood as follows. When the number of individuals in the  
253 environment,  $N_e$ , is too close to the number of individuals,  $\hat{n}$ , that are needed to exploit at  
254 least one patch –or even more so when  $N_e < \hat{n}$ , then the number of available partners is  
255 limiting. As a result, the actual number of cooperation opportunities from which individuals  
256 can choose is very low, partner choice is thus a weak force, and the benefit of investing into  
257 cooperation is low. On the other hand, when the number of individuals in the environment,  
258  $N_e$  is larger than the total number of individuals that can be accommodated on the available  
259 patches, that is when  $N_e > \hat{n}\omega$ , the number of available patches is limiting. In this case we

260 find the result described above (Fig. 2, a). The problem is rather that there are always too  
 261 many individuals on each patch than too few and partner choice is also a weak force. There  
 262 is, therefore, a range of intermediate population densities, neither too low nor too high, for  
 263 which cooperation can evolve.



264

265 *Fig 2: Effect on the population size in the environment with 20, 40 or 80 patches and an*  
 266 *optimal number of agents  $\hat{n} = 2$  and  $\sigma = 1$ . Agents have a cooperative behaviour for  $\hat{n} < N_e$*   
 267  *$< \omega \times \hat{n}$ .*

268 We then performed the same simulations again, but with more patches available in the  
 269 environment (i.e. for larger  $\omega$ , Fig. 2, b, c). We observed that the range of population  
 270 densities for which cooperation could evolve was then broader. This can again be  
 271 understood in the above framework. On one hand, the lower boundary of population  
 272 density,  $N_e \approx \hat{n}$ , below which the number of individuals is a limiting factor, is unaffected by  
 273 the number of patches available. On the other hand, the upper boundary of population  
 274 density,  $N_e > \hat{n}\omega$ , above which the number of patches is a limiting factor, increases with the  
 275 number of patches,  $\omega$ . As a result, the width of the range of population densities where  
 276 partner choice is effective increases.

## 277 4. Discussion

278 Partner choice can lead to the evolution of cooperation when individuals can compare  
 279 several opportunities for social interaction and choose the most advantageous ones. In this  
 280 article, we have shown that the conditions for this to happen are, however, quite restrictive.

281 They entail that individuals truly have access to a range of social opportunities. Yet, in many  
282 cases, social opportunities are rare because they necessitate the co-occurrence of two  
283 things at the same time: (i) at least one available partner, and (ii) an exploitable resource or,  
284 more generally, “something to do” with that partner. In this article, we have used  
285 individual-centred simulations to study the consequences of this constraint on the  
286 evolution of cooperation by partner choice. We have obtained the following results.

287 First, partner choice cannot lead to the evolution of cooperation when resources are scarce,  
288 and therefore opportunities for cooperation are rare. This explains why, in many species,  
289 social interactions show no evidence of cooperation beyond immediate self-interest  
290 (Bullinger, Melis, & Tomasello, 2011; Melis et al., 2011; Scheel & Packer, 1991). Even when  
291 individuals engage in collective actions, for example when they hunt collectively, others  
292 have so few alternative opportunities anyway that there is no need to seek to draw them  
293 into the collective actions. They will come anyway, for want of anything better to do. Even  
294 worse than that, as opportunities for cooperation are rare, not only are there always  
295 enough partners in each collective action without it being necessary to actively attract  
296 them. In fact the opposite is true: There are always too *many* individuals participating in  
297 each cooperation endeavour (see Figure 2). This has been documented for instance in pack  
298 hunting in Lions, where Packer showed that lionesses often hunt in groups that are too  
299 large compared to what would be optimal (Packer, Scheel, & Pusey, 1990). In such a case,  
300 the average gain per individual in a collective action is reduced and not increased by the  
301 participation of others, and there is therefore no selection to attract partners but rather a  
302 selection to push them away at the time of sharing.

303 Second, partner choice can lead to the evolution of cooperation when partners constitute in  
304 themselves resources. There is, in this case, no further requirement for a social opportunity,  
305 than the need to find a partner. This occurs, for instance, in sexual markets, or in the many  
306 instances of interspecific mutualisms, where the other individual alone constitutes an  
307 opportunity to cooperate. It is therefore understandable that partner choice plays a  
308 particularly important role in these two types of interactions (Andersson & Simmons, 2006;  
309 Bshary & Grutter, 2002; Schino & Aureli, 2008).



