



On potential links between inequity aversion and the structure of interactions for the evolution of cooperation

Sarah F. Brosnan^{a,b,c,d,*} and Redouan Bshary^c

^a Department of Psychology, Georgia State University, Urban Life Building, 11th Floor, 140 Decatur Street, Atlanta, GA 30303, USA

^b Department of Philosophy, Georgia State University, Atlanta, GA 30303, USA

^c Neuroscience Institute, Georgia State University, Atlanta, GA 30303, USA

^d Language Research Center, Georgia State University, Atlanta, GA 30303, USA

^e Institute of Biology, University of Neuchâtel, Rue Emile-Argand 11, CH-2000 Neuchâtel, Switzerland

* Corresponding author's e-mail address: sarah.brosnan@gmail.com

Accepted 3 March 2015; published online ???

Abstract

Despite the fact that most models of cooperation assume equal outcomes between individuals, in real life it is likely rare that this is the case. Does it make a difference for our understanding of the evolution of cooperation? Following a taxonomy of cooperation concepts that focuses on costs and benefits, we explore this question by considering the degree to which inequity aversion may provide one mechanism to stabilize cooperation. We suggest a key role for inequity aversion in some contexts in both biological markets and direct reciprocity, and highlight the potentially unique role of positive inequity aversion for human reputation games. Nevertheless, a key challenge is to determine how different animal species perceive the payoff structure of their interactions, how they see their interaction with their partners, and the degree to which simpler mechanisms, like contrast effects or the associative learning seen in optimal foraging, may produce similar outcomes.

Keywords

cooperation, inequity, inequity aversion, game theory.

1. Introduction

Here is a quiz: two jackals are hunting together. When the prey is caught, both get some food, but one gets more than the other. What should the less well-fed jackal do?

That turns out to be a very complicated question. On the one hand, the less well-fed jackal may be better off than it would have been had it attempted to hunt alone. After all, some food is better than no food, and what this jackal needs is enough food to successfully reproduce. If it gets that, it should focus on its absolute gains and continue to cooperate irrespective of what its social partner got. On the other hand, the less well-fed jackal might have produced virtually as many offspring without this meal, and now it has helped someone else get more resources than it has. Therefore, even though its net payoffs are positive (it got more in calories from its share of the prey than it burned on the hunt), it is now at a relative disadvantage to its social partner. Moreover, it might have done even better had it hunted with another partner who more evenly divided the prey. Therefore the answer to the quiz is murky; considering absolute gains, it did the right thing. Considering relative gains, it is possible that the jackal made the wrong decision.

Of course, while this is a thought experiment, scenarios like this occur regularly, in jackal (Lamprecht, 1978) and in other species that cooperate, and while there is a vast and growing body of literature regarding cooperation in humans and other animals, very little of it has thus far been dedicated to understanding how inequality influences cooperative decision-making. Typically in models, there is the assumption that both parties gain equally, yet the gains of cooperation are rarely exactly identical, especially within a single interaction. Across interactions, the value of the resources gained may vary, or, even if they are identical, the actual value to the individual may vary. A few bites of gazelle are much more valuable to a jackal on the edge of starvation than to its well-fed compatriots, and a high ranking jackal may expect more than a lower-ranking conspecific.

This is not merely an academic question. We know that animals judge the value of their resources relative to those of their partners. Ten years' worth of experimental work shows that several species of primates, including humans, as well as corvids and domestic dogs, all respond negatively to getting less than a social partner, as compared to a situation where both get the same or, critically, a situation where a preferred food is shown, but the less preferred

food is given to both partners, an outcome often referred to as inequity aversion (reviewed in Brosnan, 2013; see also Bräuer & Hanus, 2012). Different authors have used inequity aversion differently. Here we define it as a behavioral outcome in which an individual responds negatively to receiving less than a partner. We make no assumptions about underlying mechanisms for the behavior (i.e., we do not imply that subjects understand it as such; it could instead be an evolved behavior pattern with no comprehension on the part of the individual). Unless otherwise stated, throughout the paper when we refer to inequity responses we mean a response to negative inequity, i.e., receiving less than a social partner. Even in those species in which such outcomes are seen, there is substantial individual variation in response to inequitable outcomes (reviewed in Price & Brosnan, 2012). For instance, chimpanzees respond to inequity in some studies, but in no study does every individual respond (and in some, no responses have been documented; Bräuer et al., 2007, 2009; Hopper et al., 2013), and the source of this individual variation is not clear. It has been linked to dominance (Brosnan et al., 2010), social group (Brosnan et al., 2005), personality (Brosnan et al., 2015), sex (Brosnan et al., 2010; Hopper et al., 2014) and procedure (Bräuer et al., 2007, 2009; Brosnan et al., 2010). Similar individual variation has been seen in other species that have been tested extensively, although again, it is not always clear what the underlying source is (Roma et al., 2006; van Wolkenten et al., 2007; Range et al., 2009, 2012; Silberberg et al., 2009; Horowitz, 2012; Massen et al., 2012). Moreover, only some species show the response; thus far the species pattern indicates that responsiveness is present in species that routinely cooperate with non-kin (for more detail, see Brosnan, 2013).

Tying this to cooperation, there is growing evidence that such relative valuations are important in decision-making surrounding cooperation (Brosnan & de Waal, 2014), and these assessments may influence not only who subjects chose to interact with, but also how they behave with their current partners. Regarding the former, subjects may preferentially interact with partners who provide more equitable outcomes, e.g., they use partner choice/partner switching as a partner control mechanism. In experimental studies, chimpanzees prefer to cooperate with partners who are more tolerant (operationally defined as partners who more evenly share rewards in other contexts; Melis et al., 2006a), and preferentially recruit them (Melis et al., 2006b), which may indicate that they are sensitive to their outcomes relative to a partner. Capuchins will cease cooperating with a partner who

does not ‘play fair’, despite getting at least some reward on every trial (e.g., they are more sensitive to relative outcomes than absolute ones; Brosnan et al., 2006). In at least some cases, animals seem to anticipate this hesitation to participate on the part of less-well-endowed social partners, changing their behavior when necessary to secure their partner’s continued participation (Melis et al., 2009; Proctor et al., 2013). As an example of immediate responses to a partner’s behaviour, cleaner fish punish social partners who do not follow the rules (Raihani et al., 2010, 2011).

One challenge that is common to many, if not most, instances of cooperation is that they very frequently entail differences in payoffs in the short term. Even in by-product mutualism, in which individuals share an immediate benefit without paying a cost, meaning that both animals are better off participating even in one-shot interactions with strangers, it is very likely that the magnitude of the outcomes will differ. There are theoretical reasons to assume that this is important for the evolution of cooperation; as outlined above, continuing to help a partner achieve more than one achieves oneself may not be a beneficial strategy. But for natural selection to be able to act on differences in outcome, animals must be able to identify them. We here emphasize that we do not mean that animals must *understand* that they are getting less than a partner, much less that they must understand why this is a problem. Natural selection can act on different outcomes if individuals are able to recognize such discrepancies and change their behavior. For instance, emotions (getting frustrated) may be sufficient motivation to change the current situation, and if the behavioral outcome of this frustration or anger results in a better outcome over the long term, then this will be selected. Recent experiments show that animals will, in some cases, refuse to work with a partner who does not distribute the rewards of cooperation fairly, even if it means the loss of an absolute gain (Brosnan et al., 2006; see below for a more detailed discussion of this study).

