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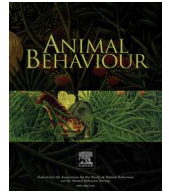
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Grooming decisions under structural despotism: the impact of social rank and bystanders among wild male chimpanzees



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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.

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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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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

& Newton-Fisher, 2015a; Newton-Fisher & Lee, 2011). Our specific focus is on the initial phase of grooming bouts, before the partner reciprocates, as previous work suggests this is an important decision period for chimpanzees during which they assess the costs and benefits of continuing to invest in the bout (Kaburu & Newton-Fisher, 2016a; Machanda et al., 2014). As in previous studies, and following Barrett et al. (1999) and Manson, Navarrete, Silk, and Perry (2004), we define a bout as an interaction rather than the behaviour of a single individual, and thus one or both members of a dyad could groom within a single bout (Kaburu & Newton-Fisher, 2015b, 2015a, 2016a; Newton-Fisher & Lee, 2011).

Chimpanzees are an ideal species for such an investigation, as their fission–fusion social system shuffles the identity and number of community members within a subgroup or party so that the number, and mix, of bystanders varies across opportunities for grooming exchange. Spatial proximity between individuals changes frequently and unpredictably (Newton-Fisher, 1999) such that parties represent local markets separated by substantially greater search costs than those required to find alternative partners within parties. In addition, chimpanzee grooming bouts can take various and complex forms (Kaburu & Newton-Fisher, 2013; Newton-Fisher, 2002b; Watts, 2000). Within a bout, grooming effort (Newton-Fisher & Lee, 2011) is typically broken up into short episodes of varying number and duration, the exchange of which can be highly dynamic. At its simplest, a bout consists of a single episode of continuous unbroken grooming performed by one individual, but typically a groomer will perform a sequence of episodes interspersed by short breaks (<30 s: Newton-Fisher, n.d.). In unidirectional bouts, this sequence of episodes terminates without the recipient responding either because the groomer has stopped or because the recipient departs. In bidirectional bouts, both individuals perform a sequence of episodes that may be asynchronous, such that individuals alternate roles, or overlapping such that grooming is simultaneous (mutual grooming). Sequences of grooming episodes are typically not aligned or necessarily matched in duration, so that most mutual grooming appears to result from coincidental overlap, and can end or resume purely as the result of individual grooming decisions. Many bouts include a combination of these structures (Machanda et al., 2014). In only a small proportion of bouts (e.g. 3% for the Sonso community, 1994–1995: Newton-Fisher & Lee, 2011) do individuals start simultaneously and groom in this manner throughout. Our study community is typical for chimpanzees in showing a mixture of unidirectional and bidirectional grooming bouts.

We focus on grooming interactions of adult males as they exhibit higher rates of grooming, and are more gregarious, than adult females (Halperin, 1979; Wrangham & Smuts, 1980). Furthermore, they engage in a broad range of cooperative behaviours such as support in agonistic interactions and sharing of food (Goodall, 1986; Nishida, 2011) with social exchanges little influenced by kinship (Langergraber, Mitani, & Vigilant, 2007). Male chimpanzees also demonstrate marked dominance relationships and rank hierarchies (Hayaki, Huffman, & Nishida, 1989; Muller & Wrangham, 2004; Newton-Fisher, 2004; Nishida & Hosaka, 1996), and are direct reproductive rivals in that they compete with one another for the same limited set of paternity opportunities (Boesch, Kohou, Néné, & Vigilant, 2006; Inoue, Inoue-Murayama, Vigilant, Takenaka, & Nishida, 2008; Newton-Fisher, Emery Thompson, Reynolds, Boesch, & Vigilant, 2010; Vigilant, Hofreiter, Siedel, & Boesch, 2001; Wroblewski et al., 2009).

With regard to the two paradigms, relationships versus direct economics, key predictions of the relationship model as applied to chimpanzee grooming have not been supported by recent work (Kaburu & Newton-Fisher, 2016a; Machanda et al., 2014), yet while there is some support for a biological markets model for

chimpanzee grooming (Kaburu & Newton-Fisher, 2015a, 2015b, 2016a), not all predictions are supported (Newton-Fisher & Lee, 2011) and more work is needed. With these analyses, we provide the first investigation of the influence of both dominance rank and bystanders on the grooming behaviour of wild male chimpanzees under strong structural despotism. While we showed recently that number of bystanders can influence the initial phase of grooming among chimpanzees of another community (Kaburu & Newton-Fisher, 2016a), those males exhibited a much flatter, structurally egalitarian hierarchy with shallow rank relationships (hierarchy steepness = 0.30), and did not trade grooming for agonistic support (Kaburu & Newton-Fisher, 2015a). As a strong relationship between grooming and coalitional support is considered typical for male chimpanzees (Mitani, 2009a; Nishida & Hosaka, 1996; Watts, 2002), it is possible that the bystander effects that we reported previously were due to unusual demographic or other conditions. One aim of this study, therefore, was to determine the generality of these previously reported findings.

From our consideration of the direct economic models, we generated a series of predictions concerning the initial phase of grooming bouts. First, we predicted that male chimpanzees should groom for longer during this initial phase when recipients are higher ranking than they are. Thus, with greater rank distance between groomer and recipient, the groomer increases initial investment (prediction 1). We also predicted that initial investment should be lower, and delivered in smaller parcels, with increasing numbers of bystanders (prediction 2). Initial investment and parcel size should be smaller when a bystander is high ranking (prediction 3), and when the high-ranking bystander outranks the current recipient (prediction 4). Thus, individuals should groom less in the initial phase if there are more bystanders and if a high-ranking bystander is present (as such an individual should be an attractive option for defection from the current partner). We also predicted that subsequent grooming by the recipient within the bout (i.e. the occurrence of a bidirectional bout) should be more likely with fewer bystanders (prediction 5) and small rank distances between partners (prediction 6). We predicted that grooming bouts should be more likely to be abandoned (resulting in a unidirectional bout) by the groomer in the presence of more bystanders (prediction 7) and with large rank distances between partners (prediction 8).

To aid interpretation of our results under a relationship model paradigm, we also investigated the effect of relationship (i.e. grooming) history on the initial investment in grooming bouts. Frequent or highly reciprocal grooming is commonly used as a marker of strong, high-quality, affiliative relationships in nonhuman primates (Mitani, 2009b; Silk et al., 2010). Therefore, we predicted that if the relationship model holds, a groomer's initial investment should be greater when grooming an individual who is a frequent grooming partner and/or one with whom the groomer has a history of reciprocal grooming (prediction 9), as either or both of these measures of prior grooming history indicate the likelihood that the groomer's investment will be returned. Predictions and the outcomes of our tests are summarized in Table 1.