310 Third, partner choice can lead to the evolution of cooperation when the environment is rich  
311 or, said differently, when individuals are efficient at finding opportunities for cooperation in  
312 their environment. Living in an environment rich in opportunities, and/or having skills that  
313 increase the effective number of opportunities one can exploit, brings with it the possibility  
314 of *choosing* between different opportunities. This puts greater pressure on individuals, who  
315 are then competing to attract partners on their own opportunity, rather than on another,  
316 and thus selects for cooperation beyond immediate self-interest.

317 This entails that the evolution of cooperation is related to the evolution of cognitive  
318 abilities, which sheds particular light on the case of the human species. The link between  
319 cooperation and cognition is a debated issue and several hypotheses have been put forward  
320 in the literature. The social brain hypothesis, in particular, posits that cooperation, and  
321 social life more generally, constitutes in itself a selection pressure favouring the evolution  
322 of greater cognitive capacities meant to deal with the complexity of social life. More  
323 recently, Dos Santos & West (Santos & West, 2018) have hypothesised that the cognitive  
324 ability to cooperate efficiently, and to coordinate with others in particular, could jointly  
325 evolve with cooperation itself. Both hypotheses, however, are about the joint evolution of  
326 cooperation with cognitive capacities that are *specifically* dedicated to cooperation itself.

327 Here we show that cognitive abilities that have nothing to do with cooperation or sociality  
328 per se, namely the sheer ability to extract resources from the environment, could also play a  
329 role in the evolution of cooperation. This occurs because enhanced cognitive abilities allow  
330 to transform and extract high-value resources from the environment (Kaplan, Hill,  
331 Lancaster, & Hurtado, 2000), thereby creating more opportunities for cooperation. As a  
332 result, a given environment contains more opportunities for cooperation for individuals  
333 with strong cognitive skills, such as human beings, than for the individuals of other species.  
334 This then affects the state of the market for cooperation, increasing the amount of  
335 competition between alternative social opportunities, thereby selecting for more  
336 investment into cooperation to attract partners.

## 337 5. Conflict of Interest

338 The authors declare that there is no conflict of interest.

## 339 6. References

340 Aktipis, C. A. (2004). Know when to walk away: Contingent movement and the evolution of  
341 cooperation. *Journal of Theoretical Biology*, 231(2), 249–260.

342 <https://doi.org/10.1016/j.jtbi.2004.06.020>

343 Aktipis, C. A. (2011). Is cooperation viable in mobile organisms? Simple Walk Away rule  
344 favors the evolution of cooperation in groups. *Evolution and Human Behavior*, 32(4), 263–  
345 276. <https://doi.org/10.1016/j.evolhumbehav.2011.01.002>

346 Alvard, M. S., & Nolin, D. A. (2002). Rousseau's Whale Hunt? *Current Anthropology*, 43(4),  
347 533–559. <https://doi.org/10.1086/341653>

348 Andersson, M., & Simmons, L. W. (2006). Sexual selection and mate choice. *Trends in*  
349 *Ecology and Evolution*, 21(6), 296–302. <https://doi.org/10.1016/j.tree.2006.03.015>

350 André, J.-B., & Baumard, N. (2011). The evolution of fairness in a biological market.  
351 *Evolution*, 65(5), 1447–1456. <https://doi.org/10.1111/j.1558-5646.2011.01232.x>

352 André, J. B., & Baumard, N. (2011). The evolution of fairness in a biological market.  
353 *Evolution*, 65(5), 1447–1456. <https://doi.org/10.1111/j.1558-5646.2011.01232.x>

354 Barclay, P. (2011). Competitive helping increases with the size of biological markets and  
355 invades defection. *Journal of Theoretical Biology*, 281(1), 47–55.

356 <https://doi.org/10.1016/j.jtbi.2011.04.023>

357 Barclay, P. (2016). Biological markets and the effects of partner choice on cooperation and  
358 friendship. *Current Opinion in Psychology*, 7, 33–38.