Of course, just because animals can notice and respond to inequity does not mean that they always do, nor does it mean that it is even to their benefit to do so. In some cases, it may be that absolute outcomes (i.e. what I got) trump relative ones (i.e., what I got in comparison to you). In order to fully understand the impact of unequal outcomes on cooperation, it is necessary to consider this question with respect to different types of cooperation. There are numerous taxonomies of cooperation, but when the question revolves around the impact of relative payoffs, it is important to consider cooperation

from an evolutionary perspective focused on costs and benefits. Therefore, we here follow the taxonomy put forth by Bshary & Bergmuller (2008), which takes a functional, evolutionary approach focused on the costs and benefits to each partner. We shall argue that it may often depend on the structure of the interaction whether inequity aversion offers a meaningful mechanism to maximize one's own payoffs. Furthermore, we will discuss issues about potential cognitive constraints.

In a first step, we will define key psychological concepts that may play a role in the assessment of payoffs and corresponding responses, like inequity aversion and contrast effects. We then start with types of cooperative interactions for which we expect no influence of inequity on subjects' behaviour, because subjects' outcomes are not influenced by their partner. We argue that for any type of interaction in which cheating is an option, inequity aversion may help to stabilise cooperation in the sense that it could be the psychological mechanism that leads to termination of an interaction and/or to partner switching and/or to return defection and/or to punishment (note that cheating is not the only way that inequalities can emerge, however our argument is that inequalities should be salient when they tell the actor something about the partner's behavior, and cheating is the most relevant source of such informative inequalities). We discuss each of these direct responses separately, and then discuss the degree to which various indirect forms of cooperation based on the assessment of reputation may be motivated by inequity aversion. Another important issue to consider is the degree to which partner selection within a biological market selects for the ability to compare offers/outcomes and how that relates to inequity aversion. Hopefully, our paper will stimulate additional perspectives on how to study an animal's ability to cooperate in a way that maximizes own payoffs within the appropriate framework (absolute or relative) for the given situation.

2. Defining key psychological concepts

Unfortunately definitions vary across disciplines, often leading to confusion, so here we provide our operational definitions of the important concepts in our paper. We consider inequality to be a situation in which actual outcomes differ, whereas inequity is a situation in which outcomes do not match the relative contributions of each individual (Brosnan, 2013). For example, an equal outcome is when two individuals who hunted together received the

same quantity of food, irrespective of their contribution, but it is only equitable if they both contributed equally. If one lagged behind and did not participate fully in the hunt, then an equal outcome would be inequitable (the laggard deserves less relative to its contribution; see below for a discussion of comparing relative inputs or efforts). Additionally, even equal outcomes may be perceived as of different value because different individuals will have different preferences and needs (again, a bite of antelope is more valuable to a starving jackal than the same sized bite is to a sated one). While we can measure outcomes, it is very difficult to determine whether inputs were the same, or whether even identical gains had the same actual value to the individuals involved, so for this paper we assume that outcomes are rarely, if ever, identical and refer to inequity. On a related point, when we talk about relative gains, we mean the comparison between actual gains, and do not take into account relative value differences (e.g., based on hunger or rank), which typically cannot be assessed.

Another important distinction is that individuals' contributions consist of two components. Here we follow a useful framework put forth by behavioural ecologists investigating parent–offspring interactions and consider contributions to be made up of two components: measureable inputs into the cooperative relationship and the effort invested. Measurable inputs are aspects that are visible to all, such as food or services provided or time spent in an activity. Effort is essentially the amount of energy an individual put into the interaction (e.g., was a hunter running as fast as it could have). Effort is the more difficult to assess, either for the experimenter or the individual engaged in the interaction (Packer, 1988). After all, how do I assess whether the other hunter tried as hard as I did, or as hard as he could? Cheating by slacking should be under strong pressure to evolve because it is so difficult to detect or, even if detected, to discriminate from other, unintentional situations (I am injured and so cannot run, or I got tangled in branches and so was slower). In fact, while there is quite a lot of evidence for inequity aversion in the context of rewards in other species, there is little evidence that they discriminate different levels of effort (but see Takimoto & Fujita, 2011 for an exception in a case in which effort was easy to observe), which may be in part due to this challenge. Measuring inputs, however, is fairly straightforward. Moreover, even though one still cannot easily judge the difference between an individual who cannot participate (e.g., due to injury) or will not

participate (e.g., due to slacking), it likely does not matter from the perspective of equity. If individuals are sensitive to inputs and invest accordingly (regardless of cause) then it is still unlikely that cheating through slacking will evolve. Therefore we find it unlikely that in most cases there has been much pressure to detect differences in effort/inputs and so here focus on how individuals assess outcomes.

Subjects must also make comparisons to judge their outcomes, and whether an outcome is related to equality depends on whether or not these outcomes are compared to another individual's outcomes. Psychology discriminates inequity (or inequality) aversion, in which subjects compare their current outcomes to the current outcomes of others (Brosnan, 2013) from contrast effects, in which subjects compare their current outcomes to their own previous expectations (Tinklepaugh, 1928; Reynolds, 1961; Brosnan, 2013). In both cases expectations are formed, but the key difference is whether those expectations are social (based on another's outcomes; inequity) or not (based on one's own previous outcomes; contrast). Additionally, there is an implicit assumption in the case of social expectations, or inequity, that the expectation is formed because this is a situation in which animals *should* get relatively similar outcomes, for instance because they are cooperating (Brosnan & de Waal, 2014). This distinction is critical as the social aspect distinguishes inequity aversion mechanistically from the way animals make decisions in non-social situations of comparison, such as optimal foraging theory; animals are able to compare food availability in different patches and hence adjust the duration of stay accordingly (Cuthill & Houston, 1997) without any evidence that they attribute to patches the status of social interaction partners. Similarly, animals learn discrimination tasks based on positive or negative reinforcement in the absence of any social component. Given that the ability to discriminate between payoffs should be present in all freely moving animal species, we thus have to ask under which circumstances the addition of inequity aversion specifically allows individuals to significantly improve their decision making.

A related question involves the psychological mechanisms required in order to be able to judge inequity (Brosnan, 2006a). At bare minimum, subjects must be able to recognize that their own outcomes differ from those of others, but this ability is presumably present in any species that can learn socially (which appears to be the large majority of animal species). Additionally, contrast effects are widespread in the animal kingdom (e.g., Freidin et al.,

2009), so again, most animal species likely share the ability to recognize when expectations are violated. In fact, this requires little more than operant conditioning. Thus, the underlying cognitive abilities that allow an individual to recognize inequity should be fairly widespread across species, meaning that the limiting factor is whether this ability evolved, not whether species have the cognitive ability to do so.

Finally, it is essential to distinguish between inequity and fairness. Many times the two are conflated, but what we have discussed thus far is not fairness; fairness implies a balancing of contributions such that they are, on average, appropriate to some standard (Baumard et al., 2013; Brosnan & de Waal, 2014). Thus, for fairness there is the assumption of concern about both inequity that harms the self and inequity that benefits the self, but violates principles of fairness (e.g., overbenefitting). We have discussed only those outcomes in which the subject is rewarded relatively less well than others, and while the two are clearly related, there is little evidence for fairness in the animal kingdom, possibly excepting some highly encephalized species (Brosnan & de Waal, 2014). In this paper, unless we state otherwise, when we refer to inequity, we explicitly mean inequity that does not benefit the self.

