Animal Behaviour 128 (2017) 153–164

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Grooming decisions under structural despotism: the impact of social rank and bystanders among wild male chimpanzees

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ARTICLE INFO

Article history:
Received 1 July 2016
Initial acceptance 3 October 2016
Final acceptance 29 March 2017

MS. number: 16-00588R

Keywords:
biological markets
Budongo
cooperation
Pan troglodytes
parcelling
Sonso

Understanding the evolution of cooperation remains a central concern in studies of animal behaviour, with fundamental issues being how individuals avoid being cheated, or ‘short-changed’, and how partners are chosen. Economic decisions made during social interactions should depend upon the availability of potential partners nearby, as these bystanders generate temptations to defect from the current partner. The influence of bystanders is highlighted in two theoretical approaches, biological markets theory and parcelling, both economic models of behaviour. Here, we tested predictions of these models using the grooming behaviour of wild male chimpanzees, *Pan troglodytes*, living under strong structural despotism, where grooming is exchanged both for agonistic support and for itself, and so we provide the first investigation of both presence and value of bystanders on chimpanzees' grooming decisions. We found that male chimpanzees took into account the relative value (rank) of bystanders compared to that of their current partner, with this more important than bystander numbers. High-ranking bystanders appeared to generate incentives to defect from a potentially cooperative interaction and we found that grooming effort was parcelled into discrete episodes, with smaller parcels used when a bystander outranked the current partner. The number of bystanders also generated a temptation to defect, as bidirectional (reciprocated) bouts were more likely to occur with fewer bystanders. Such bouts were more likely with smaller rank distances between groomer and recipient. We found no influence of grooming relationship on initial investment: groomers did not appear to trust that they would receive grooming in return, even from those with whom they had a history of strongly reciprocal grooming. Our findings are consistent with an economic-benefits, markets-based approach, but not a relationship model paradigm. Our work highlights the importance of considering the immediate social context (number and quality of bystanders) in studies of cooperation.

Understanding the evolution of cooperation remains a central concern in studies of animal behaviour (Clutton-Brock, 2009; West & Gardner, 2013; West, Griffin, & Gardner, 2007). Two questions have attracted particular attention: how an individual avoids being cheated, or ‘short-changed’, and how individuals select partners. For group-living species, choice of social partners is commonplace (Connor, 1992, 1995a, 2007; Kutsukake & Clutton-Brock, 2010; Noë & Hammerstein, 1994; Noë, van Schaik, & van Hooff, 1991; Smith, Memenis, & Holekamp, 2007; Wubs, Bshary, & Lehmann, 2016). Asymmetries exist between individuals such that the value of a particular interaction may differ between participants, and individuals have opportunities to coerce cooperation or to punish cheating (Clutton-Brock, 2009; Clutton-Brock & Parker, 1995; Jensen, Call, & Tomasello, 2007; Mulder & Langmore, 1993; West & Gardner, 2013; West et al., 2007).

Partner choice is highlighted in two particular theoretical approaches, Connor's parcelling model (Connor, 1992; 1995b; 1995a; 2010), itself presaged by Friedman and Hammerstein (1991), and Noë and colleagues' biological markets theory (Hammerstein & Noë, 2016; Noë & Hammerstein, 1994, 1995; Noë et al., 1991). Central to the parcelling model is the concept that the presence of bystanders, individuals within the vicinity of a cooperating dyad but not otherwise participating, generates a temptation to defect from the current partner. In turn, this drives the

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http://dx.doi.org/10.1016/j.anbehav.2017.04.012

parcelling (subdividing) of a social interaction by the actor, such that its partner is forced into cooperating in order to extract significant benefit from the interaction, while minimizing the actor's costs should the partner defect, i.e. refuse to cooperate, or select another partner. When individuals have easy opportunities to find alternative partners, such that the costs of searching are low, defection is more likely to occur and the actor should give smaller parcels in order to limit its losses (Connor, 1992, 1995a). Superficially similar to parcelling is raise-the-stakes (RTS: Roberts & Sherratt, 1998). However, bystanders are not a feature of this model: RTS actors are concerned solely with their investment, and whether or not it is matched; the presence or absence of third parties is irrelevant. To date, RTS has received little empirical support (Kaburu & Newton-Fisher, 2013).

Biological markets theory also incorporates the influence of bystanders. It predicts that individuals should alter their investment in an interaction in relation to the availability of other potential partners. If individuals cluster into discrete groups, those who are close at hand, i.e. bystanders, form the local marketplace of 'traders' with whom an individual can interact (Kaburu & Newton-Fisher, 2016a). The conditions of the local market may be more important in influencing levels of investment than those of the wider marketplace (the social group) due to search and opportunity costs (Noë & Hammerstein, 1994). Unlike parcelling, however, biological markets theory predicts only the total amount of investment as a function of market conditions, not the internal structuring of interactions. Thus, while both parcelling and biological markets theory predict a bystander effect, the latter neither predicts nor accounts for the division of behaviour into parcels.