METHODS

We collected data from December 2003 to August 2004 in the Sonso region of the Budongo Forest Reserve in western Uganda. Chimpanzees, *P. t. schweinfurthii*, of the study community were habituated in 1994, and have been studied continuously ever since (Newton-Fisher, 1997; Reynolds, 2005). At this time, the Sonso community consisted of 63 individuals, including eight adult males (≥ 16 years old) and 21 adult females (≥ 14 years old) (Emery Thompson, Newton-Fisher, & Reynolds, 2006). This research

Table 1
Summary of predictions

Predictions	Outcome
With greater rank distance to the recipient, the groomer should:	
(1) increase initial investment	Supported
With more bystanders, the groomer should:	
(2a) decrease initial investment	Not supported
(2b) decrease parcel size	Not supported
When a bystander is high-ranking, the groomer should:	
(3a) decrease initial investment	Supported
(3b) decrease parcel size	Supported
With greater rank distance between current recipient and the highest-ranking bystander, the groomer should:	
(4a) decrease initial investment	Supported
(4b) decrease parcel size	Not supported
Reciprocation of grooming by the recipient (a bidirectional bout) is more likely when:	
(5) there are fewer bystanders	Supported
(6) groomer and recipient are similar in rank	Supported
Groomers are more likely to abandon grooming in the initial phase:	
(7) when there are more bystanders	Not supported
(8) rank distance between groomer and recipient is large	Not supported
If the relationship model holds, the groomer's initial investment should be greater among dyads who, prior to this bout:	
(9a) groomed frequently	Not supported
(9b) strongly reciprocated grooming	Not supported

Outcomes that support predictions are shown in bold.

complied with regulations set by the Ethics Committee of the University of Kent, the protocols of the Budongo Forest Project (now BCFS) and the legal requirements of Uganda.

Data on grooming and agonistic interactions were collected using all-occurrence sampling (Altmann, 1974) within focal parties (i.e. all occurrences of these interactions that occurred in a party that contained a nominal focal animal, where 'party' is the subgroup produced by the fluid fission–fusion social system). Parties were followed for as long as possible from first encounter until nesting; focal animals were identified to allow unbiased decisions on which animals to observe when parties fissioned. If contact with chimpanzees was lost due to terrain and/or chimpanzee movement patterns, we searched for and observed the next party encountered containing one of the predetermined focal animals. We recorded a total of 1109.5 h of observation over 159 days/follows (median per day = 7 h). Individual adult males were under observation for a mean (\pm SD) of 358.8 ± 74.5 h (median = 356.7 h). We used 5 min-interval instantaneous scan sampling to record the identities of individuals present in the same party as the focal animal (i.e. association) as well as their activity (i.e. resting, grooming, travelling or feeding) every 10 min. We defined a party operationally as a cluster of independently associating individuals with a maximum radius of around 35 m, showing coordination in behaviour (Newton-Fisher, 1999). Participation in 'pant-hoot' choruses was used to confirm this definition, as this provided an active demonstration of coordination (Mitani & Nishida, 1993).

We defined grooming as the visual examination, searching and manipulation of the skin and hair with one or both hands, with the aid occasionally of the lower lip. Grooming bouts consisted of one or more episodes, with an episode defined as a period of unbroken continuous grooming by one individual, ending when the groomer removed both hands from his partner's body (Barrett et al., 2000; Kaburu & Newton-Fisher, 2013, 2016a). A bout was deemed to have ended when both members of the dyad engaged in activities other than grooming, including resting, for at least 30 s after the last social grooming movement by either individual (Newton-Fisher & Lee, 2011). For all bouts, we recorded: (1) the identity of the individual who approached the partner either to give or receive grooming, and time of the approach; (2) changes in the identity of

groomer and recipient; (3) start and end times of each grooming episode, and thus the total bout; and (4) how the bout ended (i.e. whether terminated by groomer or recipient). We excluded from analysis bouts where partners started grooming each other simultaneously ($N = 45$ bouts). We also excluded those that started prior to observation, and those that could not be accurately observed due to poor visibility.

We defined the initial phase of the bout as the period from initiation until either the bout ended (resulting in a unidirectional bout) or the receipt by the initiator of grooming from his partner (a bidirectional bout). The total duration of grooming performed in this phase we refer to as the initial investment in the bout. Any phase of grooming may consist of multiple episodes, each a period of unbroken continuous grooming by a single individual. We regard each episode as a putative parcel, and so refer to the mean duration of episodes (here, within an initial phase) as the parcel size.

Individuals in the party at the start of a grooming interaction but not part of the grooming dyad were defined as bystanders. Since the number of bystanders may be contingent on the context in which grooming occurs, we extracted from the scan samples the activities of all adult males in the party prior to the beginning of each bout. We classified four contexts: feeding, resting and travelling, where this was the activity of all the males in the party (individuals who were grooming were classified under 'resting'), and mixed, where males were engaged in multiple activities. We also noted whether the grooming bout was interrupted by aggression, either from third parties or by one of the participants in the grooming bout.

As grooming in chimpanzees is not restricted to dyadic interactions, but can develop into triadic or larger chains and clusters (Goodall, 1986; Nakamura, 2000), an individual initiating a grooming bout can do so with another who is already occupied with a grooming partner. We considered members of these grooming chains, as well as other individuals also involved in grooming, to be bystanders as they clearly represented possible alternative partners for the initiators. Thus we did not distinguish between recipients who were already engaged in a grooming interaction, and those who were not. While in principle this grooming by third parties may influence the behaviour of both initiator and recipient, we found no difference in our substantive results whether we ran our analyses including all grooming bouts or including only bouts that were neither part of grooming chains nor occurring when bystanders were engaged in their own grooming. In the interests of brevity, we present only results from the more inclusive data set.

We used directed aggressive interactions to determine relative social dominance (Newton-Fisher, 2017). We distinguished winners and losers from the outcome of each interaction, in particular using behaviours such as screaming, cowering or running away, or receiving but not returning physical violence and/or wounds, to identify the loser. Interactions that escalated, such that they consisted of multiple acts of aggression, were considered as single interactions. We discarded aggressive behaviours that provoked no response from the target, judging these to be ineffective in influencing social dominance relationships. We used these data to calculate Elo-ratings (Albers & de Vries, 2001) using the R function 'elo.sequence' (Kaburu, Inoue, & Newton-Fisher, 2013; Neumann et al., 2011; Newton-Fisher, 2017). This allowed us to track rank over time, and to determine dominance ranks of interacting males on any day for which grooming was recorded. We included in this analysis aggression performed as part of a coalition, as we have no reason to assume that such aggression would not result in the winner/loser effects assumed by the Elo-rating method. Following convention, ordinal rankings assigned a value of 1 to the highest-ranked individual (the alpha male), with numerically larger

values indicating lower-ranked individuals. We confirmed ranks were consistent with the direction of pant-grunt vocalizations (performed by subordinates towards dominants: Bygott, 1979; Goodall, 1986). We determined rank distance by subtracting the (ordinal) rank of the recipient from the (ordinal) rank of the groomer, so positive rank distances in the analysis below correspond to grooming directed from subordinates to dominants.