3. Does inequity ever influence cooperation?

It has previously been proposed that recognizing inequity could serve as a mechanism by which individuals can determine whether they are in a beneficial cooperative relationship; if outcomes are equal, they should continue the interaction, but if outcomes become unequal it may be better to consider other options (Brosnan, 2013). However, there are many forms of cooperation, and this does not apply to all of them, for instance because the partners' gains are independent of one another or because there are no alternate options. Below we consider in what situations inequity should and should not influence cooperation, but prior to this it is necessary to demonstrate that in at least some cases we have evidence that inequity does influence decisions about whether to cooperate.

One such study was done in capuchin monkeys, a species that cooperates in the wild in a variety of situations (e.g., hunting, coalitions, grooming, food sharing; Perry & Rose, 1994; Gros-Luis et al., 2003; Perry et al., 2003; Crofoot et al., 2011) and seems to very easily extend this to experimental situations. One common method for testing cooperation is a barpull device in

which individuals must work together to pull in a heavily counterweighted tray in order to obtain a food reward (de Waal & Berger, 2000; de Waal & Davis, 2003; for a review of this work, see Brosnan, 2010). In one experimental version, both monkeys always received a reward, but the value of those rewards differed (Brosnan et al., 2006). In two of the conditions, both individuals either got a highly preferred grape or a less preferred, but still appreciated, apple slice. In the third condition, one got the grape and the other got the apple slice. Who got which reward was determined by the monkeys themselves; subjects were tested in their home enclosure, rather than a testing chamber, and were not constrained in their choice, thus they determined who pulled for which outcome. Moreover, years of experience with the barpull apparatus demonstrated that the monkeys would not steal the reward in front of their partner's pull; subjects always got whatever they chose to pull for.

Despite the fact that both monkeys would *always* benefit in any situation, they did not cooperate all the time. However, contrary to what would be expected if they were simply focused on relative outcomes on a trial by trial basis, the monkeys cooperated at the same level across all conditions, whether they got the same outcome as their partner or not. What did vary was their response to each individual partner; subjects cooperated in all three conditions with a partner with whom they alternated who got the more preferred reward in the unequal, apple and grape, condition. However, when one member of the pair dominated the more preferred grape in this condition, their partner refused to cooperate in all conditions, not just the one in which they would be at a relative disadvantage.

This is a critical point — the monkeys did not seem to be responding to getting less than a partner on some occasions, rather they were responding when their partner did not behave in a manner that was equitable over the long term. If the monkeys had been calculating on a trial by trial basis, they should have refused to cooperate after any trial in which they got less (which would have been half of the trials if the subjects had alternated perfectly). Nor did they seem to be focused on only those situations in which they had the chance of inequity, as they quit cooperating in *all* conditions, not just those in which inequity was possible (and inequity was only possible in one of the three conditions). Instead they seemed to be reacting against the partner who routinely took the better reward when there was the option to do

so. Thus cooperation seems to be based on more than just getting an absolute benefit.

A second critical point: the monkeys who were successful sustained cooperation *despite* each of them receiving the less preferred reward approximately half of the time. Therefore these animals seemed to be extrapolating over the longer term, taking into account at least a couple of trials, and continuing to cooperate if this accounting was acceptable. This is critical because, as we point out above, cooperation is extremely unlikely to result in exactly equal payoffs to all involved on every single trial in which it occurs. Results such as these make it clear that not only do relative payoffs matter more than absolute ones, but the very success of cooperation in this test and in natural situations throughout the animal kingdom make it clear that we have evolved strategies for coping with such differences. In another study, capuchins ceased cooperating when rewards were clumped, such that one member of the pair could claim all rewards (de Waal & Davis, 2003; note that in Brosnan et al., 2010, discussed above, rewards were separated, not clumped). Moreover, they cooperated much less often from the very first trial, indicating that they were making this decision based on a history of similar experiences rather than on the experience gained within this specific context. This pattern was the same whether their partner was related (mother/offspring pairs) or unrelated.

Considering apes, chimpanzees may also make choices based on relative rather than absolute outcomes. Melis and colleagues (2009) gave pairs of chimpanzees a choice between two trays that could be cooperatively pulled forward to obtain the rewards. On one tray, the rewards were split evenly (5/5), whereas on the other they were uneven (10/1). If they did not work together, neither partner received anything. If absolute gains are sufficient, then they should have pulled the unequal 10/1 tray; dominant chimpanzees would obviously have preferred to get 10 rather than 5, and the subordinate would presumably prefer 1 over nothing, so should pull to get some benefit. In practice, however, subjects most often pulled either the even 5/5 tray or neither of them, indicating that the subordinate would rather receiving nothing than get substantially less than the dominant. Chimpanzees also appear to make decisions about whether or not to cooperate based on previous experiences, outside of the immediate context. Chimpanzees, as mentioned earlier, preferred to cooperate with or, given the opportunity to do so, recruit, the chimpanzee who was more tolerant in an earlier sharing situation, which could indicate

that they are sensitive to relative outcomes (Melis et al., 2006a, b), although more recent research indicates that given the choice, they prefer to work by themselves rather than with any partner (Bullinger et al., 2011).

4. Conditions under which inequity does not play a role

In many types of cooperation, one individual's actions benefit another, but incidentally. The actor is doing something that it would be doing anyway, for its own benefit, and happens to provide benefits to another individual. In these cases, the results are not the result of joint actions or investments and therefore inequality of outcome should be of little concern, even if the outcomes are very different, because the outcomes do not tell either interactor anything about their partner's worth as a cooperative partner. Below we consider each specific type of cooperation for which this is relevant in more detail.

4.1. By-product mutualism

In by-product mutualism, neither partner makes any investment in the other, and the benefits to others are due to entirely self-serving actions by the actor (Brown, 1983). In this case, of course, there is no reason for either partner to be sensitive to inequity; the actor's behaviour provides benefit to the actor regardless of the benefit to the partner, and because the partner is benefitting incidentally they should not change their behaviour if they get less than the actor. In fact, if they do seek out a situation in which they get a better outcome, this is far more similar to the asocial situation of a bird searching for a better food patch than the social situation of a jackal searching for a hunting partner who will share equitably.

4.2. Direct positive pseudo-reciprocity

In direct positive pseudo-reciprocity, the donor provides a benefit that is returned by an action that is self-serving on the part of the partner, but nonetheless provides benefits to the donor. For example, in ant mutualisms, partner species provide food (e.g., nectar) to ants in exchange for defence (for example Pierce et al., 2002; Heil & McKey, 2003). Here the ants provide the defence for their own benefit (protecting their food source) that also serves to provide a return benefit to the partner species. This is why it is defined as pseudo-reciprocity; despite the provision of different benefits that necessarily entails a reciprocal trade, there is no incentive for the partner

species to fail to reciprocate, because it is in the partner's best interests to provide a return benefit. Therefore the initial investment is not subjected to the risk of being cheated and the partner need not worry about assessing relative payoffs. The self-serving nature of the act that leads to return benefits means that there is no need for sensitivity to inequity on the part of the donor.

5. Interactions with the potential for sensitivity to inequity

We propose that any social interaction in which individuals have to pay attention to their partner's behaviour in order to avoid being cheated has the potential to involve inequity aversion. At the same time, stable cooperation based on partner control mechanisms can be achieved without needing to pay attention to inequity. For an extreme example, a plant that increases root growth in areas with nitrogen fixating bacteria shows a self-serving strategy that performs well without the need to assess whether less performing root areas lack bacteria or lack nitrogen or harbour cheating bacteria that do not fix nitrogen (Kiers et al., 2003). Thus, whether or not individuals understand the concept of inequity, we maintain that for inequity sensitivity to apply to cooperative decision-making it is necessary that individuals (a) perceive an interaction as social and (b) are able to compare own payoffs with that of the partner or with that of alternative partners. The nitrogen fixing example above does not meet this criterion because the plant does not care if the interaction is social and can achieve the same outcome without this information.