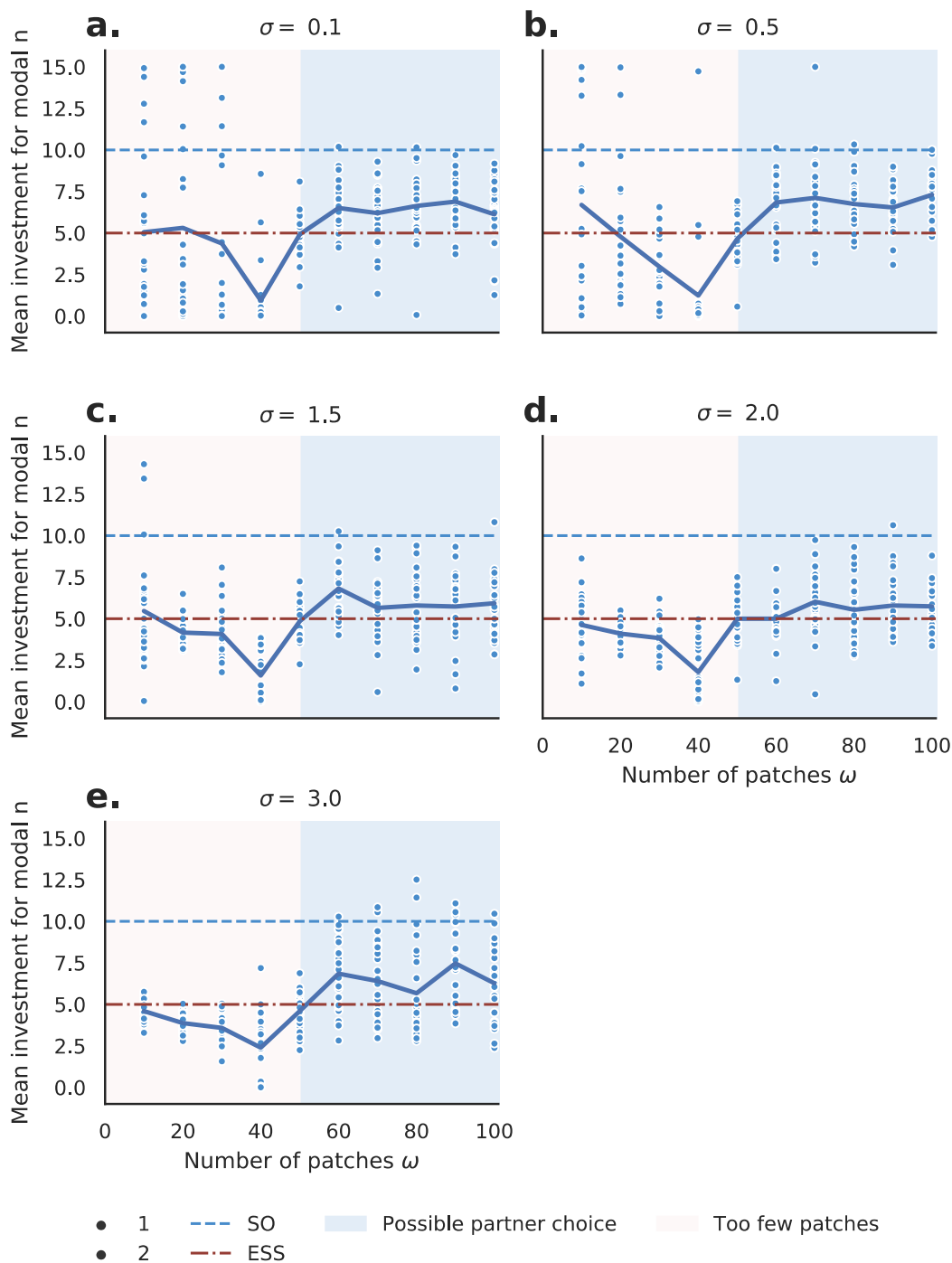
359 <https://doi.org/10.1016/j.copsy.2015.07.012>