We used mixed-model analysis to test our predictions. We used the function 'lmer' for linear mixed models (LMM) and 'glmer' for generalized linear mixed models (GLMM) with a binomial structure, from the R package 'lme4'. We used the 'drop1' function to compute a likelihood ratio test and thereby assess whether the independent factor(s) exerted a significant effect on the dependent variable. We used random-intercept models that included the identities of both initiator and recipient as random factors with crossed structure, to control for repeated observations of individuals and possible idiosyncratic behavioural tendencies.

To test whether rank distance (prediction 1) and number of bystanders (prediction 2) affected initial phase grooming, we constructed two separate LMMs: one with initial investment (total duration) and one with parcel size (mean episode duration) as the dependent variable. In both models, we included the number of bystanders (continuous), rank distance between groomer and recipient (continuous), context (categorical) and whether the bout was interrupted (binomial) as fixed factors.

To test whether the presence of a high-ranking bystander resulted in lower initial investment and smaller parcel size, we constructed further LMMs with these as separate dependent variables, and absolute (ordinal) rank of the highest-ranked bystander (prediction 3) and the rank distance between this male and the recipient (prediction 4) as fixed factors. As above, we also included context and whether a bout was interrupted as fixed factors. Necessarily, we excluded bouts in which there were no male bystanders from this analysis.

To test whether the number of bystanders (prediction 5) or the rank distance within the grooming dyad (prediction 6) influenced participation in the bout by the recipient (i.e. the occurrence of a bidirectional bout), we constructed a GLMM with outcome (unidirectional or bidirectional bout) as the dependent variable, and rank distance between partners, number of bystanders, context and whether the bout was interrupted as fixed factors. In this analysis, we used the absolute value (modulus) of rank distance, as we were interested specifically in testing the effect of whether individuals were close or distant in rank. To test whether groomers were more likely to abandon grooming in the initial phase if more bystanders were present (prediction 7), or if rank distances between groomer and recipient were large (prediction 8), we constructed a second GLMM with the role of the individual terminating the initial phase (groomer versus recipient) as the dependent variable, and the number of bystanders, within-dyad absolute rank distance, the context and whether the bout was interrupted as fixed factors. In this second GLMM, we restricted analysis to unidirectional bouts (given our focus on the initial phase we did not examine responsibility for ending bidirectional bouts).

To test prediction 9, we calculated the grooming history for each dyad in the month prior to each grooming bout in our data set, as both the frequency (number of bouts) and the degree of grooming reciprocity. This approach was preferable to calculating measures across our data set, as that would conflate both prior history and future events relative to each grooming bout and the choices or decisions made therein. We reasoned that a period of a single month should be sufficient to capture recent prior history and thus the state (or quality) of the relationship: if such relationships are stable, then these measures should be similar whether sampled over the preceding month or over longer timeframes. If these

relationships are unstable, data accumulated over a longer period risk misrepresenting the state of the relationship at the time of any particular grooming interaction, and this risk increases with the length of accumulation period (a similar problem is faced by traditional methods of determining dominance relationships: Newton-Fisher, 2017). However, we also ran these analyses using a 2-month prior history, but as our results were no different we report only those using the 1-month period. We excluded from these analyses any bout where the dyad had not been recorded as grooming in the previous month.

We calculated frequency as the number of bouts recorded relative to the time that both males were present in the same party; for the degree of grooming reciprocity, we calculated the reciprocity index RI (Newton-Fisher & Lee, 2011; Nishida, 1988):

$$RI = 1 - \left| \frac{gAb}{(gAb + gBa)} - \frac{gBa}{(gAb + gBa)} \right| \quad (1)$$

in which gAb is the grooming that individual A directed towards B, gBa is the grooming that B directed towards A and $gAb + gBa$ is the total grooming exchanged between A and B. This index ranges from 0 (no reciprocity) to 1 (complete reciprocity). We constructed two LMMs, each with initial investment as the dependent variable, and with either grooming frequency or the reciprocity index (RI) as the fixed factor. As above, we included the identities of groomer and recipient as random factors in both models.

RESULTS

We analysed 377 bouts (39.9 h of grooming), collectively containing 14.5 h (52 210 s) of initial-phase grooming. Mean duration of grooming (\pm SD) was 138.5 ± 180.1 s (median = 80 s): 149.6 ± 191.3 s (median = 86 s) in unidirectional bouts (by definition, this is equal to the total bout) and 89.7 ± 98.8 s (median = 50.5 s) for the initial phase of bidirectional bouts. The initial phase of unidirectional bouts consisted on average of 2.3 ± 2.2 episodes (median = 2; range 1–19), 64.4 ± 55.7 s (median = 47 s) in duration. The initial phase of bidirectional bouts consisted on average of 1.8 ± 1.5 episodes (median = 1; range 1–8), 50.5 ± 57.5 s (median = 41.1 s) in duration. Only 6% of bouts were interrupted ($N = 24$), and the likelihood of interruption was not related to the number of male bystanders ($\beta \pm$ SE: 0.013 ± 0.147 , $Z = 0.092$, $P = 0.926$). Most grooming occurred in a resting context (73%), with fewer bouts occurring during mixed (18%), travelling (6%) or feeding (2%) contexts. Seventy per cent ($N = 263$) of bouts were initiated by lower-ranking towards higher-ranking males, and 75% of initial-phase grooming (10.9 h) was directed from subordinates to dominant partners (binomial test: $P < 0.001$). Furthermore, the dominance rank of recipients was on average significantly higher (mean Elo-rating: 2100) than that of the most dominant male among bystanders (mean Elo-rating: 1994; Mann–Whitney signed-rank test: $V = 34 914$, $P = 0.003$), suggesting that male chimpanzees tended to select the highest-ranking male available when initiating grooming.

Results of the mixed-model analyses testing predictions 1–8 are presented in full in Tables 2–4. Here, we provide a summary of key findings in relation to our predictions. A groomer's initial investment was significantly predicted by within-dyad rank distance ($P = 0.028$) supporting prediction 1: subordinates tended to invest more in the initial phase of a bout than did dominants, with this difference increasing with the rank distance between partners (Fig. 1). The number of male bystanders, however, did not predict the groomer's initial investment so we found no support for prediction 2. Similarly, neither context nor interruptions were significant influences on the level of initial investment. None of these

Table 2

Mixed-model analyses (LMM) showing the effect of number of male bystanders and rank distance on the duration of groomer's initial investment and parcel size

Dependent	Predictor	β	SE	t	P
Initial investment	Intercept	96.399	38.456	2.506	
	Rank distance	8.649	3.540	2.443	0.028
	No. of bystanders	-6.493	6.390	-1.016	0.344
	Context	24.533	16.751	1.465	0.127
	Interrupted	24.365	38.662	0.630	0.517
Parcel size	Intercept	56.138	13.109	4.282	
	Rank distance	-1.100	1.217	-0.904	0.426
	No. of bystanders	-3.508	1.988	-1.765	0.082
	Context	3.805	5.203	0.731	0.454
	Interrupted	22.031	12.179	1.809	0.077

Initial investment is defined as duration of grooming in the initial phase; parcel size is defined as the mean episode duration. Significant results are presented in bold.