5.1. Negative pseudo-reciprocity

In negative pseudo-reciprocity, individuals cooperate in order to avoid a situation in which the partner performs the self-serving action of terminating the interaction or the relationship prematurely (Bshary & Bergmüller, 2008). Premature termination can in principle work without the leaving individual accounting for any future interactions in its lifetime (Johnstone & Bshary, 2002; McNamara et al., 2004). Selective abortion as a form of sanction has been used as an example of this (Pellmyr & Huth, 1994); in some pollination mutualisms, the pollinator female also lays eggs into the developing fruit, where too many hatching larvae would eat all the seeds. Plants, however, can assess larval densities in single fruits and abort those fruits that contain too many (Pellmyr & Huth, 1994), which from the plants' perspective is best characterised as a biological market; the plant receives many simultaneous offers and continues the collaboration with the best offers (Noë et al., 2001).

More generally, leaving a cheater seems to be typically associated with a biological market, in which switching implies that a new partner will on average behave more cooperatively than the current, cheating, partner, with whom the individual has an inequitable relationship. In a biological market, partners exchange goods/commodities where the exchange rate depends on the market law of supply and demand (Noë & Hammerstein, 1995). In this framework, the existence of alternative partners offers the possibility to leave a current partner that does not pay the proper price (Johnstone & Bshary, 2008), which involves some form of recognizing inequity (for instance, between what one is getting from the current partner and what one could get from a new one). However, how such decisions are made in different species is not well understood and may also involve absolute thresholds rather than relative comparisons. Nonetheless, as pointed out in the section on psychological terms, the vast majority of animal clades are certainly able to evaluate the payoff consequences of an act and adjust behaviour accordingly, through operant conditioning. Operant conditioning experiments also show that animals can compare the relative payoffs of different acts. Thus most species likely have the cognitive capacity for such comparisons.

However, such comparisons may be challenging in market situations. For instance, the comparison of payoffs obtained for the same act but with either the same partner (repeated interactions) or with different ones should be slightly more difficult. This is for three reasons. First, a simple evaluation 'good' or 'bad' does not suffice to make appropriate decisions because under such circumstances the partner would be under selection to provide the bare minimum that leads to a positive assessment. Thus, small differences in payoffs must be assessed in order to make proper responses. Second, if one finds a profitable partner one should try to have repeated interactions. This requires some sort of individual recognition. In some cases, the absence of mobility may allow such recognition in the absence of sophisticated cognitive machinery. Potential examples are the mutualisms between plants and mycorrhizae, the many mutualisms involving ants protecting sessile partner species against predators, and marine cleaning mutualisms in which client reef fish may seek or avoid territorial cleaner species by seeking or avoiding the location of their cleaning station (Brosnan et al., 2010). If all potential partners are mobile, however, individual recognition due to individual characteristics is necessary in order to seek partners that offer higher payoffs and to avoid partners that offer lower payoffs. Third, it has been argued

that repeated situations offer a particular difficulty because there is a time delay, which requires subjects to remember interactions over an extended period, which may be beyond the cognitive ability of many species (Stevens & Hauser, 2004). Therefore it may be anticipated that subjects would be more likely to recognize inequity when both individuals obtain their benefit simultaneously (as in the case of the jackals) rather than when they must compare a current outcome to a previous, or future, one. This may be particularly challenging when subjects must remember different currencies.

Even if animals do have the requisite cognitive mechanisms, the ability to compare payoffs obtained during interactions with different partners in order to make fitness increasing choices is not necessarily based on inequity aversion as a mechanism. The ability to remember many interactions and to calculate an average payoff is a standard ability necessary for optimal foraging decisions, where individuals have to decide what food to prefer and how long to remain in a patch before moving on to a new one. In some cases, then, for instance when the market situation with the law of supply and demand will determine exchange rate, own payoff optimisation during interactions with partners seems to be sufficient to make the appropriate decisions, without any comparison to one's partners' outcomes. Again, this boils down to the challenge of determining equity in a complex system. In particular in the many cases in which traders exchange different services/commodities, it seems to be virtually impossible to use inequity aversion as a mechanism to stabilise cooperation because the relevant comparisons are either too computationally complex or the required information is simply unavailable. Food against protection or transport, as in ant mutualisms and pollinator mutualisms, and food for sex or grooming for tolerance in primate species are examples of cooperation with the exchange of different currencies. In such cases, it is likely impossible to compare relative inputs between partners as the basis to establish equitable shares of the cooperative act; at least from the perspective of human experimenters we know of no example in which the fitness consequences of two types of input have been quantified. The exception applies to situations in which the market is a strong reflection of relative investment. The one obvious example is the mating market, where females are typically rare because of their higher investments in reproduction. Nevertheless, a partner who offers an exchange rate that is below the market average violates a focal individual's expectation. Given that plants and insects can respond appropriately to low payoffs we doubt that a psychological construct like inequity aversion is necessary to refuse the interaction.

This raises the important question what inequity aversion could add to make trading in a market efficient beyond a pseudo-rational payoff comparison. We propose that conditions that are likely to promote the evolution of inequity aversion in a biological market are such that (a) individuals trade the same commodity and hence can monitor relative contributions, (b) trading occurs within a relatively set subset of individuals, such that there is a reasonable expectation that animals can keep track of their trades across multiple partnerships, and/or (c) trading occurs in a communication network (McGregor, 1993) that allows bystanders to assess the exchange rate for competitors that offer the same service/commodity. This means that sensitivity to inequity may be most likely in species with very stable social groups that are small enough — or form small enough sub-groups — that individuals are able to keep track of their payoffs across these different partnerships and assess them relative to others' payoffs.

5.2. *Direct reciprocity*

Positive direct reciprocity occurs when individuals engage in repeated interactions where they simultaneously or alternately provide benefits to one another (or one-shot interactions, if they are structured in a 'parcelling' format, i.e., involving repeated decisions Raihani & Bshary, 2015, as with egg switching in hermaphroditic fish or grooming in impala; Connor, 1995; Fischer, 1988). This is the basis of tit-for-tat style reciprocity; individuals cooperate when their partners cooperate, but begin to cheat when their partner cheats (Dugatkin, 1997). In this case, it is extremely important to monitor relative outcomes so as to avoid getting taken advantage of. After all, outcomes are entirely dependent upon the partner's actions, and it would be both absolutely and relatively costly to continue to provide benefits to a partner, at a cost to oneself, while receiving nothing in return. While contingent helping is notoriously difficult to demonstrate (Raihani & Bshary, 2015), there are by now a few experimental examples under natural conditions (Krams et al., 2008; Cheney et al., 2010; Borgeaud & Bshary, 2015). Such monitoring may be more challenging than it appears. First, as discussed above, individuals need to be sensitive to cheating by investing less effort as well as cheating by failing to try at all (Packer, 1988). This is critical because cheating by omission may be easier for individuals to identify than cheating by investing less, particularly if the partner invests only slightly less on any given interaction, and this is further complicated by the fact that effort is extremely difficult to

assess. That being said, this may turn out to be less of an issue because, as we argued above, it may be best for individuals to ignore effort and focus entirely on their partners' inputs.

