



Review Article

Strategies for cooperation in biological markets, especially for humans

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ABSTRACT

When organisms can choose whom to interact with, it can create a biological market where individuals need to outbid their rivals for access to cooperative relationships. Each individual's market value is determined by the benefits it can confer (and is willing to confer) upon others, which selects for tendencies to actively confer benefits on others. In this article, I introduce the basics of biological markets and how they relate to traditional models of cooperation, and then elucidate their impact on human cooperation, especially in the tasks of choosing partners, competing over partners, and keeping partners. Since "generosity" is necessarily rated relative to one's rivals, this can result in tendencies to compete over relative generosity, commit to partners, help when help is unnecessary, give strategically, and attack or suppress others' helpfulness. Biological markets explain and make novel predictions about why we desire to associate with particular individuals and how we attract them, and are therefore a useful incorporation into models of cooperation.

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1. Introduction

When explaining the puzzle of human cooperative sentiment, researchers have long relied on reciprocity (e.g. Alexander, 1987; Axelrod, 1984; Trivers, 1971), and many elegant mathematical models and computer simulations have since demonstrated the power of direct and indirect reciprocity. In recent years, others have broadened the discussion about human non-kin cooperation beyond reciprocity alone to include mutualisms, stake in others' well-being, and signaling of one's qualities (reviewed by Barclay & Van Vugt, in press). Perhaps the most important addition to early models of cooperation is that humans (like some other organisms) exercise choice as to whom they will associate with, and do not equally accept all individuals as partners in cooperative ventures like friendships, coalitions, or alliances.

On what basis do people choose these friends and cooperative partners? What causes one to prioritize among equally available options? Why are friendships sometimes one-sided, where one person gives much more emotionally and practically to the partnership, and the other fails to reciprocate? Such questions make sense if one looks at all interactions through the metaphor of a biological market for partners, where one's choice of partners is

ultimately affected by the benefits they provide and the costs of maintaining such partnerships, and where an individual's desirability as a partner depends not just on its absolute qualities but on its qualities relative to others. Some biologists have investigated how these "biological markets" affect the behavior of non-humans (e.g. Barrett & Henzi, 2006; Bshary & Schäffer, 2002; Noë & Hammerstein, 1994, 1995), but little work has applied this paradigm to the study of human cooperation.

The purposes of this paper are to explicate the implications of such biological markets for human cooperative behavior, and to show how a focus on markets complements and extends some previous ways of looking at human altruism, coalitions, partnerships, and friendships. After explaining what biological markets are and how they relate to traditional models of cooperation, I present ways in which the presence of biological markets leads to different strategies than would be present in non-market-based models of cooperation.

Before beginning, a quick note on terminology, as this varies widely. Here, I use the words "altruism," "generosity," and "helping" very broadly and somewhat interchangeably to refer to behaviors that function to increase the well-being or biological fitness of the recipient but involve some cost to the actor (at least temporarily), regardless of the exact psychological mechanisms, intention to benefit, or possibility of repayment. By "altruistic or cooperative sentiment," I refer to any genuine intent to benefit the recipient without desire for personal gain, whether that sentiment be empathy (Batson et al., 1997), oneness with others (Cialdini et al., 1997), "warm glow" (Andreoni,

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1990), or some other proximate psychological mechanism. Those with concerns about this usage should substitute their preferred terms for these concepts.

2. What is a biological market?

2.1. The basics of biological markets

Noë and Hammerstein (1994, 1995) formally introduced the idea of biological markets (see also Noë, 1990). Under this view, natural selection will favor organisms that spend more time in partnerships or coalitions with the “best” partners with whom they gain the most fitness benefits (per unit investment). These fitness benefits can come from actively provided “commodities” such as coalitional aid or food, as well as passively provided “commodities” such as shelter, tolerance, or even metabolic byproducts in the case of interspecific mutualisms. Any organism that chooses partners (whether consciously or not) based on maximizing these fitness benefits will have a selective advantage over another who does not maximize its long-term ratio of benefits to costs. When individuals actively provide benefits to their partners, these benefits can come in different currencies that can be traded for other currencies (e.g. food for coalitional aid, etc.), the value of which depends on how these currencies convert into fitness.

When partner choice exists, individuals must compete or bid for time in partnerships. Those who do not provide enough or high-enough-quality commodities will be passed over in favor of those who do. Furthermore, the “price” that one can get for providing commodities depends on the relative supply and demand for the different types of commodities and how they translate into fitness. The supply and demand for these commodities can depend on the ratio of suppliers to demanders (e.g. producers vs. scroungers) and the relative production of each particular commodity (e.g. hunted meat is more difficult to acquire than gathered food, Hawkes et al., 2001), all of which can vary in space and time (Hoeksema & Schwartz, 2003; Noë & Hammerstein, 1994, 1995). For example, a good protector can demand more from potential partners when both live in an environment with many threats, especially from partners who are themselves weak. Similarly, good hunters are more desirable when food is scarce, or to those with many dependents. When mutual partner choice exists, there will be some assortative pairing such that those who are desirable partners (however defined for a given interaction) are more likely to end up with desirable partners. Environments and population structure change, and this will affect the relative supply and demand for different commodities (and thus also affect the “market value” of different individuals). As such, biological markets are inherently dynamic, which makes this viewpoint useful for predicting individual and group variation over time and across environments.

Many biologists and psychologists have implicitly or explicitly used the metaphor of markets, especially when studying mating. An explicit focus on biological markets helps researchers to recognize that different individuals will have different preferences depending on their own “market value” and who they are interacting with, that individuals may have to outbid competitors for access to partnerships, and that partner choice and partner switching can be major forces in the evolution of behavior—points that have been underappreciated by other paradigms (Barrett & Henzi, 2006; Noë, 2006). Although this viewpoint of markets has long been applied to mating behavior and coalition bargaining, it has only recently been explicitly applied to cooperative behavior. Some approaches to cooperation have been market-based without explicitly mentioning markets (e.g. Roberts, 1998; Seyfarth, 1977; Tooby & Cosmides, 1996), but the logic of markets for partners is clearly present.

2.2. Markets and traditional models of reciprocity

Biological markets are an extension of traditional models of reciprocity (Schino & Aureli, 2010). Much of the theoretical and empirical work on cooperation has used the Prisoner's Dilemma or similar paradigms where organisms cannot control either the length of the interaction or who they interact with. Several authors have created models of cooperation that included partner choice and the ability to reject uncooperative partners (e.g. Aktipis, 2004, 2011; Bull & Rice, 1991; Enquist & Leimar, 1993; Hayashi & Yamagishi, 1998; McNamara et al., 2008; Page et al., 2005; Schuessler, 1989; Sherratt & Roberts, 1998; Vanberg & Congleton, 1992). A general conclusion from such extensions is that organisms benefit from being able to leave or reject uncooperative partners and that this selects for cooperation in the population.