Table 3

Mixed-model analyses (LMM) showing the effect of the highest-ranking bystander's rank, and the rank distance between this individual and the recipient, on both the groomer's initial investment and parcel size

Dependent	Predictor	β	SE	t	P
Initial investment	Intercept	37.370	40.191	0.930	
	Highest bystander rank	16.766	6.133	2.734	0.010
	Context	29.097	17.076	1.704	0.090
	Interrupted	20.658	41.134	0.502	0.654
Initial investment	Intercept	80.881	34.603	2.337	
	Rank distance	-11.168	3.927	-2.844	0.007
	Context	28.757	17.053	1.686	0.090
	Interrupted	31.822	41.052	0.775	0.437
Parcel size	Intercept	32.233	12.441	2.591	
	Highest bystander rank	4.707	1.797	2.620	0.010
	Context	5.867	5.121	1.146	0.252
	Interrupted	18.131	12.479	1.453	
Parcel size	Intercept	46.857	11.063	4.235	
	Rank distance	-1.238	1.384	-0.895	0.351
	Context	4.930	5.165	0.955	0.337
	Interrupted	19.386	12.572	1.542	0.133

Initial investment is defined as duration of grooming in the initial phase; parcel size is defined as the mean episode duration. Significant results are presented in bold.

factors affected parcel size, as measured by mean episode duration (Table 2). However, we did find that dominance rank of the highest ranking of the male bystanders predicted both initial investment ($P = 0.010$) and parcel size ($P = 0.010$; Fig. 2). Rank distance between this highest-ranking bystander and the current recipient of the grooming also significantly influenced initial investment ($P = 0.007$; Fig. 3), although it did not affect parcel size (Table 3). These results indicate that groomers tended to invest less in the initial phase through shorter episodes when at least one male bystander was of higher rank than the current recipient, and that

Table 4

Mixed-model analyses (GLMM) showing the effect of the number of male bystanders and rank distance on the occurrence of bidirectional bouts and on the identity of the individual who terminated the bout

Dependent	Predictor	β	SE	z	P
Occurrence of bidirectional bout	Intercept	0.439	0.824	0.532	
	Rank distance	-0.328	0.136	-2.418	0.016
	No. of bystanders	-0.266	0.108	-2.476	0.013
	Context	-0.007	0.278	-0.024	0.981
	Interrupted	0.801	0.544	1.472	0.141
Who terminates bout?	Intercept	-1.178	0.675	-1.746	
	Rank distance	-0.070	0.096	-0.722	0.470
	No. of bystanders	0.063	0.110	0.576	0.564
	Context	-0.254	0.272	-0.936	0.349
	Interrupted	0.299	0.677	0.442	0.658

Significant results are presented in bold.

this effect was stronger where the difference was greater, supporting predictions 3 and 4.

Both number of bystanders ($P = 0.013$; Fig. 4) and (absolute) rank distance ($P = 0.016$) predicted the occurrence of within-bout reciprocation: bidirectional bouts were more likely when grooming partners were similar in rank, and when there were fewer bystanders, supporting prediction 5 and prediction 6, respectively. We found no evidence that a groomer's decision to abandon a bout (resulting in a unidirectional bout) was influenced by the rank distance to the recipient or number of bystanders (Table 4). Thus, we did not find support for either prediction 7 or prediction 8. Finally, we found no support for prediction 9: initial investment was not predicted by grooming relationship history, taken either as frequency of bouts (LMM: $\beta \pm SE$: -42.91 ± 76.03 , $t = -0.564$, $P = 0.521$; mean \pm SD frequency of grooming per month = 0.14 ± 0.12 bouts/h of observation) or degree of reciprocity (LMM: $\beta \pm SE$: 9.618 ± 25.831 , $t = 0.372$, $P = 0.925$; mean \pm SD reciprocity index per month = 0.49 ± 0.38).

DISCUSSION

In the Sonso community, the presence of high-ranking bystanders and the total number of bystanders both appeared to generate incentives to defect from potentially cooperative interactions. The amount of grooming that adult male chimpanzees of this community were willing to invest at the beginning of a bout increased with the rank distance between groomer and recipient: the lower ranking a groomer was relative to his partner, the more he would groom in the initial phase. Unlike our previously reported finding from M-group (Kaburu & Newton-Fisher, 2016a), this investment was not influenced by the number of bystanders. It was, however, influenced by the presence of high-ranking bystanders: males provided less grooming in the initial phase when there was a high-ranking bystander, and when the difference between the rank of this bystander and the current recipient was greater. The number of bystanders was important in influencing whether an initial phase of grooming developed into a bidirectional bout, as these bouts were more likely when the number of bystanders was small, as well as when rank distances between groomer and recipient were small.

The extreme degree of structural despotism shown by the males of the Sonso community during this study appeared to have a strong influence on grooming investment strategies. Such conditions reflect marked rank differences and the degree to which rank-related commodities such as agonistic support or tolerance are restricted to high-ranked individuals. In contrast to our findings for the substantially more structurally egalitarian M-group, the influence of bystanders on the grooming strategies of Sonso community males was mediated by a strong effect of dominance rank. These communities were of comparable size (Sonso: 63 individuals; M-group: 60 individuals) with a similar number of adult males (Sonso: 8; M-group: 10), and data were collected using comparable paradigms and for similar periods (Sonso: 1109.5 h; M-group: 800.9 h, both over 9 months). The two communities differed, however, in the number of males aged between 20 and 30 years (Sonso: 3; M-group: 7), a demographic variable that predicts hierarchy steepness across chimpanzee communities (Kaburu & Newton-Fisher, 2015a). In structurally despotic societies, high-ranking individuals either control access to commodities that low ranking individuals desire, or have the ability to extort grooming from low-ranking individuals. The apparent attraction, real or forced, of such individuals as grooming partners for nonhuman primates is not surprising (Bygott, 1979; Schino, 2006; Seyfarth, 1977, 1980; Simpson, 1973). What is novel, however, is our demonstration that the rank of bystanders, relative to the rank of the current