Social grooming provides an excellent system with which to explore such models of cooperation (Barrett, Henzi, Weingrill, Lycett, & Hill, 2000, 1999; Frank & Silk, 2009; Fruteau, Lemoine, Hellard, Noe, 2011; Kaburu & Newton-Fisher, 2015a; Machanda, Gilby, & Wrangham, 2014; Newton-Fisher & Lee, 2011; de Waal, 1997; Watts, 2002). Social grooming is a behaviour found across a variety of taxa, including ungulates (Mooring & Blumstein, 2004), bats (Carter & Leffer, 2015), rodents (Stopka & Macdonald, 1999) and birds (Radford, 2012), and is a prominent behaviour in nonhuman primates (Dunbar, 1991; Henzi & Barrett, 1999; Russell & Phelps, 2013; Schino, 2006). Time invested in grooming can vary considerably within species, making this the ideal behaviour with which to explore parcelling. Grooming provides the recipient with a variety of benefits including hygiene (Akinyi et al., 2013; Mooring & Blumstein, 2004; Zamma, 2002), stress reduction (Boccia, Reite, & Laudenslager, 1989; Shutt, MacLarnon, Heistermann, & Semple, 2007) and thermoregulation (McFarland et al., 2015), while the groomer has to endure possible energetic and opportunity costs (Dunbar, 1992) as well as increased proximity to a potentially aggressive group member (Schino & Alessandrini, 2015). While these costs may be small, in some cases perhaps trivial (Dunbar, 1988), or also incurred by the recipient, fitness is relative and even marginal gains may be important. Where recipients are reproductive rivals of groomers, providing these rivals with benefits generates net costs for the groomer (Newton-Fisher, 2014). Both parasite load and stress are driven by factors extrinsic to an individual and so will accumulate with time, creating an ongoing demand for grooming that varies between individuals.

Under economic models such as biological markets theory and parcelling, animals are viewed as following behavioural strategies that lead them to behave as if they make partner-choice decisions influenced by market conditions of supply and demand (Connor, 1992, 1995b; Hammerstein & Noë, 2016; Kaburu & Newton-Fisher, 2015a; Kutsukake & Clutton-Brock, 2010; Noë & Hammerstein, 1994; Noë et al., 1991; Smith et al., 2007). Animals living in social groups may trade grooming for commodities such as agonistic support, valued food or social tolerance where these are rank related or rank restricted (Barrett, Henzi, Weingrill, Lycett, & Hill, 1999; Clutton-Brock, 2009; Clutton-Brock & Parker, 1995; Jensen et al., 2007; Kaburu & Newton-Fisher, 2015a; Mulder & Langmore, 1993; West & Gardner, 2013; West et al., 2007), and 'grooming up the hierarchy', a well-known pattern in primate social grooming, may be the result of lower-ranking individuals attempting to access these commodities (Barrett et al., 1999; Henzi & Barrett, 1999; Kaburu & Newton-Fisher, 2015a; Noë & Hammerstein, 1994, 1995; Noë et al., 1991; Schino, 2006). Alternatively, grooming may be exchanged through varying degrees of reciprocity, with individuals trading grooming in an effort to receive grooming in return (Barrett et al., 1999; Hemelrijk & Ek, 1991; Newton-Fisher & Lee, 2011; Watts, 2002). When individuals have easy opportunities to find other partners and high-ranking individuals are close at hand, such that the costs of searching are low and switching partners is beneficial, the likelihood of defection (i.e. lack of reciprocation) should increase. Individuals attempting to trade grooming for itself should therefore adjust the amount of grooming they give, especially at the beginning of a bout when they are uncertain whether they will receive grooming in return, while recipients should decide whether it is worth reciprocating their partner's effort (Connor, 1992, 1995a; Kaburu & Newton-Fisher, 2016a). Faced with the risk of nonreciprocation, a parcelling strategy will reduce the likelihood of, or limit losses in the event of, this happening. The recipient's dominance rank, the availability of potential partners nearby and the dominance ranks of these bystanders could all affect both initial investment in a grooming bout and the likelihood of reciprocity.

Increasing support for economic models such as biological markets theory (Barrett et al., 2000; Clutton-Brock, 2009; Fruteau et al., 2011; Fruteau, Voelkl, van Damme, & Noë, 2009; Gumert, 2007; Kaburu & Newton-Fisher, 2015a; Machanda et al., 2014; McFarland et al., 2015; Newton-Fisher & Lee, 2011; Tiddi, Aureli, di Sorrentino, & Janson, 2011; de Waal, 1997; Wei et al., 2012; West & Gardner, 2013; West et al., 2007) represents a challenge to the relationship model (Dunbar, 1988; Silk, Alberts, & Altmann, 2003), which has been the dominant paradigm used to understand social interactions in nonhuman primates. In this model, social interactions such as grooming are seen as mechanisms to build relationships that in turn deliver functional benefits. The fundamental difference between the two perspectives is not one of timeframes (cf. Frank & Silk, 2009; Mitani, 2009b; Sanchez-Amaro & Amici, 2015), an often-misunderstood aspect of market-based approaches (Kaburu & Newton-Fisher, 2016b), but the link between the behavioural interaction and fitness. Under the relationship model, fitness benefits derive from the relationships established through interactions, whereas under a markets-based approach fitness benefits derive from the interactions themselves. The debate between these two perspectives remains unresolved.

Here we focus largely on testing predictions from biological markets theory and parcelling, but we also test a prediction drawn from the relationship model, and we consider our results from the perspectives of both paradigms. We test the effects of both dominance rank and bystander presence on grooming interactions among wild male chimpanzees, *Pan troglodytes*, of the Sonso community of the Budongo Forest Reserve (Uganda). These chimpanzees showed a strongly structurally despotic hierarchy at the time of this study (hierarchy steepness = 0.70: Kaburu & Newton-Fisher, 2015a), more so than during an earlier study (steepness = 0.40) and when compared to other communities (Kaburu & Newton-Fisher, 2015a). These chimpanzees used grooming both to trade for rank-restricted commodities and as part of grooming exchanges with varying degrees of reciprocity (Kaburu