Biological markets are in turn an extension of basic partner choice models in at least three ways:

- 1) *Relative cooperation matters*: cooperation is a continuous trait rather than a discrete “cooperator/defector” dichotomy, and the desirability of a partner depends not on their absolute level of cooperation, but on how cooperative they are relative to other potential partners in the market. This in turn allows individuals to “outbid” each other (Schino & Aureli, 2010).
- 2) *Choosing based on more than just reciprocity*: traits other than reciprocity are included such that organisms choose partners based on a multitude of traits (Barclay, 2011). For example, biological markets are not limited to reciprocity, but also affect mutualisms (Noë & Hammerstein, 1994, 1995). All else equal, a partner who does not reciprocate is less desirable than one who does, such that one should want to switch partners if better reciprocators are available (Trivers, 1971). However, since all else is not always equal, non-reciprocators can occasionally be highly desirable partners if they possess other desirable qualities such that one benefits from associating with them despite their non-reciprocation (Hayashi & Yamagishi, 1998).
- 3) *Supply and demand*: because the value of all traits changes with shifting supply and demand, one's market value (and thus the value of one's reciprocation) will change, both over evolutionary time and within an individual's lifetime.

By focusing on reciprocity as but one strategy within a broader market, biological markets theory makes several interesting novel predictions about apparent imbalances in reciprocity. For example, it would predict that (a) long-term imbalances in one domain will be more likely when one partner has a higher market value on other traits than the other partner does, such that the latter must provide benefits to the former (or tolerate more inequity) to entice him/her to stay; (b) greater inequalities in market value will be associated with greater apparent imbalances in reciprocity on both a dyadic and group level, as there is greater potential for imbalanced market values; (c) actual short-term imbalances will exist when one individual would benefit from signaling his/her generosity to attract other potential partners (instead of decreasing one's cooperation in response to free-riding); but at the same time (d) the presence of other potential partners will make such imbalanced relationships more likely to dissolve. A market-based perspective would also predict that organisms will not always try to associate with the best cooperators or best reciprocators: although it would generally be advantageous to pair with such individuals, some individuals (e.g. non-reciprocators) are unlikely to be successful at pairing with good reciprocators because they have low market value. As such, all else being equal, anyone who cannot or will not reciprocate should avoid the costs of searching and rejection by good partners, and instead seek out fellow non-reciprocators who *would* accept them.

3. Strategies within biological markets for cooperators

When there is no partner choice (as in traditional models of cooperation using the Prisoner's Dilemma), individuals are forced to interact with specific partners. This greatly simplifies behavior because one's strategy set is limited: one can use partner control mechanisms like conditional cooperation and punishment to enforce a partner's cooperation (e.g. Axelrod, 1984; Fehr & Gächter, 2002), but one cannot use partner choice to assort with better cooperators or enforce cooperation by threatening to leave (e.g. Aktipis, 2004; André & Baumard, 2011). When some individuals can choose partners, this can select for psychological adaptations for choosing the best partners, attracting the best or the most partners, and for maintaining partners (Table 1). Each of these additional tasks will be examined in turn.

Before discussing these strategies, it is worth mentioning that one can have partners in biological markets on multiple different timescales. One might bid for and choose partners for short timescales, as occurs when cleaner fish service their clients (Bshary & Grutter, 2002, 2005, 2006), when female baboons exchange grooming for immediate access to infants (Barrett & Henzi, 2006), or when male macaques exchange grooming for sex (Gumert, 2007a). Alternately, one might bid for and choose partners for much longer timescales, as occurs within marriage markets (Frank, 1988) or similar markets for friends, allies, or coalition partners. Different timescales will likely involve different cognitive or emotional processes (Clark & Mills, 1979). On a similar note, the term "partner" is sometimes used liberally within markets, as it need not be an all-or-none affair. Instead, market forces can affect how much time to allocate among a number of associates within one's social network, whom to associate with more than others, and whom to support most often.

3.1. Choosing partners for cooperation

Partner choice can be as simple as heuristics like "walk away if not satisfied with a current partner" (Aktipis, 2004, 2011). What determines what is deemed "satisfactory?" In markets where organisms can choose from among multiple candidate partners who vary in their market value, it can be advantageous to use more complex decision rules for assessing others' market values and setting one's threshold for "satisfaction" accordingly.

3.1.1. Similarities to sexual selection

Most work on partner choice has been on mate choice. Mating is just one form of social selection (West-Eberhard, 1979, 1983), so many principles from sexual selection will generalize to other forms of partner choice, including competition over cooperative partners (Nesse, 2007). For example, it is costly to search for, assess, and attract partners, so choosiness will only evolve when candidate partners vary on important traits; this applies to mating partners (Kokko et al., 2003) as well as cooperative partners (McNamara et al., 2008). Also, once individuals choose partners, one must then explain what maintains the variation in partners, whether this variation is the variation in male traits despite strong directional selection by females ("lek paradox," e.g. Kokko et al., 2003) or the existence of defectors in a world where cooperation has higher payoff (Sherratt & Roberts, 2001). Individuals must also choose whether to maintain multiple partners with less investment in each versus fewer partners and more investment in each; this is true whether deciding between being polygynous versus monogamous marriages or deciding how to form one's social network. While some phenomena may be unique to mating (e.g. paternity uncertainty), there is considerable scope for importing other principles from mate choice into the cooperation literature via partner choice within biological markets (and vice versa: Miller, 2007).

While the similarities to mating markets allow many principles of partner choice to be incorporated into cooperation, markets for cooperative partners differ in one important way which warrants mention. Within mating markets, there are usually two distinct "trader classes" (males and females), but this is often not the case with other biological markets. Many market models of cooperation do assume different trading classes such as buyers and sellers, proposers and responders, or host and symbiont; this assumption is made either for mathematical simplicity or because of the inter-species systems they model (e.g. André & Baumard, 2011; Johnstone & Bshary, 2008; Noë & Hammerstein, 1994). However, two trading classes are not strictly necessary, because market models are possible where all individuals are of one class and are mutually choosing each other for interactions (Barclay, 2011; McNamara et al., 2008; Nesse, 2007). This would represent interactions like friendships, alliances, and coalitions.

3.1.2. Choosing based on the benefits for association

Within a biological market, individuals benefit from assessing the market value of potential partners in order to choose the best attainable partners such that they maximize the benefits they receive from those partners and/or minimize the costs of attaining those partners (Frank, 1988; Hayashi & Yamagishi, 1998; Noë & Hammerstein, 1995). Kummer (1978) argues that the value of a given partner depends on his/her *qualities*, *tendencies*, and *availability* (for a similar argument, see Tooby & Cosmides, 1996). A partner's *qualities* affect his/her relative ability to provide benefits, whether intentionally (e.g. food, coalitional support) or incidentally (e.g. popularity by association, opportunities to learn from). A partner's *tendencies* affect his/her willingness to impart such benefits, which includes generosity to partners and in general, as well as commitment to the focal individual. Finally, a partner's *availability* determines whether a willing and capable partner is actually present to impart benefits and is not physically prevented from doing so. The total benefits received from a partner will be the product of these three partially overlapping (and possibly fluctuating) factors. The best partners are willing and able to provide benefits and are available to do so, whereas partners who are willing but unable to help (or vice versa) end up conferring fewer benefits upon their partners.

