



Social instability raises the stakes during social grooming among wild male chimpanzees



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Explaining cooperative behaviour is a fundamental issue for evolutionary biology. The challenge for any cooperative strategy is to minimize the risks of nonreciprocation (cheating) in interactions with immediate costs and delayed benefits. One of a variety of proposed strategies, the raise-the-stakes (RTS) strategy, posits that individuals establish cooperation by increasing investment across interactions from an initial interaction. This model has received little quantitative support, however, probably because individuals of many social species engage in repeated interactions from a young age. In some situations, however, such as following conflicts, after prolonged absences or during social instability, established relationships may become unreliable predictors of future behaviour, creating an environment for RTS. We investigated grooming interactions among wild male chimpanzees, *Pan troglodytes*, testing RTS in these specific contexts. We found evidence to support the view that male chimpanzees employed RTS during social instability, but not under the other conditions. However, we also found that the duration of episodes (discrete parcels) of grooming was negatively related to aggression risk and in consequence suggest that the patterning of grooming interactions indicative of RTS was less to do with preventing cheating, and more to do with avoiding the elevated risks of intramale aggression during the period of social instability. We interpret the apparent support for RTS in our data as a by-product of the way chimpanzees cope with fluctuating (here, elevated then diminishing) risks of aggression. We suggest that social instability raises the stakes for grooming by creating a more hazardous marketplace in which to trade.

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Explaining cooperative behaviour is a fundamental question for evolutionary biology (West et al. 2006). While cooperation between related individuals is often accounted for by indirect benefits and inclusive fitness theory (Hamilton 1964a, b), cooperation between unrelated individuals is typically explained by invoking the theory of reciprocal altruism (Trivers 1971) with its exchange of direct costs and benefits, albeit delayed in time. Functionally, however, this is mutualism rather than altruism as all actors receive direct fitness benefits and is better described as direct reciprocity (Clutton-Brock 2009).

The challenge for any cooperative strategy is to minimize risks of nonreciprocation (cheating) in interactions in which costs are immediate but benefits are delayed. A variety of strategies have been proposed, building on the iterated prisoner's dilemma (IPD) model suggested by Trivers (1971). Axelrod & Hamilton's (1981) 'tit-for-tat' strategy (TfT), under which individuals start out cooperating and match their opponent's behaviour in previous interactions,

refusing to cooperate only if the partner does so first, is evolutionarily stable. TfT has found some support but seems restricted to simple social exchanges (e.g. serranid coral reef hermaphroditic fish: Fischer 1988), or artificial experimental situations (e.g. predator inspection by sticklebacks and guppies: Milinski 1987; Dugatkin 1988). Strategies based on an IPD model assume cooperation to be an 'all-or-nothing' affair, and that interacting individuals have no other potential social partners (Noë 1990, 2001); in consequence, a variety of further models with more applicability to biological systems have been proposed, such as biological markets theory (Noë & Hammerstein 1994, 1995; Noë 2001, 2006), pseudoreciprocity (Connor 1986), parcelling (Connor 1992) and raise-the-stakes (Roberts & Sherratt 1998; Sherratt & Roberts 2002).

Raise-the-stakes (RTS) describes a strategy in which cooperators increase investment in a social interaction if the partner matches or betters its opponent's last move. It allows cooperation to be incremental, rather than 'all-or-nothing', and individuals' investment in a relationship can vary over a series of interactions (Roberts & Sherratt 1998; Sherratt & Roberts 1999). RTS allows the animals to 'test the water', before investing in potentially costly cooperative behaviours; at the very least, it allows them to limit their losses.

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This strategy is robust against 'subtle cheaters', that is, individuals that invest less than in previous interactions (Roberts & Sherratt 1998; Van den Berg & Dewitte 2006), and generates predictions that can be easily tested in animal systems (Keller & Reeve 1998). Support for RTS has been found in species as diverse as the sawfly *Perga affinis*, in which cohesion among gregarious larvae is maintained through tapping signals (Fletcher 2008), and humans, in which subjects increased monetary donations to a social partner if that partner matched their investment (Roberts & Renwick 2003; Majolo et al. 2006; Van den Berg & Dewitte 2006) but not if the partner was a previously established friend (Krebs 1970; Majolo et al. 2006).

The initial presentation of the RTS strategy was supported by data on reciprocity in social grooming interactions of impala, *Aepyceros melampus* (Roberts & Sherratt 1998). Such grooming should be an ideal behaviour with which to test the usefulness of RTS as an explanation for reciprocity: the total amount of grooming that one individual performs for another is easily broken down into smaller 'episodes' of investment, and that investment can be quantified by time spent giving grooming (Keller & Reeve 1998; Roberts & Sherratt 1998). Grooming offers benefits to the recipient, in terms of ectoparasite removal (Zamma 2002; Mooring et al. 2004; Akinyi et al. 2013) and stress reduction (Gust et al. 1993; Aureli et al. 1999; Kaburu et al. 2012) at some costs to the groomer, such as reduced vigilance (Maestriepieri 1993; Cords 1995; Mooring & Hart 1995) and resting time (Dunbar 1992). Studies of grooming in nonhuman primates, suggested as an example system for RTS by Keller & Reeve (1998), have failed to find support for this strategy, however (Barrett et al. 2000; Manson et al. 2004; Fruteau et al. 2011).