- 360 Barclay, P., & Vugt, M. van. (2015). The Evolutionary Psychology of Human Pro-sociality:  
361 Adaptations, Byproducts, and Mistakes. *Handbook of Prosocial Behavior*, 37–60.  
362 <https://doi.org/10.1093/oxfordhb/9780195399813.013.029>
- 363 Barclay, P., & Willer, R. (2007). Partner choice creates competitive altruism in humans.  
364 *Proceedings of the Royal Society B: Biological Sciences*, 274(1610), 749–753.  
365 <https://doi.org/10.1098/rspb.2006.0209>
- 366 Baumard, N., André, J. B., & Sperber, D. (2013). A mutualistic approach to morality: The  
367 evolution of fairness by partner choice. *Behavioral and Brain Sciences*, 36(1), 59–78.  
368 <https://doi.org/10.1017/S0140525X11002202>
- 369 Bshary, R., & Grutter, A. S. (2002). Experimental evidence that partner choice is a driving  
370 force in the payoff distribution among cooperators or mutualists: The cleaner fish case.  
371 *Ecology Letters*, 5(1), 130–136. <https://doi.org/10.1046/j.1461-0248.2002.00295.x>
- 372 Bshary, R., & Grutter, A. S. (2006). Image scoring and cooperation in a cleaner fish  
373 mutualism. *Nature*, 441(7096), 975–978. <https://doi.org/10.1038/nature04755>
- 374 Bull, J. J., & Rice, W. R. (1991). Distinguishing mechanisms for the evolution of co-operation.  
375 *Journal of Theoretical Biology*, 149(1), 63–74. [https://doi.org/10.1016/S0022-](https://doi.org/10.1016/S0022-5193(05)80072-4)  
376 [5193\(05\)80072-4](https://doi.org/10.1016/S0022-5193(05)80072-4)
- 377 Bullinger, A. F., Melis, A. P., & Tomasello, M. (2011). Chimpanzees, Pan troglodytes, prefer  
378 individual over collaborative strategies towards goals. *Animal Behaviour*, 82(5), 1135–1141.  
379 <https://doi.org/10.1016/j.anbehav.2011.08.008>
- 380 Campennì, M., & Schino, G. (2014). Partner choice promotes cooperation: The two faces of  
381 testing with agent-based models. *Journal of Theoretical Biology*, 344, 49–55.  
382 <https://doi.org/10.1016/j.jtbi.2013.11.019>
- 383 Debove, S., Andre, J.-B., & Baumard, N. (2015). Partner choice creates fairness in humans.  
384 *Proceedings of the Royal Society B: Biological Sciences*, 282, 20150392.  
385 <https://doi.org/10.1098/rspb.2015.0392>

- 386 Debove, S., Baumard, N., & André, J.-B. (2015). Evolution of equal division among unequal  
387 partners. *Evolution*, 69(2), 1–9. <https://doi.org/10.1111/evo.12583>
- 388 Debove, S., Baumard, N., & André, J. B. (2017). On the evolutionary origins of equity. *PLoS*  
389 *ONE*, 12(3), 5–7. <https://doi.org/10.1371/journal.pone.0173636>
- 390 Eshel, I., & Cavalli-Sforza, L. L. (1982). Assortment of encounters and evolution of  
391 cooperativeness. *Proceedings of the National Academy of Sciences of the United States of*  
392 *America*, 79(4 I), 1331–1335. <https://doi.org/10.1073/pnas.79.4.1331>
- 393 Fruteau, C., Voelkl, B., Van Damme, E., & Noë, R. (2009). Supply and demand determine the  
394 market value of food providers in wild vervet monkeys. *Proceedings of the National*  
395 *Academy of Sciences of the United States of America*, 106(29), 12007–12012.  
396 <https://doi.org/10.1073/pnas.0812280106>
- 397 Geoffroy, F., Baumard, N., & Andre, J.-B. (2019). Why cooperation is not running away.  
398 *bioRxiv*, 316117. <https://doi.org/10.1101/316117>
- 399 Hammerstein, P., & Noë, R. (2016). Biological trade and markets. *Philosophical Transactions*  
400 *of the Royal Society B: Biological Sciences*, 371(1687), 20150101.  
401 <https://doi.org/10.1098/rstb.2015.0101>
- 402 Johnstone, R. A., & Bshary, R. (2008). Mutualism, market effects and partner control. *Journal*  
403 *of Evolutionary Biology*, 21(3), 879–888. [https://doi.org/10.1111/j.1420-](https://doi.org/10.1111/j.1420-9101.2008.01505.x)  
404 [9101.2008.01505.x](https://doi.org/10.1111/j.1420-9101.2008.01505.x)
- 405 Kaplan, H., Hill, K., Lancaster, J., & Hurtado, A. M. (2000). A theory of human life history  
406 evolution: diet, intelligence, and longevity. *Evolutionary Anthropology*, 9(4), 156–185.  
407 [https://doi.org/10.1002/1520-6505\(2000\)9:4<156::AID-EVAN5>3.3.CO;2-Z](https://doi.org/10.1002/1520-6505(2000)9:4<156::AID-EVAN5>3.3.CO;2-Z)
- 408 McElreath, R., Clutton-Brock, T.-H., Fehr, E., Fessler, D. M. T., Hagen, E., Hammerstein, P., ...  
409 Wilson, M. (2003). Group report: The Role of Cognition and Emotion in Cooperation. In  
410 *Genetic and cultural evolution of cooperation*.  
411 <https://doi.org/10.4337/9781781006948.00023>