Do people actually choose partners based on these three factors? Multiple research areas converge on these factors (or conceptually related ideas) as prime bases for partner choice. First, the field of social perception finds that warmth and competence (i.e. willingness and ability to help) are the two most important dimensions on which people universally rate each other, and these dimensions underlie many other traits and are responsible for most of the variance in perceptions of others (reviewed by Fiske et al., 2007). Second, the literature on trust within organizations finds that the three most important factors predicting trust in a person are that person's ability to repay the trust ("ability") and their willingness to do so, either to the trustor specifically ("benevolence") or to people in general ("integrity") (reviewed by Mayer et al., 1995). Third, within evolutionary studies, people prefer to associate with competent partners (reviewed by Henrich & Gil-White, 2001) and those who can generate benefits for others (Tooby & Cosmides, 1996); chimpanzees apparently share this preference (Melis et al., 2006). In terms of tendencies, much work suggests that all else being equal, people like partners who are willing to help others (e.g. Barclay, 2010a; Milinski et al., 2002a). Finally, in terms of availability, proximity appears in many psychology textbooks as one of the most important factors in friendships and relationships (e.g. Myers, 2002; Westen, 1996). Thus it appears that the three most important bases of partner choice are indeed a partner's ability to provide benefits, willingness to do so, and availability.

This is not to suggest that people consciously track the benefits for association, or that they are aware of the market-based factors that affect their assessments, their interpersonal attraction, or their

Table 1
Useful strategies (and relevant sub-tasks) for cooperation within biological markets.

Broad goal	Examples of important strategies	Examples of relevant sub-tasks
Choose partners	1. Choose partners who give cues of being able, willing, and available to provide net benefits	<ul style="list-style-type: none"> Assess the relative benefits provided by each potential partner: use cues that discriminate (somewhat) reliably among individuals Assign value to partner-produced commodities based on supply and demand, and on one's specific needs Balance the trade-off between the quality of one's partners (ability to provide net benefits) and their willingness to help
Attract partners	2. Approach potential partners according to one's own relative market value	<ul style="list-style-type: none"> Assess one's own market value relative to those who compete for the same partners Avoid wasting effort trying to ally with those of much higher market value, especially when competition for these partners is severe or when approach costs are high
	3. Balance the trade-off between having weak connections with many partners and strong connections with few	<ul style="list-style-type: none"> Assess relative payoffs for forming associations that are strong and narrow versus weak and distributed
Maintain partners	1. Signal traits that are desirable to partners, including ability, willingness, and availability to provide net benefits	<ul style="list-style-type: none"> Signal one's qualities such as abilities and resources: difficult-to-perform cooperative actions ("extravagant helping"); difficult-to-perform actions in non-cooperative domains (displays of athleticism, conspicuous consumption, etc.) Signal one's willingness to help: mundane help; generalized help; frequent help; displays of commitment; expressions of morality; signals of allegiance to group or shared goals Signal one's availability to help: maintain physical proximity and/or social contact
	2. Use generosity to compete over partners	<ul style="list-style-type: none"> Compare one's generosity relative to others who compete over the same partners Calculate the marginal costs and benefits of increasing or decreasing one's generosity relative to others Escalate one's generosity when this grants better access to partners (competitive helping), provided that they are worth the additional cost
	3. Impression management	<ul style="list-style-type: none"> Monitor own reputation: increase helping when one's (relative) reputation is too low, decrease if unnecessarily high Appear helpful, even when help is unnecessary If reputational benefits for helping are low, avoid situations that obligate helping Balance the benefits of anonymously cheating with the risk of being detected; err on side of safety when average reputational costs are high Determine when such suppression will be effective, against whom, and how to frame the attack to maximize effectiveness
	4. Suppress, downplay, or attack the generosity of competitors	<ul style="list-style-type: none"> Assess the benefits provided by current partner(s) relative to alternative partners Determine the costs of switching, including search costs, time to build trust, and opportunity costs of lost cooperation If long-term payoffs favor staying with current partner(s), then offer commitment Continue to provide the commodities that attracted them to you Continue to signal one's qualities, tendencies, and availability, especially if others believe these might have changed recently Assess the risk of partners leaving for better alternatives When risks of abandonment are high, provide more benefits and tolerate more asymmetries in cooperation Become irreplaceable by providing commodities that others do not; maintain such monopolies when possible
	1. Determine whether to stay with a current ally or switch to better long-term alternatives	<ul style="list-style-type: none"> Limit their access to, and/or knowledge of, high-value competitors Impose costs to prevent allies from straying
	2. Entice desirable partners to stay	
	3. Prevent useful allies from leaving	

The proximate psychological mechanisms will vary, and might include either deliberately strategic planning or adaptive modulation of more general psychological mechanisms (e.g. increased "liking" of particular individuals, heightened empathy in certain situations). This list of strategies is not meant to be exhaustive, and many strategies are useful in both mating and non-mating contexts.

emotional and behavioral responses. Sometimes these decisions are deliberate and Machiavellian, but often will not be. Instead, natural selection favors psychological mechanisms that *function* to perform these assessments and target interpersonal attraction accordingly—a market-based approach identifies what traits will be deemed socially attractive, to whom, and why. Under this view, emotional responses (e.g. "attitudinal reciprocity," de Waal & Luttrell, 1988) are one *proximate* or *psychological* cause of such social attraction, and biological markets help explain *ultimate* or *functional* causes—why organisms would have such proximate mechanisms in the first place and what tends to trigger them. Similarly, a market perspective is agnostic about which *developmental* factors influence market-based behavior and the way in which genes and social environment interact to produce a well-functioning psychology (e.g. gene-culture interactions). For a discussion of this distinction between psychological, developmental, and functional causes, see levels of analysis by Tinbergen (1968) (see also Barrett et al., 2002). As long as the resulting choices are adaptively tailored according to partners' market value, then natural selection will favor whatever psychological mechanisms or developmental processes led to that result.

People will use various cues to assess partners' relative ability and willingness to provide benefits (and fluctuations thereof), just as they do when assessing mate value (Miller & Todd, 1998). For example, physical and intellectual competence both predict someone's ability to provide benefits, and these could be cued or actively signaled by specific physical traits and demonstrated skills (e.g. size, hunting ability, sports acumen, or reputation thereof) or various intellectual skills and abilities (e.g. wit, vocabulary, problem solving). Similarly, Ego could predict Alter's willingness to help him/her by assessing Alter's warmth for Ego (or toward people in general), which is cued by Alter's past instances of help toward Ego (or toward people in general), or Alter's reputation, expressed morals, group membership, emotional expression, or any cues thereof. Perceived similarity and group membership could be used as cues of common goals (Tooby & Cosmides, 1996) or the likelihood of receiving reciprocity (Yamagishi & Kiyonari, 2000). More generally, many features investigated by social psychologists may be cues of ability to provide benefits and future likelihood of doing so.

The exact cues and signals used will be extremely varied. These cues may also vary in their usefulness at predicting ability and/or willingness to help, or in the factors that maintain the honesty of such

cues and signals (e.g. signal costs or differential benefits: Gintis et al., 2001; McNamara & Houston, 2002; Zahavi & Zahavi, 1997). As with traits in sexual selection, these cues of ability and willingness to help can differ between populations, with more inter-population variation in cues occurring where there is stronger competition for partners (West-Eberhard, 1983). The nature, usefulness, maintenance, and variance of such cues and signals require further investigation; reviewing the existing work is beyond the scope of this article (for a review of signaling systems in non-humans, see Searcy & Nowicki, 2005). For this article, we merely need to assume that individuals do vary in their ability and/or willingness to provide benefits to partners and that this can be at least partially assessed. As such, some potential partners are more desirable than others and that there is at least some agreement about which partners are more desirable, just as there is some agreement over what mates are most desirable.