What may be more important, then, is that while in the context of models it makes perfect sense for individuals to sanction their current partner or find a new one after an instance of cheating, in real life there may be mistakes or other contingencies that lead to an unequal outcome despite no intention to cheat on the part of the partner. These situations should be treated very differently, because individuals may lose longer-term benefits by responding too quickly to all inequalities as if they were cheating, thereby losing out on what has been a very good partner. For instance, a partner may intend to cooperate, but either make a mistake or be unable to. This can be mitigated by strategies such as tit-for-two-tats, a 'forgiving' or 'generous' strategy whereby over time individuals do better by occasionally forgiving or ignoring an instance of cheating despite the inequality inherent in the interaction (although this 'forgiveness' may also be taken advantage of in other contexts; Axelrod, 1984). Additionally, in many situations it may not be possible to trade exactly the same amount as the partner previously gave on a trial-by-trial situation, yet over time, the investments even out. Thus the relationship between inequality and direct positive reciprocity is complicated; subjects do better by recognizing situations of inequality, but do best by extrapolating over a series of interactions rather than only a single instance.

As we discussed in the third section, some animals are clearly capable of this calculus. Capuchin monkeys accept inequity on specific trials if outcomes are equal over the long-term (note that while the action of the monkeys in this task was a mutualism — both pull for a joint reward — the payoffs required reciprocity as individuals alternated receiving the superior outcome; Brosnan et al., 2006b). This does not necessarily require calculation, either, which would likely be so cognitively advanced as to preclude most species (Stevens & Hauser, 2004). Instead, such reciprocity may be based on so-called attitudinal reciprocity, in which individuals base their decisions on their attitude towards their partner, which is in turn based upon the partner's earlier behaviour and so is therefore both partner specific and contingent (Brosnan & de Waal, 2002; see also Schino & Aureli, 2009, 2010).

To come back to our opening example of the jackal hunting, we emphasise that one needs a lot of detailed information in order to be able to classify the interaction according to our categories. The joint hunting itself can be

classified as a by-product mutualism, as during the study period, two individuals working together had a six times higher probability of catching a gazelle fawn as compared to single hunters (Lamprecht, 1978). The increased success is due to alternating attacks on the fawn: whoever gets close is attacked and chased away by the mother, opening the opportunity for the partner to get to the fawn, eventually leading to a killing bite. The key question is what happens after the fawn is killed. In the jackal case, the carcass could in principle be monopolized by the stronger individual, but that does not seem likely for three reasons. First, there is enough meat for both. Second, most other predator species are dominant over jackals, which therefore have to eat as fast as possible in order to reduce the risk of losing their prey. Third, hunting partners are typically established pairs with shared stakes in reproduction and hence interdependent fitness (Roberts, 2005). Indeed, there are no reports that prey consumption depends on who killed the fawn or of aggression between partners (Lamprecht, 1978). Therefore in this case inequity, if it matters at all, likely matters most during the initial stages of pair formation, when individuals may be assessing each other's value, and likely matters less once the interdependency is established because of the high costs of finding a new partner (Brosnan, 2013).

In other cases of cooperative hunting, like in fish and in dolphins, the problem of sharing does not exist as whoever captures a prey swallows it whole (Gadza et al., 2005; Bshary et al., 2006; Strübin et al., 2011). The situation becomes more complex when individuals play different roles that predictably lead to different probabilities to capture the prey but are necessary to increase overall hunting success. In such cases, fair sharing becomes necessary, independently of resource holding power, in order to maintain cooperation. In fact, in groups of chimpanzees that necessarily hunt collaboratively in groups due to ecological conditions, food sharing following the hunt is based most heavily on participation in the hunt (Boesch, 1994, 2002), a pattern not seen at other sites that rely less strongly, or not at all, on group hunting (Gilby, 2006).

Finally, negative direct reciprocity occurs when individuals punish those who fail to cooperate or fail to provide benefits at their own expense. Critically, punishment differs from partner choice sanctions in that it requires repeated interactions; if a cheated individual switches partners (partner choice), this is not negative direct reciprocity because the action of partner

switching does not change their partner's behaviour (at least for the individual in question, who has already found a new partner). As with positive direct reciprocity, negative direct reciprocity may involve individuals recognizing inequities between themselves and the individual that they punish.

Punishment is interesting to consider because of its rarity in the animal kingdom (Jensen, 2010; Raihani et al., 2012a). In fact, while there are anecdotal examples of punishment, there are very few documented examples. One such example is punishment in cleaner fish. Cleaner fish clean clients in pairs, and when one member of the partnership cheats (e.g., eats the client's mucus rather than parasites), the partner will punish the cheater, which changes its behaviour (Bshary et al., 2008). This behaviour benefits both the punisher and the client fish, who is the victim (Raihani et al., 2010). Males, who are the typical punishers, also adjust their punishment based on what they risk losing (Raihani et al., 2011), and females pre-emptively cooperate more with males who are more likely to punish them (Raihani et al., 2012b). This may imply that punishment is best sought in situations in which partner switching is difficult or costly (Raihani & McAuliffe, 2012; Raihani et al., 2012c; Brosnan, 2013).

5.3. Indirect forms of cooperation based on reputational effects

We call cooperation 'indirect' if the benefits of helping accrue due to the action of third parties rather than from the recipient of the helping act. For the purpose of the current paper we will focus on 'reputation-based' concepts. These concepts share the notion that the decision to help or to punish is based on prior observation of the focal individual's behaviour towards third parties. In forms of indirect pseudo-reciprocity, focal individuals help recipients either to be chosen self-servingly by bystanders for mutually beneficial interactions, or to avoid a situation in which bystanders perform a self-serving action that reduces the fitness of the focal individuals. An example for the former is reef fish clients choosing to interact with cleaners that they observed being cooperative towards another client (Bshary & Grutter, 2006). An example of the latter involves helpers helping offspring to avoid being expelled by the breeder parents (as suggested for cooperatively breeding cichlids; Bergmüller & Taborsky, 2005). Indirect forms of reciprocity comprise interactions in which each act by either focal individual or bystander involves an investment.

Currently, studies that have documented behavioural adjustments of observed individuals due to reputational effects on the bystanders (so-called

audience effects) have focussed on a competitive context (McGregor, 2005). Nevertheless, we consider it likely that reputation effects in the context of pseudo-reciprocity are widespread in the animal kingdom, while there is currently no evidence for forms of indirect reciprocity based on reputation in non-human species. We consider it possible that the presence of sophisticated inequity aversion in humans that is largely absent in other species may play a role in this difference. As we see it, indirect reciprocity is complex for at least three reasons. First, bystanders have to assess the actions and resulting payoffs of third parties through observation rather than personal experience. This ability is nevertheless likely to be widespread, at least in vertebrates, as it is also a requirement of indirect pseudo-reciprocity. Second, the key response by bystanders involves an investment: helping helpful individuals and punishing defectors (e.g., third party punishment; Fehr & Fischbacher, 2004). As these responses do not involve personal experience, they need to be based on some value system that is rather general (e.g., social norms or a moral system), for which there is little to no evidence outside of humans (although there is evidence that our system of morality evolved from building blocks found in other species, these other species lack sophisticated values systems similar to ours; Flack & de Waal, 2000; Brosnan, 2014). Third, while the punishment of defectors may be based on negative inequity aversion, i.e. jealousy about the gains by the defector, the helping of co-operators must be based on positive inequity aversion. The bystander must feel the need to compensate the helper for the losses due to helping. Again, there is very little evidence that other species even notice when they are benefitted with respect to others (Silk et al., 2005; Vonk et al., 2008; although see Brosnan et al., 2010; Proctor et al., 2013), and in the few cases in which it occurs, there is currently no evidence that the underlying mechanism is a prosocial feeling (Silk & House, 2011; Brosnan, 2013).