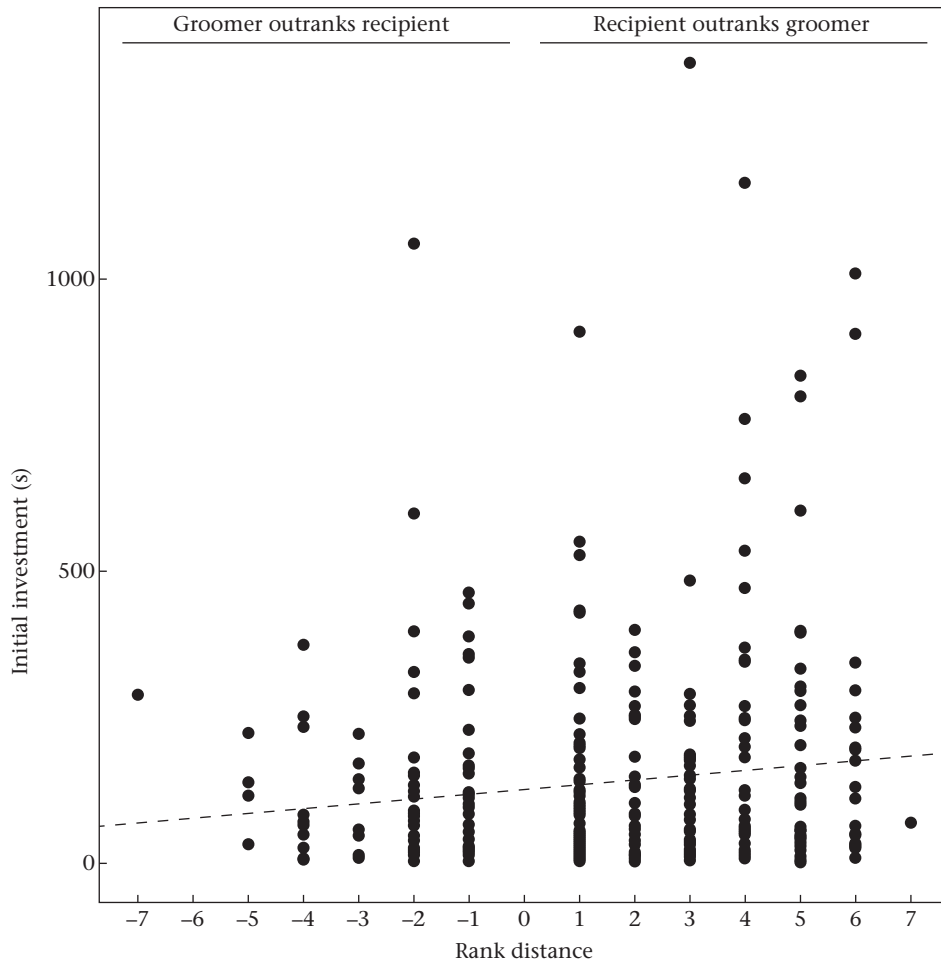


Figure 1. Relationship between rank distance (rank of groomer – rank of recipient) and initial investment (duration of grooming, s) in the bout by the groomer (the individual initiating the bout), prior to any response by the recipient. Data points represent individual grooming interactions. The dashed line is the relationship predicted by linear mixed modelling (Table 2).

partner, is taken into account when making grooming investment decisions, and furthermore that such rank considerations appear to be more important than the number of bystanders when structural despotism is high. We found that rank was less important in the more structurally egalitarian M-group, where it affected only the length of grooming episodes, and subordinates did not direct a greater proportion of their grooming towards dominants (Kaburu & Newton-Fisher, 2015a). Sensitivity to bystander ranks has been shown in agonistic decision making (e.g. Engh, Siebert, Greenberg, & Holekamp, 2005; Kitchen, Cheney, & Seyfarth, 2005; Perry, Manson, Muniz, Gros-Louis, & Vigilant, 2008; Silk, 1999; Slocombe & Zuberbuehler, 2007); here we showed this in an affiliative context. The importance of our results are: (1) that we demonstrated that an influence of bystanders on grooming decisions is generalizable across populations with differing dominance hierarchies and not an artefact of the egalitarian group structure in our previous study (Kaburu & Newton-Fisher, 2016a), and perhaps more importantly (2) that the nature of bystander influence differs in the manner predicted by biological markets theory. Given the broad reach of biological markets theory, these results have implications beyond our study species.

These findings strengthen our previous suggestion (Kaburu & Newton-Fisher, 2016a) that the spatially dispersed subgroups operate as local markets when it comes to grooming decisions: that is, the opportunity and search (or sampling) costs (Noë &

Hammerstein, 1994) associated with selecting social partners from other parties bias individuals to make decisions based on their immediate social environment. With high sampling costs, such local markets may become isolated, but whether they do so should depend on individuals weighting the potential gains from cooperating with a partner chosen from the current array against the expected average returns from the supply in the global market, devalued by sampling costs.

Our finding that bouts were more likely to be bidirectional, with the initiator's investment reciprocated to some degree, when the number of alternative partners was low suggests that the costs incurred by male chimpanzees searching for new partners in other parties must be relatively high, leading to strong discounting with decisions made largely on the basis of the current party composition. It also supports the hypothesis that male chimpanzees may form small parties to facilitate prolonged grooming interactions (the tactical association hypothesis: Newton-Fisher, 1999). Our finding that male chimpanzees evaluate both (1) their rank relative to the highest-ranking adult male bystander and (2) the rank of this individual relative to that of the current recipient of their grooming shows that they not only select a partner close at hand, but also appear to weigh their options from this current array of potential partners.

However, the fission–fusion dynamics in chimpanzee society allow individuals to leave current associates and subsequently

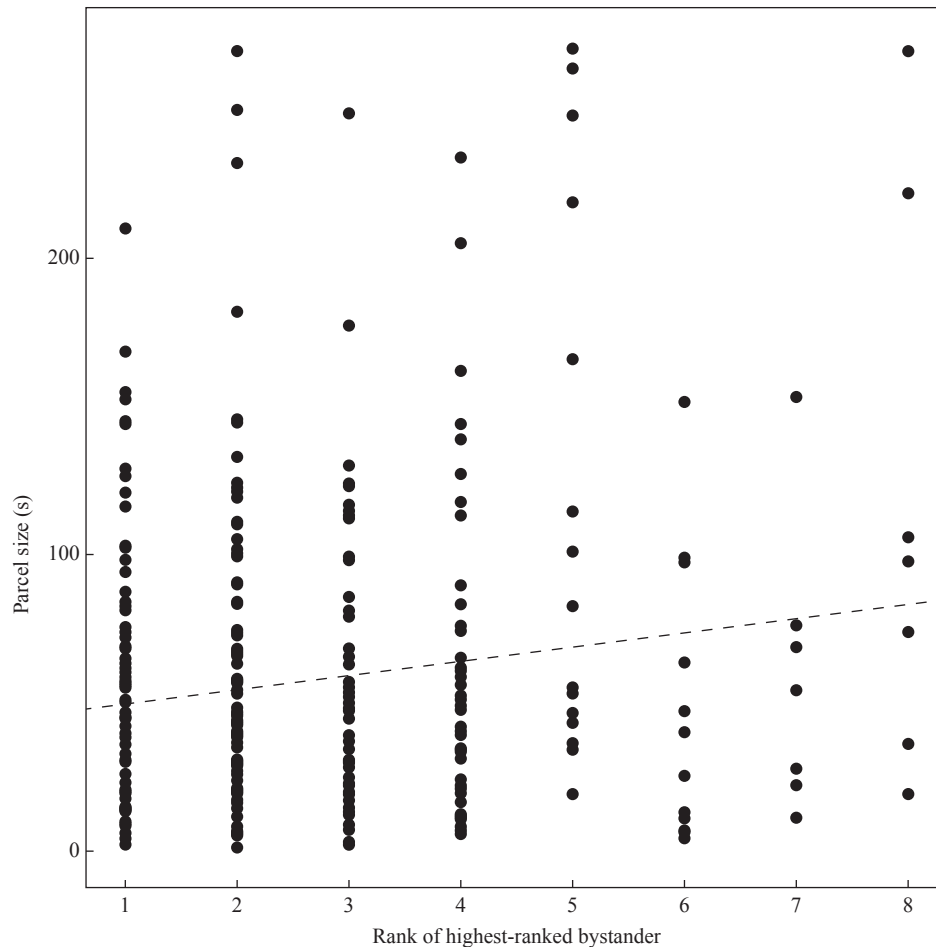


Figure 2. Relationship between the rank of the highest ranking of bystanders to a grooming bout and the size of grooming parcels (mean duration, s, across grooming episodes in the initial phase of the bout, prior to any response by the recipient). Data points represent individual grooming interactions. The dashed line is the relationship predicted by linear mixed modelling (Table 3).