3.1.3. *Idiosyncratic partner preferences*

Despite there being at least some agreement over what traits (and therefore what partners) are more desirable than others, individuals may nevertheless weigh some traits and cues more heavily than others do. This can cause idiosyncratic preferences for partners. Potential causes of these individual differences in partner preferences include the following: variation in levels of relatedness to different partners (Chapais, 2006; Seyfarth, 1977), variation in one's own market value (Frank, 1988), variation in the particular types of benefits that individuals need from partners (Hoeksma & Schwartz, 2003), variations in whom the available partners appear to want to pair with and commit to (Tooby & Cosmides, 1996), or differing assessments of what cues best predict ability and willingness to help (possibly based on past experience with those cues). There could even be variation in choosiness itself due to frequency-dependent selection, with some individuals entirely avoiding the cost of assessing partners (e.g. Foster & Kokko, 2006). Future work should further investigate the causes of these individual differences in partner preferences, how they interact, and what effects they will have on the overall market for partners.

In terms of who actually approaches and pairs with whom, individuals must also assess their own market value in order to direct their efforts toward those who are relatively more likely to partner with them; this helps avoid the costs of search and rejection associated with aiming too high (Frank, 1988; Seyfarth, 1977). Thus, in a biological market, even when there is mutual agreement about who is most desirable, many individuals cannot fulfill their preferences because they are outcompeted. Possessing low market value may cause individuals to adaptively adjust their actual preferences for social partners, as in mating markets (e.g. Little et al., 2001).

3.2. *Attracting partners for cooperation*

Choosing partners is of little value if they do not choose you. Some markets have discrete classes of “chooser” and “chosen” (e.g. buyers and sellers, females and polygynous males), but many cooperation markets will have either mutual choice between two classes (e.g. plant–fungus mycorrhiza, monogamous matings) or all members being of a single class that choose amongst each other (e.g. friends, allies, coalition partners). In all of these, to attract a particular partner, one must be more desirable than available rivals are. To get a good partner, one must *be* a good partner. How might one do so? Given that organisms should choose partners who have the ability, tendency, and availability to provide net benefits, it becomes a good strategy to advertise these characteristics to whomever one might want to ally with. There are many ways to do so that are unrelated to cooperation, such as demonstrating competence, good genes, and resource-holding potential. In addition to these, and related to the focus of this paper, we can ask: “How might one use cooperative behavior as a means of competing for social partners?”

3.2.1. *Increasing one's market value via generosity*

Many individuals have qualities that allow them to provide benefits to partners through mere association or through mutualistic benefits (Clutton-Brock, 2009; Sachs et al., 2004). For example, learned individuals provide opportunities for infocopying (Henrich & Gil-White, 2001). Those who watch for or repel predators, violence, or harassment, provide environments free of such threats. Hunters who hunt to feed themselves may provide opportunities for scrounging (Barclay & Van Vugt, *in press*). In economic jargon, these individuals are desirable because they generate “positive externalities” (Tooby & Cosmides, 1996).

In addition to such passive provision of benefits, one could also become a valuable partner by intentionally providing benefits directly to a partner rather than doing so only incidentally (Seyfarth, 1977), and individuals vary in their ability to do so. It is obviously desirable to interact with those who are willing to directly provide such benefits to partners, and ample research demonstrates that people prefer to associate with others who have demonstrated a tendency toward generosity (e.g. Barclay, 2010a; Barclay & Willer, 2007; Milinski et al., 2002a). In order to attract partners who are willing to provide one with benefits, one may then have to provide them with benefits in kind or in different currencies—this becomes the basis of reciprocity (Trivers, 1971). In fact, market-based bidding over mutualistic partners may have been an evolutionary precursor to reciprocity, because this strategy can invade a population where no one actively provides benefits (Barclay, 2011).

This provision of benefits—and signals thereof—could be directed toward specific individuals to court or keep them as allies (Seyfarth, 1977), or broadcast toward a large audience to attract multiple persons at once (Smith & Bliege Bird, 2000). The relative benefits of these two types of generosity should depend on the availability of novel partners, the ease of switching partners, and the possibility of receiving attention from multiple partners at once. While signaling to multiple individuals is highly beneficial, audiences should be more skeptical of anything signaled to a large crowd because of the increased payoff for deception (Andrews, 2001; Barclay & Willer, 2007). As such, audience members should place more value on a signal of benefit-provision if that signal is directed at themselves alone rather than at a large crowd.

3.2.1.1. Extravagant helping: giving to signal high quality. Zahavi (1977) argued that helping could serve as an honest signal of one's abilities, as long as only those individuals who possessed sufficiently high quality would be able to help. In this argument, some kinds of helping are sufficiently difficult or costly to perform that only those of high competence or resources can afford to be magnanimous, such that the magnanimity itself is a signal of those highly desirable traits. Originally controversial, this idea of “costly signaling” has been generally accepted since Grafen (1990) mathematically proved that such signals could work if high-quality individuals experienced a lower marginal cost than did higher-quality individuals. Other researchers have used similar models to explicitly show that helping can function as an honest signal of quality and can be used to attract partners (Gintis et al., 2001).

Audience members benefit from attending to public generosity because it can convey information about the giver's abilities, resources, or cooperative intent (Gintis et al., 2001, see also Zahavi & Zahavi, 1997). When there exists variation in these traits, it pays for audiences to choose partners based on signals of those traits (McNamara et al., 2008). Public generosity may be particularly effective at signaling such traits because crowd members have a vested interest in attending to such generosity in order to receive a share (Smith & Bliege Bird, 2000).

Several forms of helping have been described as costly signals of individual quality. Extravagant donations to charity or lavish examples of sharing may function to advertise one's resources

(Boone, 1998). For example, we may know that Warren Buffett is exceedingly rich because of the billions of dollars he has donated to charity. Field examples of this include Kwakiutl potlatches (Goldman, 1937; Rohner & Rohner, 1970) and New Guinea mokas (Strathern, 1979). Hunting large game requires physical skill, such that some anthropologists have argued that hunters in some groups deliberately target hard-to-acquire big game to “show-off” and to attract social status or mates (Hawkes & Bliege Bird, 2002; Smith & Bliege Bird, 2000, but see Marlowe, 1999). These hunters seem to benefit from this signaling: Meriam turtle hunters in the Torres Strait have more children than non-hunters (Smith, 2004; Smith et al., 2003), and good Ache hunters have more children with other men's wives than do poor hunters (Hill & Kaplan, 1988). In these examples, generosity primarily signals resources and/or abilities, although its secondary function could be to signal cooperative intent if one gives resources to others rather than destroying them (Smith & Bliege Bird, 2005). Even if the primary function of such acts is trade rather than signaling, they can still have secondary function of signaling one's qualities (Lotem et al., 1999).