- 412 McNamara, J. M., Barta, Z., Fromhage, L., & Houston, A. I. (2008). The coevolution of  
413 choosiness and cooperation. *Nature*, *451*(7175), 189–192.  
414 <https://doi.org/10.1038/nature06455>
- 415 McNamara, J. M., & Leimar, O. (2010). Variation and the response to variation as a basis for  
416 successful cooperation. *Philosophical Transactions of the Royal Society B: Biological Sciences*,  
417 *365*(1553), 2627–2633. <https://doi.org/10.1098/rstb.2010.0159>
- 418 Melis, A. P., Hare, B., & Tomasello, M. (2008). Do chimpanzees reciprocate received favours?  
419 *Animal Behaviour*, *76*(3), 951–962. <https://doi.org/10.1016/j.anbehav.2008.05.014>
- 420 Melis, A. P., Schneider, A. C., & Tomasello, M. (2011). Chimpanzees, Pan troglodytes, share  
421 food in the same way after collaborative and individual food acquisition. *Animal Behaviour*,  
422 *82*(3), 485–493. <https://doi.org/10.1016/j.anbehav.2011.05.024>
- 423 Noë, R., & Hammerstein, P. (1994). Biological markets: supply and demand determine the  
424 effect of partner choice in cooperation, mutualism and mating. *Behavioral Ecology and*  
425 *Sociobiology*, *35*(1), 1–11. <https://doi.org/10.1007/BF00167053>
- 426 Noë, R., Van Hooff, J. A., & Hammerstein, P. (2001). *Economics in nature: social dilemmas,*  
427 *mate choice and biological markets*. Cambridge University Press.
- 428 Packer, C. (1986). 19. The Ecology of Sociality in Felids. In D. I. Rubenstein & R. W.  
429 Wrangham (Eds.), *Ecological aspects of social evolution* (pp. 429–451).  
430 <https://doi.org/10.1515/9781400858149.429>
- 431 Packer, C., Scheel, D., & Pusey, A. E. (1990). Why lions form groups: food is not enough.  
432 *American Naturalist*, *136*(1), 1–19. <https://doi.org/10.1086/285079>
- 433 Packer, G., & Rutan, L. (1988). The evolution of cooperative hunting. *American Naturalist*,  
434 *132*(2), 159–198. <https://doi.org/10.1086/284844>
- 435 Raihani, N. J., & Bshary, R. (2011). Resolving the iterated prisoner's dilemma: theory and  
436 reality. *Journal of Evolutionary Biology*, *24*(8), 1628–1639. [https://doi.org/10.1111/j.1420-](https://doi.org/10.1111/j.1420-9101.2011.02307.x)  
437 [9101.2011.02307.x](https://doi.org/10.1111/j.1420-9101.2011.02307.x)