interact with members of other parties. While cooperation is not the only reason individuals might seek new social environments, this flexibility to change associates might suggest that sampling costs related to selecting social partners are both variable and not necessarily prohibitive. The extent to which partner choice decisions are influenced by social opportunities elsewhere remains to be determined, as does the degree to which searching for other parties is costly for male chimpanzees, as well as how such costs are influenced by knowledge of the location of other individuals, for example from recent association, predictable ranging patterns (Murray, Gilby, Mane, & Pusey, 2008; Newton-Fisher, 2002a, 2000) or vocal signals (Mitani & Nishida, 1993).

While fission–fusion dynamics shown by chimpanzees provide an obvious opportunity to explore the concept of local markets, such market structuring should exist in other species (e.g. long-tailed macaques *Macaca fascicularis*: Gumert, 2007). Where social groupings are more cohesive, interindividual proximity may be an important factor in generating local market conditions within these groups. The relatively small effect of the number of bystanders for the chimpanzees in this study may have been due, in part, to the spatial arrangement of males within parties (Newton-Fisher, 1997) and considering interindividual distances, and the dynamics of these, will be an important refinement for future studies.

Our results also support the hypothesis that chimpanzees make use of a parcelling-like strategy in their grooming (Kaburu & Newton-Fisher, 2016a; Machanda et al., 2014), with grooming

investment in the initial phase varying in a manner consistent with the predictions of Connor's parcelling model (Connor, 1992; 1995a, 1995b, 2010). In parties containing an adult male who outranked both the groomer and recipient, the groomer reduced the length of episodes (parcel size) and initial investment as predicted by Connor's model. However, our predictions regarding the number of bystanders were not supported.

As might be expected given the level of structural despotism, the presence of a high-ranking male appeared to generate an incentive to defect from a potentially cooperative interaction (bouts were more likely to end without reciprocation in the presence of such individuals), while the presence of multiple lower-ranked males was not relevant to these grooming decisions (unfortunately, we were not able to determine whether groomers limited their investment to encourage reciprocation or to cut losses that they might incur). A possible alternative explanation is that shortening of episodes might, instead, have been an indication of increased vigilance, given that grooming potentially distracts animals from the presence of predators or aggressive group members (Maestripieri, 1993; Mooring & Hart, 1995). Male chimpanzees will disrupt grooming interactions, especially during periods of social instability (Nishida & Hosaka, 1996; de Waal, 1982), and we reported previously that male chimpanzees of M-group performed shorter grooming episodes during a period of social instability when aggression rates were high (Kaburu & Newton-Fisher, 2013). Increased vigilance may account for our finding that decreasing

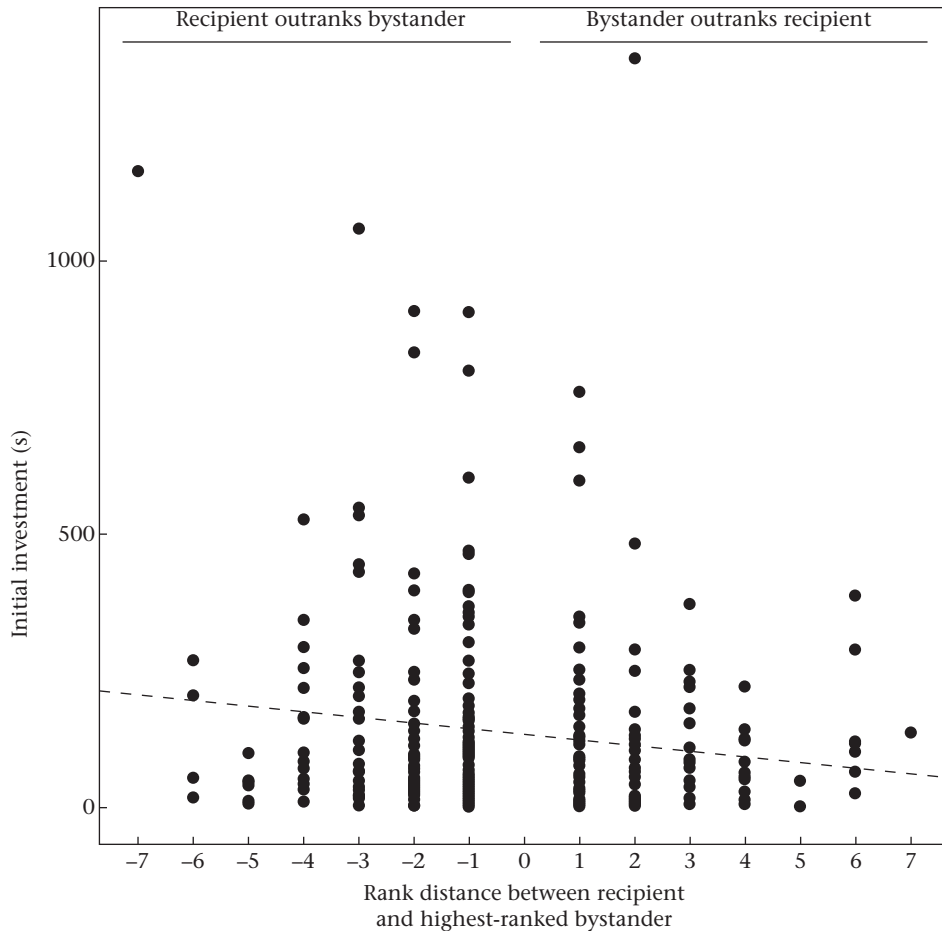


Figure 3. Influence of bystander rank relative to that of current recipient (rank of recipient – rank of highest ranked bystander) on the initial investment (duration of grooming, s) in the bout by the groomer (the individual initiating the bout), prior to any response by the recipient. Data points represent individual grooming interactions. The dashed line is the relationship predicted by linear mixed modelling (Table 3).

episode length was related to the absolute rank of the highest-ranked bystander but not to the difference in rank between this individual and the current recipient. It is evident that groomers were able to recognize and respond to this difference, as they adjusted their grooming effort accordingly.