3.2.1.2. Mundane helping: giving to signal willingness or compensate for low quality. Individuals may also help others not to advertise extravagant qualities, but to compensate for a lack of them. For example, the literature on primate grooming consistently shows that low-ranking group members spend more time giving grooming to high-ranking group members than vice versa (for a meta-analysis, see Schino, 2001). Some of this is undoubtedly appeasement (trading grooming for tolerance, e.g. Ventura et al., 2006), but it can also occur because low-ranking primates have less to offer in terms of coalitional support, such that they must compensate for their low market value by offering more grooming in exchange (Schino, 2001, 2007; Seyfarth, 1977). Similarly, the mating literature has noted that physically attractive males perform less brood care and invest less in relationships than do less attractive males, and that females are attracted to the former despite this lower investment because of the higher benefits for associating with high-quality males (e.g. Burley, 1988; Frank, 1988; Gangestad & Simpson, 2000; Gangestad et al., 2007; Møller & Thornhill, 1998); low-quality males must compensate for their low market value by offering more commitment and investment. Physically attractive men are also less cooperative than unattractive men in experimental games (Takahashi et al., 2006; Zaatari & Trivers, 2007). Such findings would suggest that it is often the low-quality individuals who provide the most help, at least in men.

Why would high-quality individuals help less? Helping others involves an opportunity cost in terms of time, energy, and resources that cannot be spent elsewhere. However, not all individuals pay equal opportunity costs. Some individuals—like high-quality males in polygynous species—receive high returns for investing in mating effort or in directly advertising their high quality to potential partners and allies (Burley, 1988; Møller & Thornhill, 1998). Although there are reputational benefits for helping and cooperation, these benefits may not outweigh the high opportunity costs experienced by high-quality individuals, who may receive a better return investment for their time and effort by investing directly in mating effort (Barclay, 2010a). For example, highly athletic or competent individuals may benefit more from directly advertising these highly desirable qualities instead of performing low-cost acts of helping that anyone could perform. The relative costs and benefits of various acts currently require empirical testing. Those who lack competence or desirable physical qualities (less desirable partners) do not have the option of advertising those qualities, and would instead need to advertise their willingness to invest more in relationships in order to attract partners. Similarly, highly physically attractive or competent individuals can get away with being less cooperative specifically because they have those other qualities to offer in a relationship (Takahashi et al., 2006; Zaatari & Trivers, 2007).

The difference between this “mundane helping” and the more “extravagant” forms like hunting and philanthropy is in whether all individuals pay the same fitness cost to perform it (Barclay & Reeve, 2012). When high-quality individuals experience lower fitness costs for helping (e.g. risky heroism for athletes versus klutzes, philanthropy for billionaires versus paupers), then helping behavior can honestly signal the possession of desirable qualities. However, some forms of help are equally costly for everyone, such as grooming, volunteering, or anything else that is simply an investment of time. In these cases, those with lower opportunity costs will help more (e.g. unattractive males with fewer mating opportunities). In this latter case, helping is an honest signal of future cooperation not because of differential costs, but differential benefits: cooperation at time A is worth the cost for those who intend to reap the long-term future rewards of mutual cooperation, but is not worth it for those who intend to defect later (André, 2010; Bolle, 2001; Ohtsubo & Watanabe, 2009; Smith & Bliege Bird, 2005).

It is potentially problematic to group all forms of helping together because they have different kinds of costs—opportunity costs versus performance costs—and will be performed by different individuals (Barclay & Reeve, 2012). As such, it is useful to distinguish between extravagant helping and mundane helping (Barclay and Reeve called these “quality-dependent” and “quality-independent” help, respectively). We should predict that researchers will find stronger relationships between helping and individual quality (or any other measure of individual differences) if they separate the two types of helping than if they combine them.

3.2.1.3. Commitment. Organisms can respond to fluctuations in others' market value on very short timescales (e.g. Barrett & Henzi, 2006; Fruteau et al., 2009), but they can also opt for longer-term strategies. When partner choice is based on long-term cooperation, this can select for genuine concern for long-term partners because of the commitment problem. In any long-term cooperative relationship, whether monogamous mates, allies, or otherwise, there is a risk of abandonment. Partners can be lost to rivals, especially after a drop in market value, and we have many negative terms for those who readily switch partners too easily (e.g. “fair-weather friends”). Because of this risk of abandonment, one should seek cues that others are genuinely concerned for one's welfare and will continue to provide benefits even if one's market value decreases (Frank, 1988; Tooby & Cosmides, 1996).

Emotions like love serve to commit people to romantic relationships (Frank, 1988), and other emotions presumably serve the same function in long-term friendships. Those possessing such emotions have an advantage in being more desirable as partners, such that partner choice selects for displays of genuine concern toward committed partners. The honesty of such displays can be maintained by signals of commitment that are costly to signaler and only beneficial in the long-term, thus deterring those who would exploit in the short term (André, 2010; Ohtsubo & Watanabe, 2009). Such signals of commitment could include the direct provision of benefits to partners, but because this invites exploitation, one might rely on signals that are costly to produce but provide no benefit to partners, such as investments of time (Bolle, 2001; Sozou & Seymour, 2005).

Of course, there is a trade-off between the long-term benefits of committing to one or a few “close friends” versus the benefits of “playing the field” by responding immediately to others' short-term fluctuations in market value. This latter strategy may involve maintaining shallower alliances with more partners, possibly to use some of them to replace current partners. This trade-off currently requires more theoretical and empirical work, especially as partners may demand signals of commitment. We might tentatively expect some stable baseline level of commitment to existing partners and only minor fluctuations in response to short-term changes in their market value (especially in domains that “don't really matter for true

friendship”), with these fluctuations in commitment becoming larger and more permanent if the partners’ new market value appears increasingly permanent (Frank, 1988).

One reviewer has noted that the trade-off between “committing to close friends” and “playing the field” resembles the trade-off between males seeking monogamous versus polygynous romantic relationships. In romantic relationships, some individuals (e.g. high-quality males) benefit more from investing in short-term mating effort toward multiple partners, whereas others (e.g. low-quality males) must direct long-term mating effort toward fewer partners (Gangestad & Simpson, 2000). Analogously, for platonic relationships, highly desirable partners may be better able to “play the field” by courting multiple allies or by responding more quickly to others’ fluctuations in market value, whereas low-value partners may have to offer deeper commitment to fewer partners. I would suggest there may even be a non-mating equivalent of the polygyny threshold model (e.g. Alcock, 2005), whereby individuals must choose between befriending high-value partners who offer less time to each of many friends versus befriending low-value partners who offer much more devotion to fewer friends.

3.2.2. Competitive helping

One of the most important implications of biological markets on cooperation is that “generosity” is an inherently relative term. If all individuals can increase their biological market value via generosity—whether extravagant displays or more mundane willingness to help—then those who make the most generous public displays or provide the most benefits to their partners will have access to the most (or the best) partners. This market force provides an incentive (conscious or not) for individuals to *compete* to be more generous than others in the biological market (Roberts, 1998). By being more generous than others, an individual is signaling greater abilities, greater resources, or greater willingness to provide benefits than others. This phenomenon has been called *competitive altruism* (Barclay, 2004; Roberts, 1998; Van Vugt et al., 2007) or *competitive helping* (Barclay, 2011). It can occur whenever reputational benefits are a limited resource such that the best cooperators give and receive more social benefits than the next-best cooperators, and so on down the line, and when these additional benefits outweigh the costs of the investment in generosity (Barclay, 2004).