RTS assumes an initial interaction from which reciprocity can develop and so appears most applicable to situations in which individuals are forming new cooperative relationships (*sensu* Hinde 1976). In many animal groups, however, most observed social interactions are merely the latest of a series of interactions that may have started in infancy: the relevance of RTS for understanding persistent reciprocity between members of complex social groups has therefore been questioned (Barrett et al. 2000; Barrett & Henzi 2006). That said, there are several possible scenarios under which this history of interactions may be negated, at least temporarily. These could include aggressive conflicts, prolonged absences from a group or periods of high social instability. If this occurs, and individuals cannot rely on their prior history of interactions to predict future behaviour, they may need to use strategies such as RTS to re-establish cooperative relationships. The impact of such contexts on grooming strategy has not been investigated.

We examined grooming exchanges among wild male chimpanzees, *Pan troglodytes*, for evidence of the RTS strategy. The grooming behaviour of adult male chimpanzees offers a good model system for the investigation of reciprocity. Previous work has shown that chimpanzees tend to reciprocate grooming exchanges (Newton-Fisher 1997, 2002; Boesch & Boesch-Achermann 2000; Watts 2000; Arnold & Whiten 2003; Mitani 2006; Gomes et al. 2009; Newton-Fisher & Lee 2011). Furthermore, they tend to divide grooming bouts into episodes (*sensu* Barrett et al. 2000), the length (or duration) of which can vary both within and across bouts. The chimpanzee social system is characterized by fluid associations, with any particular set of individuals often only stable on a timescale of minutes or hours, and individuals may be out of contact with particular others for hours or days as a result (Reynolds 1965; Nishida 1968).

Given the findings of previous studies of primate grooming exchanges (Barrett et al. 2000; Manson et al. 2004; Fruteau et al. 2011), we predicted that RTS would not be a strategy employed during periods of social stability (prediction 1). In contrast, we

predicted that RTS would be employed in contexts in which relationships may be 'reset', that is, where prior histories of interaction may become unreliable predictors of the behaviour of social partners, thus creating a need to re-establish grooming relationships. We focused on three specific contexts.

(1) The aftermath of aggressive conflicts. Across a range of primate species both aggressor and victim tend to be more anxious after a conflict (reviewed in Aureli & Smuçny 2000), especially where they had previously shown a high level of affiliation (Aureli 1997; Cords & Aureli 2000; Kutsukake & Castles 2001). Conflicts can potentially jeopardize the relationship between two individuals (Aureli & de Waal 2000; Cords & Aureli 2000; Aureli et al. 2002; Silk 2002) and former opponents may try to repair their relationships (Cords & Aureli 2000) by reconciling (de Waal & van Roosmalen 1979; Silk 2002), suggesting that they can no longer rely on prior history to guide future cooperation. Reconciliatory tendency in wild chimpanzees is relatively low, however, occurring in only 12–16% of dyads (Arnold & Whiten 2001; Kutsukake & Castles 2004; versus 27–35% in captivity: de Waal & van Roosmalen 1979; Preuschoft et al. 2002), so RTS may provide an alternative strategy (prediction 2).

(2) After prolonged absence. Male chimpanzees may be apart from others for many days or weeks if they pursue a consortship mating strategy, by which they isolate themselves and a single (cycling) female from the rest of the social group in an attempt to gain exclusive mating access (Tutin 1979; Goodall 1986; Nishida 1997; Matsumoto-Oda 1999). The duration of this separation, together with shifting patterns of interactions between other males, may create a context in which males rejoining the other members of the social group may be unable to rely on past history and need to employ the RTS strategy to re-establish cooperative relationships (prediction 3).

(3) During periods of social instability. Loss of key individuals through disease, predation or, particularly in chimpanzees, conspecific lethal violence (Newton-Fisher & Thompson 2012), may disrupt existing patterns of social interaction and/or destabilize rank hierarchies (Wey et al. 2008; Cheney & Seyfarth 2009). During our study period, a phase of elevated aggression rates and high instability in the male hierarchy followed the killing of the incumbent alpha male of the study community (Kaburu et al. 2013). We used this dramatic shift to examine whether male chimpanzees employ RTS in their grooming interactions in periods of high social instability (prediction 4).

METHODS

Data Collection

The study was conducted between February and November 2011 on the M-group chimpanzee community of the Mahale Mountains National Park, Tanzania (for descriptions of the field site see: Nishida 1990, 2012; Nakamura & Nishida 2012). The study group initially consisted of 10 adult males (≥ 16 years), five adolescent males (9–15 years), two juvenile males (5–8 years), three infant males (0–4 years), 23 adult females (≥ 14 years), seven adolescent females (7–13 years), five juvenile females (3–6 years) and five infant females (0–2 years). During data collection, two females gave birth, one female joined the community, two cycling females disappeared (and were assumed to have dispersed to another community) and one adult male, the alpha, was killed (Kaburu et al. 2013).

Eight adult males were followed through day-long focal sessions (Altmann 1974). Each day, the individual previously sampled less frequently was selected as the focal animal in an effort to equalize number of hours of observation across individuals. To ensure

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