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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

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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;

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

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

On the other hand, there are a number of other biological situations in which one would typically expect partner choice to also play an important role, but where no such effect has ever been demonstrated. These include most intraspecific collective actions in non-human animals. This is particularly salient in collective hunts such as collobus hunting in chimpanzees, or pack hunting in carnivores. No empirical evidence in these species suggests that individuals cooperate for reasons related to partner choice, either to attract partners or to be accepted by them in their hunts. On the contrary, the majority of available data are consistent with the more parsimonious explanation that individuals are simply doing what is in their immediate best interest at any given time (Melis, Hare, & Tomasello, 2008; Melis, Schneider, & Tomasello, 2011; Packer, 1986; Packer & Ruttan, 1988). In particular, if cooperation in collective hunts was driven in part by the need to appear as a good partner, individuals would be expected to willingly share the product of their hunts in a way that depends on everyone's actual engagement, to encourage participation in other hunts in the future. However, such voluntary and conditional sharing has never been documented in animal collective hunts (Melis et al., 2011). In evolutionary terms, therefore, collective hunting in these species is most likely an instance of *by-product* cooperation, rather than an instance of reciprocal cooperation based on partner choice. This lack of observation is all the more surprising given that, in similar collective actions, human behaviours are demonstrably driven by the need to appear as a good partner (Alvard & Nolin, 2002; Baumard et al., 2013). One may therefore wonder why the same effects did not produce the same consequences in other species.

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

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

In other cases, however, finding an opportunity for cooperation requires more than just finding a partner. This is what happens when cooperation consists of several individuals working together to exploit environmental resources. In this case, a cooperation opportunity requires both a partner(s) and a resource, which imposes an additional constraint limiting the scope of partner choice. When resources are scarce, there are always few options to compare, and partner choice cannot operate. This could explain the lack of cooperation, beyond by-product cooperation, in many instances of collective actions in the wild despite the availability of potential partners.

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

We believe that this constraint plays a central role in explaining that, in many species, although individuals do participate in collective actions, sometimes finely coordinating their behaviour with that of others, they do not actually seek to cooperate beyond what is in their immediate personal interest. In contrast, in the case of the human species, thanks to extensive cognitive skills individuals are able to extract resources from a greater variety of situations. As a result, humans actually live in an environment that is much richer in resources than other species. Hence they can compare and compete over a greater diversity of opportunities for cooperation against one another, and are thus forced to cooperate more intensively to attract partners.

2. Methods

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

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

2.1. The decision-making mechanisms

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

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

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

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

2.1.1. Phenotypic variability of cooperation

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

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

2.2. The payoff function

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

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

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

$$F(n) = e^{-(n-\hat{n})^2/(2\sigma^2)}$$

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

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

2.3. The evolutionary algorithm

Each individual has a genome composed of the weights of its two neural networks, which makes a total of 84 genes $g = (g_1,\ldots,g_{84})$ with $g_i \in]-10,10[$. We consider a population of fixed size N. The first generation is composed of N individuals with random genes for the neural network weights, drawn uniformly in $]-1,1[$. We then use a fitness proportionate evolutionary algorithm to simulate evolution. After the T time steps of a generation have taken place, individuals all reproduce and die. A new population of N individuals is built out of the previous generation by sampling randomly among the N parents in proportion to their cumulated payoff, according to a Wright-Fisher process.

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

The evolutionary algorithm is run for G generations.

Parameter	**Description**	**Value**
Environment		
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
Payoff		
a	Immediate personal benefit of cooperation	5
b	Social benefit of cooperation	5
$\hat{n}$	Optimal number of individuals per patch	variable
σ	Tolerance to variations in the number of individuals per patch	variable
Evolution		
G	Number of generations	1 500