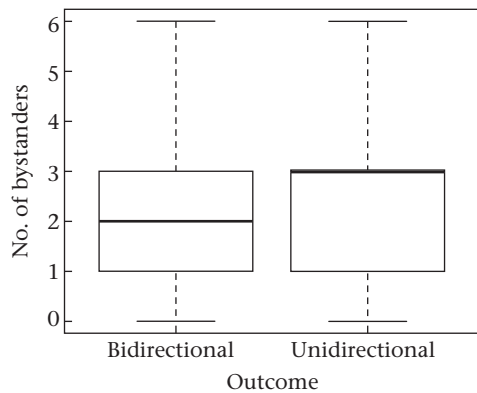


Figure 4. Influence of the number of bystanders on the outcome of the initial phase of grooming either a unidirectional bout, if the recipient does not participate, or bidirectional, if the recipient reciprocates grooming to some degree (Table 4). The thick bold line indicates the median, while the box represents 25th and 75th percentiles, with whiskers indicating the range.

That said, vigilance-against-aggression and parcelling-to-encourage-cooperation may be difficult to distinguish in practice, and may not be mutually exclusive: to determine risks of defection, a groomer needs to monitor the immediate social environment, i.e. be vigilant. If the necessary information is gained via the proxy of subgroup composition, and if both forms of risk are posed by high-ranking males, vigilant individuals inevitably gain information on the risks of both aggression and defection simultaneously (although we note that only 6% of grooming bouts in our data set were interrupted by aggression). Further work will need to establish the proximate drivers of vigilance, for example how this behaviour varies with changes in the composition of groups and in relation to variation in the aggressiveness of other party members. It may also be necessary to consider that partner choice decisions may be influenced by the possibility of reciprocity across grooming bouts (Newton-Fisher & Lee, 2011).

Considering cooperation across a series of interactions raises the notion of social relationships, so it is worth asking whether we can explain our results from a relationship model paradigm. If chimpanzees groom in order to form relationships that facilitate the coalitional behaviour that aids rank acquisition (Gilby et al., 2013; Nishida & Hosaka, 1996; de Waal, 1982), then they should prefer to form relationships with high-ranking individuals, as these males would provide the most effective support: this interpretation would match with our findings. However, given that males should compete to form such relationships, competitive exclusion should

result in a graded series of rank-matched relationships, with the most effective partner available being limited to a male of adjacent rank (cf. Seyfarth, 1977). That is, where there is competition for social partners, the relationship paradigm should predict supportive relationships between adjacently ranked individuals. While male chimpanzees do show enduring (multiyear) relationships characterized by highly reciprocal grooming (Gilby & Wrangham, 2008; Mitani, 2009b; Newton-Fisher & Lee, 2011), such dyads are not sorted strictly by rank. For example, Mitani (2009) showed that rank did not affect how enduring such relationships were, and while he reported that stronger grooming reciprocity existed between males of the same rank class, Newton-Fisher and Lee (2011) used individual level rankings to show that males close in social rank did not have more reciprocal grooming relationships. In addition, these relationships can persist over longer timescales than many shifts in social rank, which can change within as well as between years, and it seems difficult to reconcile grooming investment in particular social partners across multiple years with an effort to secure the most powerful coalition partners.

Furthermore, these enduring relationships may not be all they appear to be. In both our study of chimpanzees from the Mahale Mountains National Park (Kaburu & Newton-Fisher, 2016a) and in this study, we found no evidence that initial-phase grooming partner choice/control decisions were influenced by prior grooming history: the grooming male showed no evidence of trust that grooming would be reciprocated, even if that dyad had a prior history of strongly reciprocal grooming. Defined as a summary of a set of interactions, essentially, the interaction history, between particular individuals (Hinde, 1976), the term relationship in and of itself implies no functional consequence: it is descriptive and proximate. If interaction history does not influence grooming decisions, it seems unlikely that such relationships have much to do with building or exploiting trust.

Finally, it has also been argued (Boehm, 1999; Flack & de Waal, 2004; de Waal, 1996) that coalitional behaviour (facilitated by relationships according to the paradigm) between subordinate male chimpanzees serves to limit the despotism of the alpha male: if this is true, more or less any adult male should be an effective coalition partner, and attraction to high-ranked males as potential relationship (and thus coalition) partners would cease to be a prediction of the model, at least as applied to male chimpanzees.

Thus the rank effects that we report here are neither explicable by nor, in fact, should be predictions of the relationship model, as high-ranking bystanders should not generate temptations to defect from current social partners. On the other hand, under a model of direct economic exchange (e.g. grooming for agonistic support) low-ranking males can engage in out-bidding competition (as grooming is not rank restricted and can be provided by any individual) and so they are not excluded from gaining access to rank-restricted or rank-related commodities. In a structurally despotic society, high-ranking individuals should consistently generate temptations to defect from the current partner, which is precisely what we find. Our data on grooming decisions are not consistent with the trust-building, relationship model paradigm, but are consistent with a more direct economic benefit, markets-based, approach. That said, affiliative relationships, sometimes with strongly reciprocal grooming, are widely reported in nonhuman primates (Silk, Cheney, & Seyfarth, 2013). Explaining these remains a challenge for economic models, particularly where relationships form between unrelated individuals who are otherwise reproductive rivals, as among male chimpanzees (Newton-Fisher, 2014).

Overall, our data show that bystander effects and parcelling during the initiation phase of grooming bouts among male chimpanzees persist despite variation in the steepness of the dominance hierarchy, but that relative dominance rank (a marker of partner

quality) becomes more significant than the number of bystanders under structural despotism. Studies of cooperation across taxa will need to be mindful of both bystander effects, which may incorporate both number and quality of potential partners, and variation in these associated with the degree of structural despotism/egalitarianism. In addition, future tests of biological markets theory will need to allow for the existence of local markets, with more work necessary, in particular, on identifying and quantifying sampling costs and on examining the extent that local markets are isolated from, or embedded within, wider global marketplaces.

