

# Biological markets and the effects of partner choice on cooperation and friendship

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Cooperation is crucial to our survival and social success. People typically choose their social partners (e.g., friends, allies, mates), which allows us to avoid bad partners and preferentially interact with better ones. This creates a *biological market* where people prefer to associate with others who are willing and able to confer benefits upon partners. In such a market, it pays to compete to be (or appear to be) more willing and able to help than competitors are, causing an arms race over any behaviour that signals these traits — including generosity. Biological markets help us understand why we choose the partners we do, when and why people are cooperative and fair (and to what extent), and why individuals differ on these traits.

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Humans rely on cooperation for survival and success in social competition. Accordingly, we possess powerful emotions that lead us to value others (including non-relatives), coordinate for mutual benefit, and help others even at temporary cost to ourselves. From an evolutionary perspective, for such cooperative sentiment to evolve, helpers must receive corresponding benefits that outweigh the costs of helping (if any). Thus, much evolutionary research seeks to identify these benefits in order to understand why our cooperative sentiments exist, and how best to stimulate them.

Traditional research approaches have studied reciprocal exchange of benefits with fixed partners, such as playing ‘Tit-for-Tat’ in a Prisoner’s Dilemma, or giving to receive help from others in an existing network of ‘indirect reciprocity’. More recent approaches have extended these

models to also examine the role of partner choice in fostering cooperation, including in mutualisms. These new approaches give insight into how people choose and attract friends, allies, coalition members, mutualistic collaborators, and mates (henceforth collectively known as ‘partners’).

## Partner choice and biological markets

The most basic partner choice is the ability to leave bad partners or reject them outright. Theoretical and experimental work both show that this ability helps cooperators to preferentially assort with each other, resulting in more cooperation (Table 1). Such strategies require little cognitive complexity, which increases their generality because they apply across multiple kingdoms of life.

Strategies become more complex when organisms can actively choose partners from available alternatives, and this also results in higher cooperation (Table 1). Because people do not interact equally with everyone, there is market-like competition for the ‘best’ partners, in what is known as a *biological market* [1]. The best partners are those most willing, able, and available to confer benefits, either intentionally or incidentally [2<sup>\*\*</sup>]: choosing partners (consciously or not) based on these characteristics is highly advantageous [3]. As such, biological markets likely shaped the evolution of our proximate social emotions (e.g., liking, attraction, closeness) such that we value and partner with the best partners available to us.

The best-known biological market is the mating market: organisms choose mates based on cues of direct benefits (e.g., resource provisioning) or indirect benefits (i.e., genetic quality for offspring), and also compete to appear as better mates. Some individuals are more desirable partners, i.e., they have higher *market value*. However, sexual selection is just one component of the broader category of *social selection* [4]. As such, researchers now recognize that many principles of partner choice apply to both mating and non-mating relationships. These principles include a focus on the supply and demand of various commodities; the costs and benefits of choosing and attracting partners; the total benefits provided by a partner (including mutualistic benefits); one’s generosity relative to others (instead of absolute levels of generosity); the signals used to communicate benefit-conferral; and the effects of one’s own market value on behaviour [2<sup>\*\*</sup>].

## How to choose partners

People choose partners based on cues of their ability, willingness, and availability to confer benefits on the