Competitive helping is more than “merely” trying to appear good; it occurs when individuals actively try to outdo each other by being *more* generous than others (Barclay & Willer, 2007), either with consciously increased generosity or even with an increase in genuinely altruistic sentiment. This competitive process can create a positive feedback loop causing an escalation of generosity in a “runaway” process until very high levels of cooperation are reached (McNamara et al., 2008; Nesse, 2007). This runaway process could occur over evolutionary time, or could be the result of individuals adaptively varying their generosity in response to cues of competition.

3.2.2.1. Evidence for competitive helping. Evidence is accumulating that people actively escalate their generosity when competing over partners. People give more money to partners in cooperative games when they are observed than when anonymous (e.g. Hardy & Van Vugt, 2006; Milinski et al., 2002b; Rege & Telle, 2004), but they give the most when those observers also have an opportunity to choose whom to interact with in subsequent games (Barclay, 2004; Barclay & Willer, 2007; Sylwester & Roberts, 2010). This latter finding indicates that opportunities for partner choice create an incentive to compete via generosity, and this generosity is above and beyond the effects of simply “appearing nice.” In addition, multiple researchers have interpreted the extravagant helping described in Section 3.2.1.1 as a form of competition to help the most (e.g. Barclay, 2010b; Van Vugt et al., 2007). This competitive helping appears to pay off, in that those who give more money to others tend to be chosen more often as

partners (Barclay & Willer, 2007; Sylwester & Roberts, 2010) and are rated as possessing higher status than those who give less (Hardy & Van Vugt, 2006; Willer, 2009). In addition to competitive giving being caused by partner choice, it can also be fostered by giving prizes to people who donate the most to others, even if that prize is worth less than the donations (Duffy & Kornienko, 2006).

It is currently unknown whether non-humans also actively display this competitive helping, though the evidence is suggestive. Seyfarth (1977) argued that primates use grooming to attract high-ranking social partners and that there is competition over who gets to groom whom; two meta-analyses by Schino (2001, 2007) support these contentions. There is ample evidence that non-human grooming responds to market pressures. For example, baboon females groom mothers with infants (a desirable resource) more often when the supply of infants is low (Barrett & Henzi, 2006; Gumert, 2007b; Henzi & Barrett, 2002), baboon males groom females for longer before sex when the supply of females is low relative to the number of males (Gumert, 2007a), and low-status baboons who are experimentally granted the ability to provide food for others tend to receive more grooming when this ability is unique than when others are also granted this ability (Fruteau et al., 2009). Market effects have also been found in cleaner fish (Bshary & Grutter, 2002, 2005, 2006; Bshary & Schaffer, 2002) and plant–mycorrhiza interactions (Kiers et al., 2011). However, it is not always clear whether these market effects represent an active escalation of giving in response to immediate cues of competition, a byproduct of proximate psychological factors correlating with market pressures (e.g. stress to providers when supply is low, Henzi & Barrett, 2002), or whether they occur over longer timescales including evolutionary timescales (e.g. Kiers et al., 2011). For example, there were early suggestions that birds compete to provide food at nests or to perform “altruistic” sentinel behavior (Zahavi & Zahavi, 1997), but others have dismissed this as resulting from simpler processes such as parental effort or state-dependent selfishness (e.g. Wright, 1997; Wright et al., 2001). Because of such ambiguities, we look forward to further investigations of active competition over helping in non-humans. Such tests might use forced partner choice paradigms (e.g. Barclay & Willer, 2007) where animals can increase the benefits they give to others (including third parties) in the presence/absence of an anticipated audience and/or competitors for that audience.

3.2.2.2. Determining the optimal level of competitive helping. How much should one invest in social competition over relative reputation? Individuals should escalate their helping until the marginal cost of giving additional generosity outweighs the marginal benefits of additional audience attention (Barclay, 2011). This marginal cost of giving will vary among individuals, and the marginal benefits of audience attention should be affected by factors including: (a) the value that audiences place on the signaled traits when choosing partners; (b) the variance in quality among partners that one might attract; (c) the ability of a signaler to receive benefits from multiple observers; and (d) an individual’s need to attract partners (e.g. those who need partners will compete more vigorously). All else being equal, the optimal level is predicted to be greater in larger biological markets because of the increased competition over a larger share of benefits (Barclay, 2011).

Of course, sometimes it does not pay to compete at all. Within mating competition, it is not worthwhile to escalate competition over a mating partner when one is unlikely to win (West-Eberhard, 1979). Analogously, it is not always worth competing over cooperative partners. The following conditions would make competitive helping not worth the cost: (a) if one is so undesirable to potential partners that no amount of generosity could compensate; (b) if one is so much higher quality than competitors such that one can attract social attention without paying any costs of helping; (c) if the additional quality of a new partner(s) is not worth the cost of attracting them;

(d) if one does not need additional partners or social attention, or (e) if other means of competition provide much better benefit-to-cost ratios than competing via helping. If one is unable to compete normally, one might adopt alternative tactics for competing over partners (see below), just as individuals who cannot compete in physical competitions may develop alternative means of competition (West-Eberhard, 1979).

3.2.3. Reputation management

Whenever partner choice exists, people have a vested interest in maintaining a reputation for cooperativeness. Because audiences have imperfect information about one's abilities and cooperative intent, one can attempt to manage others' impressions of oneself, and there is wide literature on impression management (reviewed by Leary & Kowalski, 1990). Some strategies will be the same for cooperation as in any other form of impression management (e.g. when to engage in false advertising), but new interesting strategies also emerge, especially within market competition.

3.2.3.1. Wasteful giving. When in competition for social partners, everyone must send signals of cooperation to maintain their relative desirability. There is inevitably some waste and inefficiency associated with signaling one's generosity. Not all signals of cooperative intent actually benefit anyone, or provide as much benefit as they cost. For example, imagine a highly inefficient but well-known charity: each individual might not actually want to donate because of the inefficiency, but might need to give to look better than others (or to avoid losing relative standing). As a result, everyone gives despite the "charity" not actually helping anyone. Anyone who does *not* give will lose relative position to those who do (Frank, 1985) and may lose partners to more generous competitors. However, when everyone does this, it does not change the equilibrium distribution of partners. Each individual ends up paired with partners of the same quality as he/she would without the giving, only under competition he/she would have had to pay a higher cost in order to do so (Frank, 2000). Although there are indeed often public gains from many types of giving, the *signals* of cooperative intent can involve wastage that reduce such gains (e.g. giving to inefficient or bogus charities; consumerist signals of conscientiousness, Miller, 2009). As evidence for these arguments, Van Vugt and Hardy (2009) recently showed that reputational pressures can cause people to contribute money to a group project even when their contributions have no effect or are not necessary. Furthermore, people who made such contributions—even when wasteful—were rated as having higher status than low contributors had.