μ	Probability of mutation per gene per generation	0.01

3. Results

3.1. Cooperation cannot evolve when patches are scarce

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

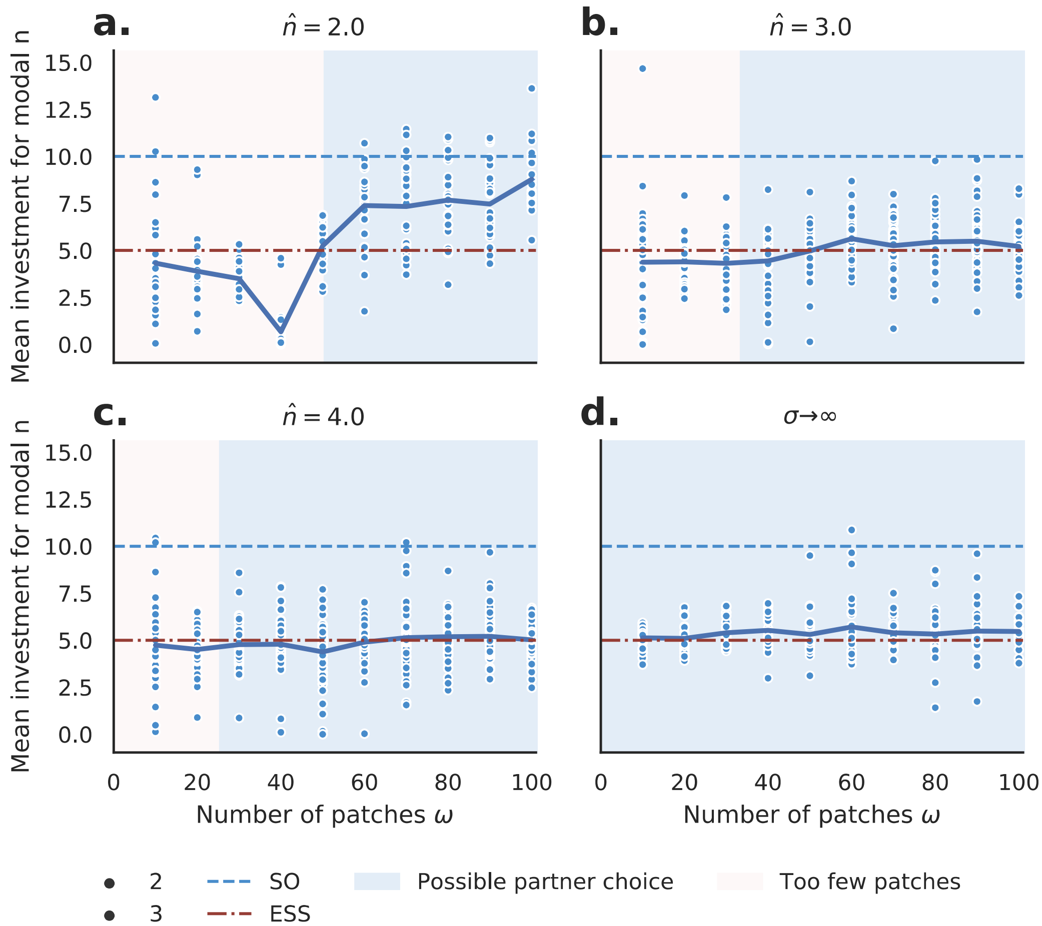

Fig 1: Mean investment in simulation for different number of opportunities ω and a fixed population of $N_e = 100$ individuals. Results after 1 500 generations. ***a.*** *When $\hat{n} = 2, \sigma = 1$ Cooperation evolves when $\omega \geq 50$.* ***b-c.*** *For $\hat{n} \geq 3, \sigma = 1$, cooperative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

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

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

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

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

3.2. Cooperation cannot evolve when there are too many partners around

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

In this case, cooperation only evolved when the number of individuals in the environment was intermediate. This can be understood as follows. When the number of individuals in the environment, N_e, is too close to the number of individuals, $\hat{n}$, that are needed to exploit at least one patch –or even more so when $N_e < \hat{n}$, then the number of available partners is limiting. As a result, the actual number of cooperation opportunities from which individuals can choose is very low, partner choice is thus a weak force, and the benefit of investing into cooperation is low. On the other hand, when the number of individuals in the environment, N_e is larger than the total number of individuals that can be accommodated on the available patches, that is when $N_e > \hat{n}\omega$, the number of available patches is limiting. In this case we find the result described above (Fig. 2, a). The problem is rather that there are always too many individuals on each patch than too few and partner choice is also a weak force. There is, therefore, a range of intermediate population densities, neither too low nor too high, for which cooperation can evolve.