Table 1

## Sample of recent theoretical and experimental studies on cooperation under partner choice.

Type of model or experiment	Sample finding and illustrative reference
Theoretical models and computer simulations of ostracism and rejection	<ol style="list-style-type: none"> <li>1. The ability to leave [53] or ostracize [54] partners helps cooperators to assort with each other, allowing cooperation to evolve</li> <li>2. Organisms divide resources unfairly when their partner has no outside option, but fairness evolves when organisms can seek better offers elsewhere [55]; reviewed by [49**]</li> <li>3. Cooperation and choosiness coevolve to high levels when individuals can assess and reject potential partners before interacting [23*]</li> </ol>
Humans in dyadic bargaining games and cooperative group games	<ol style="list-style-type: none"> <li>1. Participants divide money more evenly in bargaining games when their partner can seek better options [56]</li> <li>2. Participants cooperate more in cooperative group games when they can use gossip to exclude or ostracize non-cooperators [57]</li> <li>3. The threat of ostracism increases cooperation more than intergroup conflict does [58]</li> </ol>
Humans in artificial social networks with passive choice (the ability to leave or reject partners)	<ol style="list-style-type: none"> <li>1. Participants are more likely to cooperate when they can break or reject links with non-cooperators than when they are forced to interact [59]</li> <li>2. The level of cooperation depends on how easily or frequently one can break links with non-cooperators [60]</li> <li>3. High costs for switching partners affect participants' willingness to switch but not their cooperation, suggesting that the threat of abandonment alone is sufficient to incentivize cooperation [61]; see also [62]</li> </ol>
Humans in artificial social networks with active choice (the ability to approach specific individuals)	<ol style="list-style-type: none"> <li>1. Cooperation is even higher when participants have information about others in the population, because they use this information to selectively approach cooperators [63]</li> <li>2. More information about the pool of potential partners results in better assortment and higher cooperation [64]</li> <li>3. Cooperation suffers when information about others is too costly to be worth using [65]</li> </ol>

chooser (reviewed by [2\*\*]). These cues affect our emotional responses, such as how much we 'like' someone, which then influences who we try to befriend and ally with.

### Cues of ability to confer benefits

Many actions function to signal one's ability to confer benefits on partners, from athletic displays for signalling physical abilities, conspicuous consumption for signalling wealth (e.g., [5]), frequent affiliation with high status individuals to signal social connectedness, even war heroism signalling strength and courage [6]. Extravagant generosity may do the same, including philanthropy to signal wealth, or sharing hunted game to signal physical abilities (e.g., [7]). These examples are reliable signals of underlying qualities because they would be impossible or disproportionately costly for those who do not possess those qualities [8\*].

People tend to target wealthy, high-ability, and well-connected individuals for partnerships because of the benefits of pairing with them. Thus, people who are central in social networks receive more generosity from friends [9], healthy-looking people are more likely to have their trust reciprocated [10], and those wearing luxury brands are more likely to be hired or have their requests granted [5]. This principle generalizes beyond humanity: even rats and trout will cooperate more often with partners who are more effective or productive collaborators [11,12].

### Cues of willingness to confer benefits

Good partners are not only *able* to confer benefits, but *willing* to do so. Indeed, the latter is deemed more important among hunter gatherers [13]. Many traits that we deem 'nice' are cues of others' willingness to confer benefits [14]. For example, charitable giving is seen as a cue of trustworthiness [15], especially when the giver receives no personal benefits for giving [16]. Benefits to *us* are especially valued: 'friends' are partners who greatly value us and are emotionally committed to conferring benefits upon us, and vice versa. We distinguish between true friends and 'fair weather friends' by the attention they give us [17], especially when such attention is costly [18]; those who do not honestly value us would rather invest their limited attention elsewhere [19]. We can also assess others' cooperativeness based on whether they deliberate before helping, because good allies (e.g., true friends) help without calculating the costs [20\*]. These various actions become inputs in our estimations of others' future behaviour towards us (see [21], on 'welfare trade-off ratios'), which then affects who we trust and partner with.

### Optimal choosiness

One's optimal level of choosiness depends on multiple factors. The costs of assessing partners (and rejecting some) are only worthwhile if there are multiple candidates to choose from [22], if those potential partners differ enough in quality [23\*], and if the chooser is desirable enough to attract its top choice(s) [24]. Otherwise, choosiness does not pay. To reduce competition, it pays to pursue partners

that others are not pursuing [24,25]. If partnerships are expected to be short, then fast decisions are better than perfect decisions, so it pays to spend less time choosing and proportionally more time in the partnership [26].

### How to be chosen as a partner

There is much laboratory evidence that people prefer to associate with good cooperators, all else equal (Table 1; reviewed by [14]). Anthropological findings also demonstrates these preferences: people who help or share more often have the best reputations, are preferred as camp-mates and spouses, and consequently receive more help from others [13,27,28,29]. In online markets and auctions, sellers with more honest reputations make more sales and command higher prices than sellers with poorer reputation [30].