6. Conclusions

A sensitivity to inequity is hypothesized to be related to cooperation with non-kin, but it is not expected in all forms of cooperation. As we note above, there are numerous constraints that may influence whether or not inequity influences cooperation. In some cases, the cognitive requirements for detecting and responding to inequity, such as individual recognition, may be absent. In others, it may be that there is simply no need for it. These are

conditions under which individuals can do just as well by simply making decisions that maximize their own outcomes, without any attention paid to the partner's outcomes. Thus, a first step for any study on inequity is to identify what game the animals perceive themselves to be playing. This is particularly important for lab experiments in which the experimenter knows everything about the game while the animals may perceive it differently. For example, it has previously been hypothesized that the refusals common in inequity experiments are a behavioral manifestation of partner choice mechanisms that would be used in a natural interaction (Brosnan & de Waal, 2014). In many situations the cooperator may not be able to change the 'defecting' partner's behaviour, for instance because the defecting partner is dominant and therefore can control the rewards of cooperation (e.g., the carcass after a cooperative hunt). In these cases, the cooperator's only recourse is to try to find a new partner. In the typical lab study of inequity, the subject also cannot influence the partner's behaviour, and therefore the 'refusals' seen are not likely to be an attempt by a confused subject to influence the partner's outcome, but instead a behavioural manifestation of a subject who is walking away from the interaction that in this context appears as a refusal to participate. If this hypothesis was to be confirmed in future studies, it implies that inequity aversion is much more linked to partner switching than to other partner control mechanisms like punishment and counter-defection.

Another key point is to distinguish function from mechanism. Previous arguments that have linked inequity responses and cooperation have primarily done so at the functional level; inequity is a way in which individuals can determine whether or not they are in beneficial cooperative relationships (Fehr & Schmidt, 1999; Brosnan, 2006b, 2013). In this approach, at least some aspects of inequity responses are expected to be widespread among animals that cooperate routinely with non-kin (Brosnan & de Waal, 2014; there are other explanations for cooperation with kin). As we have repeatedly stated, this does not mean that individuals track inequity or understand the decision that they are making. It may become important in some situations to distinguish between situations in which individuals act as if they understand how their outcomes relate to those of their partners, and situations in which they actually do. This distinction may be the one that separates other animals from humans, who can conceptualize this.

One final point; although we have not discussed it in detail, it may be very difficult to always tell whether an animal is basing a response on inequity (the comparison of what they got to that of their partner), contrast

(the comparison of what they got to previous outcomes) or loss (similar to contrast, but in this case the comparison is to what was expected), or even frustration directed at a partner who cheated them (e.g., irrespective of the outcome). In experimental tests we can discriminate these to some degree with careful controls that explore how subjects respond to the same violation of expectation when the violation is due to a partner getting the more preferred outcome, the subject itself previously getting the more preferred outcome, or the experimenter giving less than was originally offered (e.g., Brosnan & de Waal, 2009; Hopper et al., 2014). However, in observational studies, or in situations in which this degree of control is not possible, we may not always be able to distinguish among these options. This may be even more problematic in species that are not highly encephalized, for whom the typical null assumption is that they lack the cognitive resources to make such comparisons. While this is a reasonable null hypothesis (for all species, not just those that are less encephalized), it is still important to test the alternative.

Of course, this raises another issue; does it matter? Does it matter if a cleaner fish punishes a partner because they were able to clean for a shorter period than expected versus because they saw their partner obtain the (more preferred) mucus? On one level, it does not; subjects are able to maximize their rewards. But on another level, identifying how they do so is critical to understanding the market in which the organism lives. Do cleaner fish conceptualize their interactions as a partnership? If so, we might make different predictions about a novel partnership than we would if we simply assume that they are blindly maximizing outcomes. There is no experimental evidence that cleaner fish respond to inequity (Raihani et al., 2012a, although inequity may motivate partner punishment; Raihani & McAuliffe, 2012), but understanding what cleaner fish — or any species — are doing requires determining how they conceptualize (or not) their interactions with their partners. We hope that our attempt to generate predictions about the role of inequity in cooperation will contribute to this endeavour.

Acknowledgements

The authors thank Peter Verbeek and Elisabetta Palagi for organizing the conference that led to the formulation of this paper. SFB was funded by National Science Foundation grants SES 1123897 and SES 1425216 during writing. RB was funded by the Swiss Science Foundation.

References

- Axelrod, R.M. (1984). *The evolution of cooperation*. — Basic Books, New York, NY.
- Baumard, N., André, J.-B. & Sperber, D. (2013). A mutualistic approach to morality: the evolution of fairness by partner choice. — *Behav. Brain. Sci.* 36: 59-78.
- Bergmüller, R. & Taborsky, M. (2005). Experimental manipulation of helping in a cooperative breeder: helpers “pay to stay” by pre-emptive appeasement. — *Anim. Behav.* 69: 19-28.
- Boesch, C. (1994). Cooperative hunting in wild chimpanzees. — *Anim. Behav.* 48: 653-667.
- Boesch, C. (2002). Cooperative hunting roles among Tai chimpanzees. — *Human Nature* 13: 27-46.
- Borgeaud, C. & Bshary, R. (2015). Wild vervet monkeys trade short-term tolerance and specific coalitionary support for grooming in experimentally induced conflicts. — *Curr. Biol.* 25: 3011-3016.
- Brauer, J., Call, J. & Tomasello, M. (2007). Chimpanzees really know what others can see in a competitive situation. — *Anim. Cogn.* 10: 439-448.
- Brauer, J., Call, J. & Tomasello, M. (2009). Are apes inequity averse? New data on the token-exchange paradigm. — *Am. J. Primatol.* 71: 175-181.
- Brauer, J. & Hanus, D. (2012). Fairness in non-human primates? — *Soc. Justice Res.* 25: 256-276.
- Brosnan, S.F. (2006a). At a crossroads of disciplines. — *Soc. Justice Res.* 19: 218-227.
- Brosnan, S.F. (2006b). Nonhuman species’ reactions to inequity and their implications for fairness. — *Soc. Justice Res.* 19: 153-185.
- Brosnan, S.F. (2010). What do capuchin monkeys tell us about cooperation? — In: *For the greater good of all: perspectives on individualism, society, and leadership perspectives on individualism, society, and leadership. Jepson studies in leadership series* (Forsyth, D.R. & Hoyt, C.L., eds). Palgrave Macmillan, New York, NY, p. 11-28.
- Brosnan, S.F. (2013). Justice and fairness related behaviors in non-human primates. — *Proc. Natl. Acad. Sci. USA* 110: 10416-10423.
- Brosnan, S.F. (2014). Evidence for moral behaviors in non-human primates. — In: *Empirically informed ethics: morality between facts and norms* (Christen, M., van Schaik, C.P., Fischer, J., Huppenbauer, M. & Tanner, C., eds). Springer, Berlin, p. 85-98.
- Brosnan, S.F. & de Waal, F.B.M. (2002). A proximate perspective on reciprocal altruism. — *Human Nature* 13: 129-152.
- Brosnan, S.F. & de Waal, F.B.M. (2009). Cebus apella tolerate intermittent unreliability in human experimenters. — *Int. J. Primatol.* 30: 663-674.
- Brosnan, S.F. & de Waal, F.B.M. (2014). Evolution of responses to (un)fairness. — *Science* 346: 1251776.
- Brosnan, S.F., Schiff, H.C. & de Waal, F.B.M. (2005). Tolerance for inequity may increase with social closeness in chimpanzees. — *Proc. Roy. Soc. Lond. B: Biol. Sci.* 272: 253-258.
- Brosnan, S.F., Freeman, C. & de Waal, F.B.M. (2006). Partner’s behavior, not reward distribution, determines success in an unequal cooperative task in capuchin monkeys. — *Am. J. Primatol.* 68: 713-724.