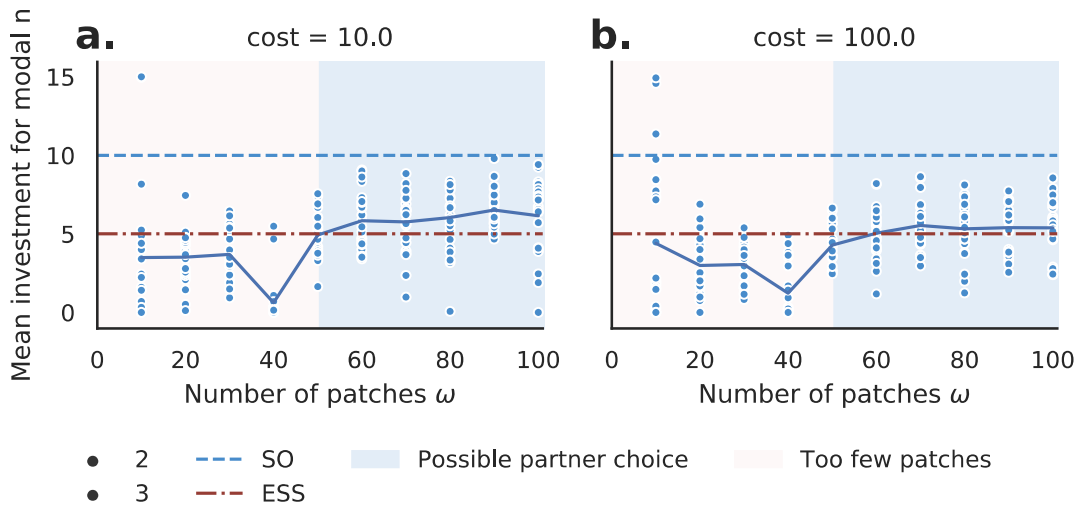
- 438 Santos, M. dos, & West, S. A. (2018). The coevolution of cooperation and cognition in  
439 humans. *Proceedings of the Royal Society B: Biological Sciences*, 285(1879).  
440 <https://doi.org/10.1098/rspb.2018.0723>
- 441 Scheel, D., & Packer, C. (1991). Group hunting behaviour of lions: a search for cooperation.  
442 *Animal Behaviour*, 41(4), 697–709. [https://doi.org/10.1016/S0003-3472\(05\)80907-8](https://doi.org/10.1016/S0003-3472(05)80907-8)
- 443 Schino, G. (2007). Grooming and agonistic support: a meta-analysis of primate reciprocal  
444 altruism. *Behavioral Ecology*, 18(1), 115–120. <https://doi.org/10.1093/beheco/arl045>
- 445 Schino, G., & Aureli, F. (2008). Grooming reciprocation among female primates: a meta-  
446 analysis. *Biology Letters*, 4(1), 9–11. <https://doi.org/10.1098/rsbl.2007.0506>
- 447 Schino, G., & Aureli, F. (2017). Reciprocity in group-living animals: Partner control versus  
448 partner choice. *Biological Reviews*, 92(2), 665–672. <https://doi.org/10.1111/brv.12248>
- 449 West, S. A., Griffin, A. S., & Gardner, A. (2007). Evolutionary Explanations for Cooperation.  
450 *Current Biology*, 17(16), 661–672. <https://doi.org/10.1016/j.cub.2007.06.004>
- 451 Zahavi, A. (1975). Mate selection-A selection for a handicap. *Journal of Theoretical Biology*,  
452 53(1), 205–214. [https://doi.org/10.1016/0022-5193\(75\)90111-3](https://doi.org/10.1016/0022-5193(75)90111-3)
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454 **7. Supplementary Material**

455

456 *Fig S1: Mean investment in simulations for different numbers of opportunities  $\omega$ , different*  
 457 *values of friction strengths  $\sigma$  and a fixed population of  $N_e = 100$  individuals. Results after*  
 458 *1500 generations. a-b. When the friction strength is strong (ie.  $\sigma \leq 1$ , see Fig. 1, a for  $\sigma = 1$ ),*

459 agents cooperate. **d-g.** When the friction strength is low (ie.  $\sigma \geq 1.5$ ), agents do not cooperate.  
 460 This is explained by the fact that too many agents (including cheaters) can come on the  
 461 resource without suffering a friction that has a strong impact on the gains. So there is a  
 462 dilution effect of responsibility that sets up in the same way as when  $\hat{n}$  is big.



463

464 *Fig S2: Mean investment in simulations for different numbers of opportunities  $\omega$ , different*  
 465 *values of cost of moving and a fixed population of  $N_e = 100$  individuals. Results after 1500*  
 466 *generations. The reference figure when the cost is 0 is available in Fig. 1, a. The greater the*  
 467 *cost is, the less cooperative the population is. Increasing the cost of moving increases the cost*  
 468 *of partner choice. When the cost is too high, it is of no interest for the agents to cooperate so as*  
 469 *to attract new partners, as if a cheater joins them, it will be too costly for them to leave the*  
 470 *opportunity with a defector.*