Such results demonstrate that one's relative cooperation (i.e., relative to competitors) increases one's market value and affects others' choice of partners. Correspondingly, people are more cooperative when their actions are public than when anonymous (for a review of laboratory experiments, see [2<sup>••</sup>,14]; for a review of field experiments, see [31<sup>•</sup>]). Even 6- to 8-year olds vary their fairness according to observation [32].

Sexual relationships are particularly important partnerships, and men use generosity to attract mates. Men are more generous in laboratory and field experiments when observed by women, whereas the reverse is not always true; this finding has been demonstrated in both developed and developing countries [33,34,35]. Men will also give more to attractive women on online fundraising sites than to unattractive women, and are more likely to match previous high donations if the previous donor was male [36<sup>•</sup>] (see also [10]). Hunting and sharing big game has often been viewed as males 'showing off' to attract partners (e.g., [7]; but see [37]).

### Competing via generosity (and cues thereof)

Biological markets theory predicts that people will compete on any dimension that increases their market value; that is, any trait that signals their willingness or ability to confer benefits upon others. These signals include public generosity, commitment to partners or groups, intelligence, athleticism, and so on. Whereas many theories predict that observation will increase cooperation, biological markets theory is unique in predicting that competition over partners will cause higher levels of cooperation than observation alone.

Such 'competitive altruism' or 'competitive helping' has been found with laboratory monetary games (e.g., [38]), online donations by men towards attractive female fundraisers [36<sup>•</sup>], and men's willingness to undergo painful procedures to benefit a group that includes a woman [34]. Furthermore, this type of competitive helping appears to

be more effective than indirect reciprocity in maintaining contributions to public goods [39<sup>•</sup>,40].

How generous ought one to be? One's optimal level of competitive helping should vary with one's costs of competing, the effect on one's market value, and the benefits of increased market value [2<sup>••</sup>]. For example, for types of helping that signal special abilities [19], it only pays to signal if one is of sufficient quality to effectively compete for partners [41<sup>••</sup>]. This phenomenon underlies the costly signalling theory of helping (reviewed by [14]).

Conversely, some individuals benefit little from being generous — especially when generosity does not signal their wealth or physical abilities — because their market value is already sufficiently high [19]. As such, selfishness is more common among high status people (e.g., [42,43]), physically attractive people [44,45], people with more power within relationships [46], and people who have already recently demonstrated their good character by previous actions ('moral licensing': [47<sup>•</sup>]). Thus, whereas cooperation that signals one's special qualities should be performed by those of high market value; more mundane forms of generosity may be a compensatory strategy by those of lower market value to 'sweeten the deal' when courting partners of higher market value [2<sup>••</sup>].

### Alternative tactics in the generosity arms race

Of course, not all competition over partners is nice. People may suppress others' generosity or sabotage competitors' reputations for cooperativeness, for example by attacking the helper's effectiveness, motivations, or character [48]. Such attacks may work: those who are perceived to benefit from their actions are seen as less prosocial than those who do not benefit [16].

### Implications and future directions

Biological markets theory has many implications. For example, partner choice may have shaped our moral systems: people offer fairness, earnings in proportion to productivity, commitment, and sometimes even impartiality, because those who are not offered these benefits will seek alternative partners who do offer them [49<sup>••</sup>]. These market-based intuitions of what is 'fair' may even have affected religion and perceptions of what supernatural agents demand and offer [50]. Partner choice is more prevalent in some cultures, which affects patterns of commitment, self-disclosure, self-esteem, and preferences for loyalty over impartiality, among other things (reviewed by [51]). Thus, some cultural differences may be explainable by differences in the local social marketplaces.

There remain many open questions about partner choice within biological markets. What specific cues do people use to assess abilities, willingness and availability? What ancestral cues did we evolve to use, and how do new cues acquire their informational value? Do signals of partner

quality also signal other traits, and does a signal in multiple domains risk being diluted? How do observers' impressions about cooperators differ according to the size and characteristics of audiences, and how does this then affect the incentives to cooperate? How much can we harness market-like competition over partners in order to promote positive social outcomes, and what limitations and unintended consequences might this have [52\*]? What developmental processes underlie which traits (and signals thereof) a person comes to value and to display? What socio-ecological factors affect the markets for partners in different cultures, and how does this then impact people's psychology? We should look forward to future investigations of such questions about how biological markets affect social interactions.

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