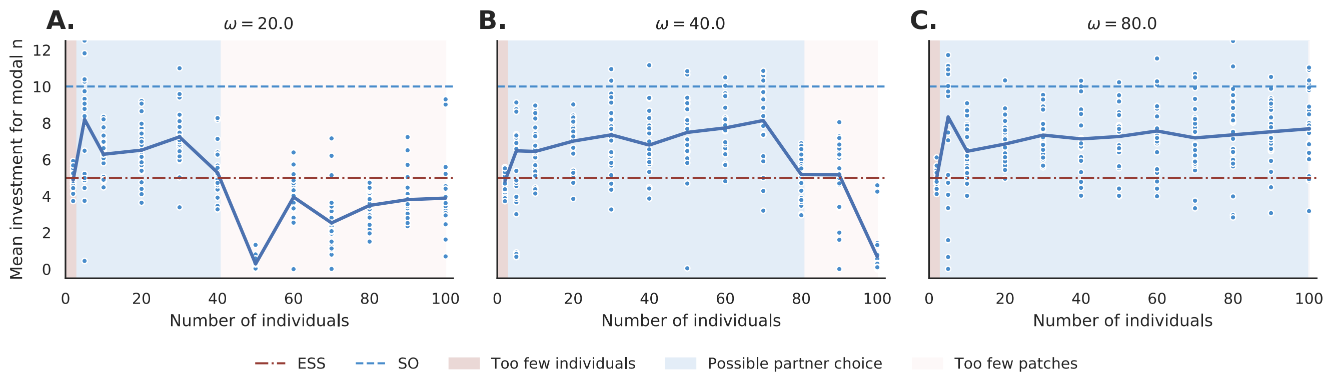

Fig 2: Effect on the population size in the environment with 20, 40 or 80 patches and an optimal number of agents $\hat{n} = 2$ and $\sigma = 1$. Agents have a cooperative behaviour for $\hat{n} < N_e < \omega \times \hat{n}$.

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

4. Discussion

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

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

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

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

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

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

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

5. Conflict of Interest

The authors declare that there is no conflict of interest.