- Brosnan, S.F., Talbot, C., Ahlgren, M., Lambeth, S.P. & Schapiro, S.J. (2010). Mechanisms underlying responses to inequitable outcomes in chimpanzees, *Pan troglodytes*. — *Anim. Behav.* 79: 1229-1237.
- Brosnan, S.F., Hopper, L.M., Richey, S., Freeman, H.D., Talbot, C.F., Gosling, S.D., Lambeth, S.P. & Schapiro, S.J. (2015). Personality influences responses to inequity and contrast in chimpanzees. — *Anim. Behav.* 101: 75-87.
- Brown, J.L. (1983). Cooperation — a biologist's dilemma. — *Adv. Stud. Behav.* 13: 1-39.
- Bshary, R. & Bergmuller, R. (2008). Distinguishing four fundamental approaches to the evolution of helping. — *J. Evol. Biol.* 21: 405-420.
- Bshary, R. & Grutter, A.S. (2006). Image scoring and cooperation in cleaner fish mutualism. — *Nature* 441: 975-978.
- Bshary, R., Hohner, A., Ait-El-Djoudi, K. & Fricke, H. (2006). Interspecific communicative and coordinated hunting between groupers and giant moray eels in the Red Sea. — *PLoS Biol.* 4: 2393-2398.
- Bshary, R., Grutter, A.S., Willener, A.S.T. & Leimar, O. (2008). Pairs of cooperating cleaner fish provide better service quality than singletons. — *Nature* 455: 964-967.
- Bullinger, A.F., Melis, A.P. & Tomasello, M. (2011). Chimpanzees, *Pan troglodytes*, prefer individual over collaborative strategies towards goals. — *Anim. Behav.* 82: 1135-1141.
- Cheney, D.L., Moscovice, L.R., Heesen, M., Mundry, R. & Seyfarth, R.M. (2010). Contingent cooperation between wild female baboons. — *Proc. Natl. Acad. Sci. USA* 107: 9562-9566.
- Connor, R.C. (1995). Impala allogrooming and the parcelling model of reciprocity. — *Anim. Behav.* 49: 528-530.
- Crofoot, M.C., Rubenstein, D.I., Maiya, A.S. & Berger-Wolf, T.Y. (2011). Aggression, grooming and group-level cooperation in white-faced capuchins (*Cebus capucinus*): insights from social networks. — *Am. J. Primatol.* 73: 821-833.
- Cuthill, I.C. & Houston, A.I. (1997). Managing time and energy. — In: *Behavioural ecology: an evolutionary approach*, 4th edn. (Krebs, J.R. & Davies, N.B., eds). Wiley-Blackwell, Cambridge, p. 97-120.
- de Waal, F.B.M. & Berger, M.L. (2000). Payment for labour in monkeys. — *Nature* 404: 563.
- de Waal, F.B.M. & Davis, J.M. (2003). Capuchin cognitive ecology: cooperation based on projected returns. — *Neuropsychology* 41: 221-228.
- Dugatkin, L.A. (1997). *Cooperation among animals: an evolutionary perspective*. — Oxford University Press, New York, NY.
- Fehr, E. & Fischbacher, U. (2004). Third-party punishment and social norms. — *Evol. Human Behav.* 25: 63-87.
- Fehr, E. & Schmidt, K.M. (1999). A theory of fairness, competition, and cooperation. — *Q. J. Econ.* 114: 817-868.
- Fischer, E.A. (1988). Simultaneous hermaphroditism, tit-for-tat, and the evolutionary stability of social systems. — *Ethol. Sociobiol.* 9: 119-136.
- Flack, J. & de Waal, F.B.M. (2000). "Any animal whatever": Darwinian building blocks of morality in monkeys and apes. — *J. Conscious. Stud.* 7: 1-29.

- Freidin, E., Cuello, M.I. & Kacelnik, A. (2009). Successive negative contrast in a bird: starlings' behaviour after unpredictable negative changes in food quality. — *Anim. Behav.* 77: 857-865.
- Gadza, S.K., Connor, R.C., Edgar, R.K. & Cox, F. (2005). A division of labour with role specialization in group-hunting bottlenose dolphins (*Tursiops truncatus*) off Cedar Key, Florida. — *Proc. Roy. Soc. Lond. B: Biol. Sci.* 272: 135-140.
- Gilby, I.C. (2006). Meat sharing among the Gombe chimpanzees: harassment and reciprocal exchange. — *Anim. Behav.* 71: 953-963.
- Gros-Luis, J., Perry, S. & Manson, J.H. (2003). Violent coalitionary attacks and intraspecific killing in wild white-faced capuchin monkeys (*Cebus capucinus*). — *Primates* 44: 341-346.
- Heil, M. & McKey, D. (2003). Protective ant-plant interactions as model systems in ecological and evolutionary research. — *Annu. Rev. Ecol. Evol. Syst.* 34: 425-553.
- Hopper, L.M., Lambeth, S.P., Schapiro, S.J. & Brosnan, S.F. (2013). When given the opportunity, chimpanzees maximize personal gain rather than "level the playing field". — *PeerJ* 1: e165.
- Hopper, L.M., Lambeth, S.P., Schapiro, S.J. & Brosnan, S.F. (2014). Social comparison mediates chimpanzees' responses to loss, not frustration. — *Anim. Cogn.* 17: 1303-1311.
- Horowitz, A. (2012). Fair is fine, but more is better: limits to inequity aversion in the domestic dog. — *Soc. Justice Res.* 25: 195-212.
- Jensen, K. (2010). Punishment and spite, the dark side of cooperation. — *Phil. Trans. Roy. Soc. Lond. B: Biol. Sci.* 365: 2635-2650.
- Johnstone, R.A. & Bshary, R. (2002). From parasitism to mutualism: partner control in asymmetric interactions. — *Ecol. Lett.* 5: 634-639.
- Johnstone, R.A. & Bshary, R. (2008). Mutualism, market effects and partner control. — *J. Evol. Biol.* 21: 879-888.
- Kiers, E.T., Rousseau, R.A., West, S.A. & Denison, R.F. (2003). Host sanctions and the legume-*Rhizobium* mutualism. — *Nature* 425: 78-81.
- Krams, I., Krama, T., Igaune, K. & Mänd, R. (2008). Experimental evidence of reciprocal altruism in the pied flycatcher. — *Behav. Ecol. Sociobiol.* 62: 599-605.
- Lamprecht, J. (1978). The relationship between food competition and foraging group size in some larger carnivores. A hypothesis. — *Z. Tierpsychol.* 46: 337-343.
- Massen, J.J.M., Van Den Berg, L.M., Spruijt, B.M. & Sterck, E.H.M. (2012). Inequity aversion in relation to effort and relationship quality in long-tailed macaques (*Macaca fascicularis*). — *Am. J. Primatol.* 74: 145-156.
- McGregor, P.K. (1993). Signalling in territorial systems: a context for individual identification, ranging and eavesdropping. — *Phil. Trans. Roy. Soc. Lond. B: Biol. Sci.* 340: 237-244.
- McGregor, P.K. (2005). *Animal communication networks*. — Cambridge University Press, Cambridge.
- McNamara, J.M., Barta, Z. & Houston, A.I. (2004). Variation in behaviour promotes cooperation in the prisoner's dilemma game. — *Nature* 428: 745-748.