3.2.3.2. Avoiding obligations to give. Some types of help are committed because a person has a genuine or unfeigned concern for the well-being of the recipient (e.g. empathy, Batson et al., 1997; oneness with others, Cialdini et al., 1997; "warm glow," Andreoni, 1990). However, other types of generosity could be performed for explicitly reputational reasons. For example, a person might not actually want to help the recipient because the costs outweigh the reputational gains, but would feel obligated and would act generously out of fear of losing his/her reputation and hence his/her rank in terms of apparent generosity (Barclay, 2009). To prevent an obligation to be generous when the reputational benefits are low, people may avoid situations that require generosity, for example by crossing a street to avoid a beggar. In an experimental analogy of this, Dana and colleagues (2006) had participants play a "Dictator Game" where they had the choice of dividing money (e.g. \$10) between themselves and a recipient, and then gave them the option of keeping \$9 and having the recipient not know that any decision had been made. Of the participants who would give money, 40% later reneged when offered the latter "quiet exit option" of having the recipient not know about the interaction. Because some help is given only grudgingly for

reputational reasons, it might thus be useful to distinguish between voluntary helping and obligated helping. This is conceptually similar to previous breakdowns like symmetry-based versus calculated reciprocity (de Waal & Luttrell, 1988) but broadened to include non-dyadic cooperation and public reputations. More generally, it is important to distinguish reputational benefits for helping from reputational costs for *not* helping, because these can differ in magnitude in different situations or for different people.

3.2.3.3. Strategic helping versus genuine concern. Cooperation can be used to attract partners, but it is often costly for partners to directly provide benefits to others. Since audiences' choices of partners must be based on information they observe or receive from others, the easiest way of avoiding these costs is to be publicly helpful but privately selfish. This involves helping when observed and not helping when anonymous, and much research shows that people give less to others when their actions are anonymous (e.g. Barclay, 2004; Bereczkei et al., 2007; Coricelli et al., 2010; Hardy & Van Vugt, 2006; Hoffman et al., 1994; Masclot et al., 2003; Rege & Telle, 2004). This modulation of behavior could be strategic, as it was in studies where participants modulated their cooperation within an experiment according to their anonymity in a particular round (Barclay & Willer, 2007; Milinski et al., 2002b; Semmann et al., 2004). At other times this modulation could be unconscious, as when subtle cues of observation influence monetary donations and other forms of helpfulness (Bateson et al., 2006; Burnham & Hare, 2007; Ernest-Jones et al., 2011; Haley & Fessler, 2005).

Despite the advantages of strategic giving, there is a risk: being discovered being selfish when one thought one was unobserved. This is a classic case of risk management (a.k.a. signal detection, the "smoke-detector principle," Nesse, 2005; "error management," Haselton & Buss, 2000). All else being equal, people are unlikely to prefer partners who have been caught being selfish, and they may switch their allegiances to more generous alternatives (Tooby & Cosmides, 1996). Partner choice allows for "punishment" of detected selfishness that is costless to the punisher (barring high costs of switching) because it is in one's interest to avoid selfish partners. This can select for a default strategy of cooperation—or at least an avoidance of unambiguous complete selfishness—so that people avoid the high costs of detected selfishness (Delton et al., 2011; Frank, 1988; Johnson & Bering, 2006; West et al., 2011). We should thus predict that people will respond to unconscious cues about the likelihood of observation and the reputational costs or benefits if observed (e.g. Haley & Fessler, 2005), but at the same time there will be some non-zero level of cooperative sentiment that remains for risk management reasons (Delton et al., 2011). It is currently unknown whether people's genuine concern for others varies as a function of audience; this would be extremely interesting to study.

3.2.4. Attacks on reputation and suppression of others' generosity

It is well established that people will attack the reputations of romantic rivals. Furthermore, competitors will launch these attacks in precisely the domains that potential mates most seek in partners, such as fidelity in females (Buss & Dedden, 1990). There is no a priori reason why this principle applies only to mating relationships, but why should we expect similar such attacks on rivals for non-mating cooperative relationships?

Generosity is a relative concept: whether one is seen as generous depends not only on one's own level of generosity, but also on the generosity displayed by others around (i.e. local norms). If a person gives X units to a charity, a public good, or a needy person, then he/she will be seen as relatively generous if all other group members give $X - 1$ and somewhat selfish if others give $X + 1$. Just as there are a limited number of dominant or high status positions within groups (Frank, 1985), there are a limited number of "highly generous" positions within groups because when one person increases his/her

generosity it makes others appear relatively more selfish by comparison. This then affects access to partnerships: when one person increases his/her access to better partners by increasing his/her generosity, this shifts the norm slightly and results in some others appearing less desirable by comparison and thus having less access to good partners. There is thus an arms race over positions of relative generosity (or relative norm-upholding). When one person increases his/her generosity, it obligates others to increase theirs to “keep up with the Joneses’ generosity” and maintain access to high-quality partners. Thus, individuals have an incentive to subtly suppress the generosity of their competitors (Zahavi & Zahavi, 1997), or even to suppress the entire market for generosity if they cannot compete in it.

There are multiple ways to maintain one’s relative position in the face of others’ escalated generosity. If another’s generosity is unambiguously altruistic, then one must follow suit to maintain one’s own relative value as a partner. However, there is ambiguity regarding many generous acts, including the exact amount of help and especially the underlying motivations (e.g. Bénabou & Tirole, 2006). One can downplay or criticize others’ benevolence to prevent that person from gaining position in the reputational arms race. Monin (2007) suggests that this “do-gooder derogation” can be done by implying that another’s morality reflects well-intentioned naivety or weakness rather than moral strength, pointing out obvious or imagined incentives a person may have been following for being generous, or implying real or imagined hypocrisy by the actor (e.g. “he’s a vegetarian for moral reasons, but wears leather shoes!”). This may also explain many people’s resistance to accepting functional explanations for the evolution of generosity and cooperative sentiment: from my experience studying altruism, when someone admits that altruists can receive benefits, others question that admitter’s motives whenever he/she is cooperative. Although anecdotal, such questioning may be part of a general phenomenon of discrediting others’ generosity. One might also downplay others’ generosity by implying that it was not actually costly or not actually helpful to the recipient. For example, members of egalitarian hunter-gatherer tribes sometimes criticize the size of game brought in by good hunters, which functions to prevent the hunters from gaining too much status and rising above everyone else (Boehm, 1999). This pattern makes sense when one considers that one person’s relative reputational gain is another person’s relative reputational loss.

Such attacks on cooperators’ reputations may explain the fact that cooperators are often punished at non-zero levels in experimental tasks (e.g. Barclay, 2006; Fehr & Gächter, 2002; Gächter et al., 2006) or publicly criticized in field experiments (Barr, 2001). This punishment of cooperators appears to be cross-cultural (Herrmann et al., 2008). Much of this is undoubtedly retaliation by free-riders for past or anticipated punishment, but some such punishment (especially from non-free-riders) could be attempts to maintain one’s position in the generosity hierarchy: by punishing or criticizing the cooperation of others, one discourages them from engaging in a generosity arms race which would make one’s own cooperation look small (and punishment-worthy) by comparison. This is especially true with criticism because the cost of being criticized depends on audience perceptions, which can be manipulated. If the criticism of cooperators precedes opportunities to criticize free-riders, then a free-rider can lower others’ impressions of what is expected, thus protecting his/her own reputation and simultaneously reducing a cooperator’s gain.