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7. Supplementary Material

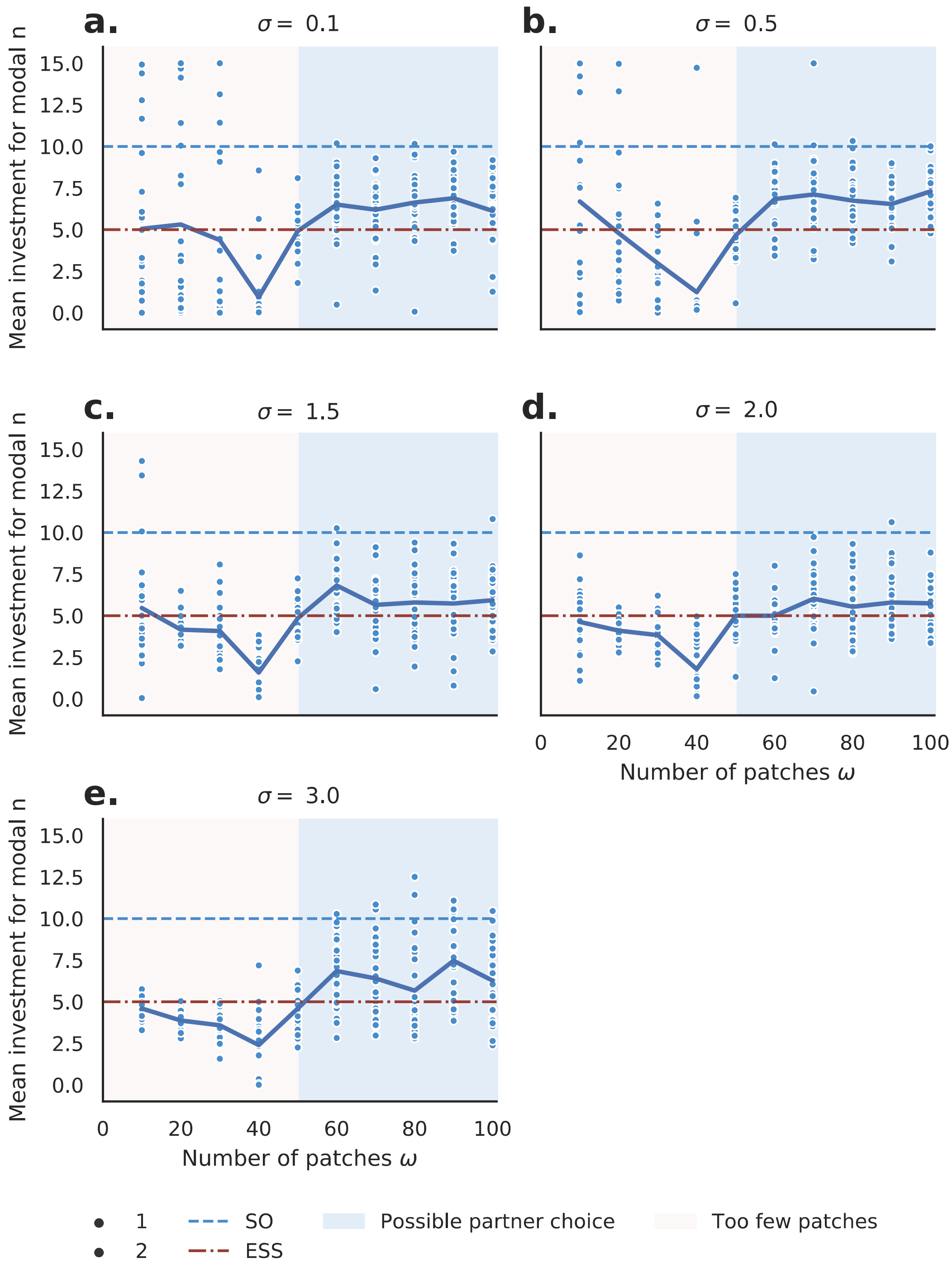

Fig S1: Mean investment in simulations for different numbers of opportunities ω, different values of friction strengths σ and a fixed population of $N_e = 100$ individuals. Results after 1500 generations. ***a-b.*** *When the friction strength is strong (ie. $\sigma \leq 1$, see Fig. 1, a for $\sigma = 1$),* *agents cooperate.* ***d-g****. When the friction strength is low (ie. $\sigma \geq 1.5$), agents do not cooperate. This is explained by the fact that too many agents (including cheaters) can come on the resource without suffering a friction that has a strong impact on the gains. So there is a dilution effect of responsibility that sets up in the same way as when $\hat{n}$ is big.*

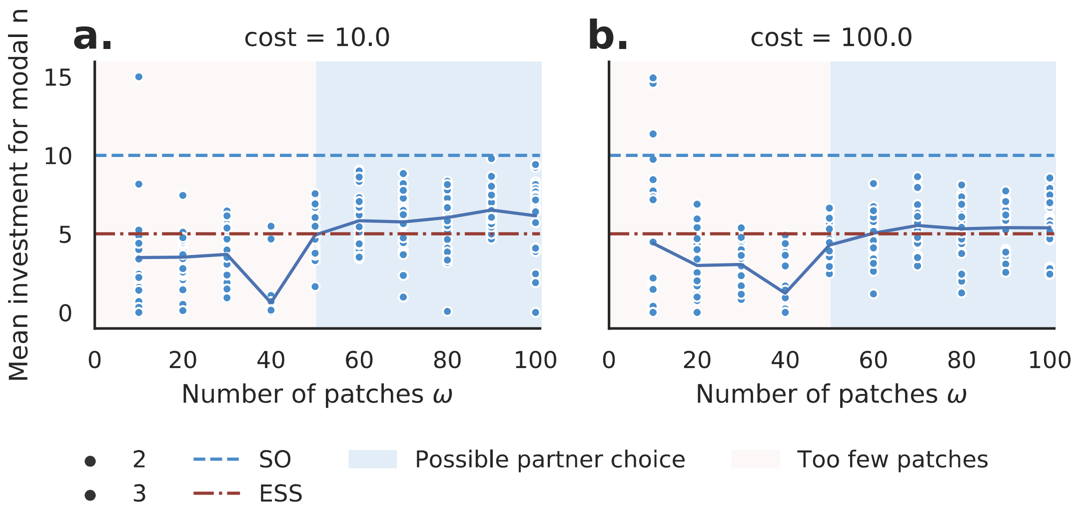

Fig S2: Mean investment in simulations for different numbers of opportunities ω, different values of cost of moving and a fixed population of $N_e = 100$ individuals. Results after 1500 generations. The reference figure when the cost is 0 is available in Fig. 1, a. The greater the cost is, the less cooperative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