- Melis, A.P., Hare, B. & Tomasello, M. (2006a). Chimpanzees recruit the best collaborators. — *Science* 311: 1297-1300.
- Melis, A.P., Hare, B. & Tomasello, M. (2006b). Engineering cooperation in chimpanzees: tolerance constraints on cooperation. — *Anim. Behav.* 72: 275-286.
- Melis, A.P., Hare, B. & Tomasello, M. (2009). Chimpanzees coordinate in a negotiation game. — *Evol. Human Behav.* 30: 381-392.
- Noë, R. & Hammerstein, P. (1995). Biological markets. — *Trends Ecol. Evol.* 10: 336-339.
- Noë, R., van Hooff, J.A.R.A.M. & Hammerstein, P. (2001). *Economics in nature*. — Cambridge University Press, Cambridge.
- Packer, C. (1988). Constraints on the evolution of reciprocity: lessons from cooperative hunting. — *Ethol. Sociobiol.* 9: 137-147.
- Pellmyr, O. & Huth, C.J. (1994). Evolutionary stability of mutualism between yuccas and yucca moths. — *Nature* 372: 257-260.
- Perry, S., Manson, J.H., Dower, G. & Wikbert, E. (2003). White-faced capuchins cooperate to rescue a groupmate from a *Boa constrictor*. — *Folia Primatol.* 74: 109-111.
- Perry, S. & Rose, L. (1994). Begging and transfer of coati meat by white-faced capuchin monkeys, *Cebus capucinus*. — *Primates* 35: 409-415.
- Pierce, N.E., Braby, M.F., Heath, A., Lohman, D.J., Mathew, J., Rand, D.B. & Travassos, M.A. (2002). The ecology and evolution of ant association in the Lycaenidae (Lepidoptera). — *Annu. Rev. Entomol.* 47: 733-771.
- Price, S.A. & Brosnan, S.F. (2012). To each according to his need? Variability in the responses to inequity in non-human primates. — *Soc. Justice Res.* 25: 140-169.
- Proctor, D., Williamson, R.A., de Waal, F.B.M. & Brosnan, S.F. (2013). Chimpanzees play the ultimatum game. — *Proc. Natl. Acad. Sci. USA* 110: 2070-2075.
- Raihani, N.J. & Bshary, R. (2015). Why humans might help strangers. — *Front. Behav. Neurosci.* 9: 39.
- Raihani, N.J. & McAuliffe, K. (2012). Does inequity aversion motivate punishment? Cleaner fish as a model system. — *Soc. Justice Res.* 25: 213-231.
- Raihani, N.J., Grutter, A.S. & Bshary, R. (2010). Punishers benefit from third-party punishment in fish. — *Science* 327: 171.
- Raihani, N.J., Pinto, A.I., Grutter, A.S., Wismer, S. & Bshary, R. (2011). Male cleaner wrasses adjust punishment of female partners according to the stakes. — *Proc. R. Soc. Lond. B Biol.* 279: 365-370.
- Raihani, N.J., Grutter, A.S. & Bshary, R. (2012a). Female cleaner fish cooperate more with unfamiliar males. — *Proc. Roy. Soc. Lond. B: Biol. Sci.* 279: 2479-2486.
- Raihani, N.J., McAuliffe, K., Brosnan, S.F. & Bshary, R. (2012b). Are cleaner fish, *Labroides dimidiatus*, inequity averse? — *Anim. Behav.* 84: 665-674.
- Raihani, N.J., Thornton, A.N. & Bshary, R. (2012c). Punishment and cooperation in nature. — *Trends Ecol. Evol.* 27: 288-295.
- Range, F., Horn, L., Virányi, Z. & Huber, L. (2009). The absence of reward induces inequity aversion in dogs. — *Proc. Natl. Acad. Sci. USA* 106: 340-345.
- Range, F., Leitner, K. & Virányi, Z. (2012). The influence of the relationship and motivation on inequity aversion in dogs. — *Soc. Justice Res.* 25: 170-194.

- Reynolds, G.S. (1961). Behavioral contrast. — *J. Exp. Anal. Behav.* 4: 441-466.
- Roberts, G. (2005). Cooperation through interdependence. — *Anim. Behav.* 70: 901-908.
- Roma, P.G., Silberberg, A., Ruggiero, A.M. & Suomi, S.J. (2006). Capuchin monkeys, inequity aversion, and the frustration effect. — *J. Comp. Psychol.* 120: 67-73.
- Schino, G. & Aureli, F. (2009). Reciprocal altruism in primates: partner choice, cognition and emotions. — *Adv. Stud. Behav.* 39: 45-69.
- Schino, G. & Aureli, F. (2010). Primate reciprocity and its cognitive requirements. — *Evol. Anthropol.* 19: 130-135.
- Silberberg, A., Crescimbene, L., Addessi, E., Anderson, J.R. & Visalberghi, E. (2009). Does inequity aversion depend on a frustration effect? A test with capuchin monkeys (*Cebus apella*). — *Anim. Cogn.* 12: 505-509.
- Silk, J.B., Brosnan, S.F., Vonk, J., Henrich, J., Povinelli, D.J., Richardson, A.S., Lambeth, S.P., Mascaró, J. & Schapiro, S.J. (2005). Chimpanzees are indifferent to the welfare of unrelated group members. — *Nature* 437: 1357-1359.
- Silk, J.B. & House, B.R. (2011). Evolutionary foundations of human prosocial sentiments. — *Proc. Natl. Acad. Sci. USA* 108: 10910-10917.
- Stevens, J.R. & Hauser, M.D. (2004). Why be nice? Psychological constraints on the evolution of cooperation. — *Trends Cogn. Sci.* 8: 60-65.
- Strübin, C., Steinegger, M. & Bshary, R. (2011). On group living and collaborative hunting in the yellow saddle goatfish (*Parupeneus cyclostomus*). — *Ethology* 117: 961-969.
- Takimoto, A. & Fujita, K. (2011). I acknowledge your help: capuchin monkeys' sensitivity to others' labor. — *Anim. Cogn.* 14: 715-725.
- Tinklepaugh, O.L. (1928). An experimental study of representative factors in monkeys. — *J. Comp. Psychol.* 8: 197-236.
- van Wolkenten, M., Brosnan, S.F. & de Waal, F.B.M. (2007). Inequity responses of monkeys modified by effort. — *Proc. Natl. Acad. Sci. USA* 104: 18854-18859.
- Vonk, J., Brosnan, S.F., Silk, J.B., Henrich, J., Richardson, A.S., Lambeth, S.P., Schapiro, S.J. & Povinelli, D.J. (2008). Chimpanzees do not take advantage of very low cost opportunities to deliver food to unrelated group members. — *Anim. Behav.* 75: 1757-1770.