Attacks on others’ generosity should be most common (all else being equal) when there is increased competition for partners, especially when groups are small such that one person’s gain is a relatively bigger loss to others. One might also predict that these attacks would come from direct competitors such as those who are closest in overall partner value to the generous person, because those people would have the most to lose from their competitor increasing in reputation. However, this is a dangerous game, as many people will realize the incentives behind such attacks, such that they could

backfire on the criticizer. One potential way around this would be if criticism comes from the friends, allies, and kin of those who are closest in overall partner value to the generous person (for a review of gossip and attacks on reputation, see Hess & Hagen, 2006).

3.3. Keeping partners

Partner choice implies the possibility of abandonment by one’s current partner in favor of a rival. Whether this abandonment is a sharp break or a gradual reduction of associations, there are obvious fitness consequences if one loses valued associates. Thus, we should predict psychological and behavioral adaptations to convince cooperative partners to stay or prevent them from leaving. Such adaptations have already been studied within mating relationships, and many of the principles can apply to non-mating partnerships as well. Rather than list all possible insights that might be brought from the mating literature into the cooperation literature, I will highlight just a few.

3.3.1. Partner maintenance

The most obvious strategy for enticing partners to stay is to keep doing whatever attracted those partners in the first place, i.e. keep providing benefits (direct or indirect) and cues thereof. This is so obvious it is barely worth saying. This being said, an organism must also monitor its own market value relative to competitors to determine whether additional enticements toward partners are required to prevent them from “trading up” for a better partner. An organism might also need to continuously signal its ability or willingness to help if it needs to assure partners that these traits have not changed recently (André, 2010); the necessity of ongoing signaling should depend on the perceived likelihood of these traits changing.

In economics, businesses have many strategies to keep customers, such as creating brand loyalty, specializing in a particular commodity to develop a comparative advantage, or creating a monopoly on a commodity. If a company has a local monopoly on a particular commodity, then its customers are forced to either purchase from that company, go without the commodity, or move. Analogously, if one organism gains a local monopoly on producing a desirable social commodity, its partners must stay with it to have access to that commodity. That organism will become irreplaceable to its partners (Tooby & Cosmides, 1996), who then have a stake or vested interest in its well-being (Roberts, 2005). Tooby and Cosmides (1996) use this concept to derive a number of predictions about people’s desire to be irreplaceable to friends and allies, including motivations to: a) develop specialized skills; b) seek partners who value them and to whom they would be irreplaceable; c) avoid and be jealous of others who could replace them; and d) seek confirmation that they are indeed irreplaceable to partners.

Many ways of keeping partners seem “nice,” as they involve providing benefits to others. However, just as there is a dark side to retaining mates, there can be a dark side to retaining other types of cooperative partners. For example, people are jealous when their mate might be attracted to someone else (e.g. Buss et al., 1992), and they are also jealous when a close friend appears to favor someone else more (DeScioli & Kurzban, 2009; Tooby & Cosmides, 1996). Just as one might sequester a mate from opportunities to stray (Wilson & Daly, 1992), one might also attempt to limit one’s ally’s exposure to alternative allies; this may be part of creating a monopoly on a social resource. It is even conceivable that some individuals might coerce allies into staying by imposing costs for leaving, just as mates will sometimes do to one another (Wilson & Daly, 1992). These are all attempts to limit others’ partner choice in order to maintain preferential access to those partners. The utility of these strategies depends on their costs relative to partner-attraction, as well as the risk of abandonment. For example, low-quality mates experience

more romantic jealousy than high-quality mates (Brown & Moore, 2003), so we might predict that people with low market value will experience more jealousy about their friends and allies than highly desirable partners do.

3.3.2. Switching partners versus maintaining partners

One might not always want to maintain current partners, especially if high-value alternatives are available. However, there are costs associated with switching partners. These include search costs, assessment costs, signaling costs to attract a new partner, and possible reputation costs (e.g. accusations of being a “fair-weather friend”). Furthermore, it takes time to build trust within a relationship and commitment does not occur immediately (Roberts & Renwick, 2003; Roberts & Sherratt, 1998), so switching partners involves lost opportunities with a current committed partner. Switching partners is only worth it when the benefits of switching outweigh these costs, and this depends on the relative quality of available partners and the expected future length of the relationship. When switching is too costly, it pays to commit to current partners in order to avoid those ongoing costs, just as it can pay to commit to mates (Frank, 1988). It would then also pay to use alternate forms of partner control such as conditional cooperation or punishment to entice cooperation.

One does not especially need to entice a partner to stay if they have no incentive to leave. Barring any differences in market value, one's partners will often experience similar trade-offs and constraints about switching partners. This means that if both partners are of similar market value, there is little incentive for either to leave because the gains do not outweigh the costs (including opportunity costs from lost commitment). If partnerships never dissolve once formed, there is little need to continually signal one's value as a partner; the main reason to continue providing benefits is to incite reciprocation. However, if there is a risk of partnerships dissolving or weakening, then one must constantly signal one's value so that one's partners do not leave for higher-value rivals. One may also opt to also signal to attract others as “backup” partners. One must also signal commitment to reassure partners, as well demand signals of commitment if there is a risk of one's own partner leaving. Thus, whether individuals persist in their partner-attraction strategies will depend on the ease of their partners (or themselves) straying.

4. Conclusions

These three main tasks—choosing partners, attracting partners, and keeping partners—all have their parallels in the mating literature. These tasks are not required in traditional models of cooperation which rely only on partner control (e.g. reciprocity, punishment) rather than partner choice. As soon as organisms can choose with whom to interact, a biological market exists, such that organisms can benefit from choosing partners, attracting more (or better) partners, and keeping good partners. Considering the importance of cooperation for many organisms, we should expect that organisms will choose partners based in part on their cooperativeness, and this will in turn select for cooperative sentiment.

By viewing cooperation as part of a biological market, one realizes that generosity is a relative concept: the definitions of cooperation and a good reputation are not fixed, but instead depend on cooperation and generosity relative to others. As such, the fitness benefits for generosity will also depend on the relative generosity of others. When reputational benefits for generosity are a limited resource, such as when individuals preferentially allocate time across partnerships based on others' generosity, we should expect to see individuals competing to be more generous than others in their actions and possibly their sentiment. This arms race over good reputations should lead to alternative tactics such as criticism or derogation of others' generosity. Competition for social partners also leads to predictions about imbalances of reciprocity within relation-

ships, the causes of individual differences in giving, and people's altruistic sentiment varying with their own market value (as well as their needs). While non-market-based perspectives might predict some of these effects, all of them are predicted by the idea that people use cooperation to increase their market value in a biological market for social partners.

Viewing human cooperation within the context of biological markets allows researchers to draw parallels with the vast literature on mating markets. The cooperation literature is ripe for incorporating many of the principles discovered within modern sexual selection theory. These principles include, but are not limited to, the various strategies for choosing partners, attracting partners, and keeping partners. At the same time, a biological markets perspective allows researchers to link the concept of reciprocity with other bases for partner choice, including mutualisms, interdependence, and byproduct benefits. Thus, a biological markets perspective is a useful addition to existing models of cooperation and is a potentially fruitful approach for generating new hypotheses about cooperation. Because of this, we should look forward to increased incorporation of a biological markets paradigm into models of cooperation.

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