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References

- Akinyi, M. Y., Tung, J., Jeneby, M., Patel, N. B., Altmann, J., & Alberts, S. C. (2013). Role of grooming in reducing tick load in wild baboons (*Papio cynocephalus*). *Animal Behaviour*, 85(3), 559–568.
- Albers, P. C. H., & de Vries, H. (2001). Elo-rating as a tool in the sequential estimation of dominance strengths. *Animal Behaviour*, 61(2), 489–495.
- Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, 49(3), 227–266.
- Barrett, L., Henzi, S., Weingrill, T., Lycett, J., & Hill, R. (1999). Market forces predict grooming reciprocity in female baboons. *Proceedings of the Royal Society of London Series B- Biological Sciences*, 266(1420), 665–670.
- Barrett, L., Henzi, S., Weingrill, T., Lycett, J. E., & Hill, R. A. (2000). Female baboons do not raise the stakes but they give as good as they get. *Animal Behaviour*, 59(4), 763–770.
- Boccia, M. L., Reite, M., & Laudenslager, M. (1989). On the physiology of grooming in a pigtail macaque. *Physiology & Behavior*, 45(3), 667–670.
- Boehm, C. (1999). *Hierarchy in the forest*. Cambridge, MA: Harvard University Press.
- Boesch, C., Kohou, G., Néné, H., & Vigilant, L. (2006). Male competition and paternity in wild chimpanzees of the Tai forest. *American Journal of Physical Anthropology*, 130(1), 103–115.
- Bygott, J. D. (1979). Agonistic behaviour, dominance, and social structure in wild chimpanzees of the Gombe National Park. In D. A. Hamburg, & E. R. McCown (Eds.), *The great apes* (pp. 405–427). Menlo Park, CA: Benjamin/Cummings.
- Carter, G., & Leffer, L. (2015). Social grooming in bats: Are vampire bats exceptional? *PLoS One*, 10(10), e0138430.
- Clutton-Brock, T. H. (2009). Cooperation between non-kin in animal societies. *Nature*, 461(7269), 51–57.
- Clutton-Brock, T. H., & Parker, G. A. (1995). Punishment in animal societies. *Nature*, 373(6511), 209–216.
- Connor, R. C. (1992). Egg-trading in simultaneous hermaphrodites: An alternative to Tit-for-Tat. *Journal of Evolutionary Biology*, 5(3), 523–528.
- Connor, R. C. (1995a). Altruism among non-relatives: Alternatives to the 'Prisoner's Dilemma'. *Trends in Ecology & Evolution*, 10(2), 84–86.
- Connor, R. C. (1995b). Impala allogrooming and the parcelling model of reciprocity. *Animal Behaviour*, 49(2), 528–530.
- Connor, R. C. (2007). Dolphin social intelligence: Complex alliance relationships in bottlenose dolphins and a consideration of selective environments for extreme brain size evolution in mammals. *Philosophical Transactions of the Royal Society of London Series B- Biological Sciences*, 362(1480), 587–602.
- Connor, R. C. (2010). Cooperation beyond the dyad: On simple models and a complex society. *Philosophical Transactions of the Royal Society London Series B- Biological Sciences*, 365(1553), 2687–2697.
- Dunbar, R. I. M. (1988). *Primate social systems*. London, U.K.: Croom Helm.
- Dunbar, R. I. M. (1991). Functional significance of social grooming in primates. *Folia Primatologica*, 57, 121–131.
- Dunbar, R. I. M. (1992). Time: A hidden constraint on the behavioural ecology of baboons. *Behavioral Ecology and Sociobiology*, 31(1), 35–49.
- Emery Thompson, M., Newton-Fisher, N. E., & Reynolds, V. (2006). Probable community transfer of parous adult female chimpanzees in the Budongo Forest, Uganda. *International Journal of Primatology*, 27(6), 1601–1617.
- Engh, A. L., Siebert, E. R., Greenberg, D. A., & Holekamp, K. E. (2005). Patterns of alliance formation and postconflict aggression indicate spotted hyenas recognize third-party relationships. *Animal Behaviour*, 69(1), 209–217.

- Flack, J. C., & de Waal, F. B. M. (2004). Dominance style, social power and conflict management: A conceptual framework. In B. Thierry, M. Singh, & W. Kaumanns (Eds.), *Macaque societies: A model for the study of social organisation* (pp. 157–182). New York, NY: Cambridge University Press.
- Frank, R. E., & Silk, J. B. (2009). Impatient traders or contingent reciprocators? Evidence for the extended time-course of grooming exchanges in baboons. *Behaviour*, 146, 1123–1135.
- Friedman, J. W., & Hammerstein, P. (1991). To trade, or not to trade; that is the question. In R. Selten (Ed.), *Game equilibrium models I* (pp. 257–275). Berlin, Germany: Springer.
- Fruteau, Lemoine, Hellard, & Noe. (2011). When females trade grooming for grooming: Testing partner control and partner choice models of cooperation in two primate species. *Animal Behaviour*, 81(6), 1223–1230.
- Fruteau, C., Voelkl, B., van Damme, E., & Noë, R. (2009). Supply and demand determine the market value of food providers in wild vervet monkeys. *Proceedings of the National Academy of Sciences of the United States of America*, 106(29), 12007–12012.
- Gilby, I. C., Brent, L. J. N., Wroblewski, E. E., Rudicell, R. S., Hahn, B. H., Goodall, J., et al. (2013). Fitness benefits of coalitional aggression in male chimpanzees. *Behavioral Ecology and Sociobiology*, 67(3), 373–381.
- Gilby, I. C., & Wrangham, R. W. (2008). Association patterns among wild chimpanzees (*Pan troglodytes schweinfurthii*) reflect sex differences in cooperation. *Behavioral Ecology and Sociobiology*, 62(11), 1831–1842.
- Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behaviour*. Cambridge, MA: Belknap Press.
- Gumert, M. D. (2007). Payment for sex in a macaque mating market. *Animal Behaviour*, 74, 1655–1667.
- Halperin, S. D. (1979). Temporary association patterns in free ranging chimpanzees. In D. A. Hamburg, & E. R. McCown (Eds.), *The great apes* (pp. 491–500). Menlo Park, CA: Benjamin/Cummings.
- Hammerstein, P., & Noë, R. (2016). Biological trade and markets. *Philosophical Transactions of the Royal Society London Series B- Biological Sciences*, 371(1687), 20150101.
- Hayaki, H., Huffman, M. A., & Nishida, T. (1989). Dominance among male chimpanzees in the Mahale Mountains National Park, Tanzania: A preliminary study. *Primates; Journal of Primatology*, 30, 187–197.
- Hemelrijk, C. K., & Ek, A. (1991). Reciprocity and interchange of grooming and support in captive chimpanzees. *Animal Behaviour*, 41, 923–935.
- Henzi, S., & Barrett, L. (1999). The value of grooming to female primates. *Primates; Journal of Primatology*, 40(1), 47–59.
- Hinde, R. A. (1976). Interactions, relationships and social structure. *Man*, 11(1), 1–17.
- Inoue, E., Inoue-Murayama, M., Vigilant, L., Takenaka, O., & Nishida, T. (2008). Relatedness in wild chimpanzees: Influence of paternity, male philopatry, and demographic factors. *Yearbook of Physical Anthropology*, 137(3), 256–262.
- Jensen, K., Call, J., & Tomasello, M. (2007). Chimpanzees are vengeful but not spiteful. *Proceedings of the National Academy of Sciences of the United States of America*, 104(32), 13046–13050.
- Kaburu, S. S. K., Inoue, S., & Newton-Fisher, N. E. (2013). Death of the alpha: Within-community lethal violence among chimpanzees of the Mahale Mountains National Park. *American Journal of Primatology*, 75(8), 789–797.
- Kaburu, S. S. K., & Newton-Fisher, N. E. (2013). Social instability raises the stakes during social grooming among wild male chimpanzees. *Animal Behaviour*, 86(3), 519–527.
- Kaburu, S. S. K., & Newton-Fisher, N. E. (2015a). Egalitarian despots: Hierarchy steepness, reciprocity and the grooming-trade model in wild chimpanzees, *Pan troglodytes*. *Animal Behaviour*, 99, 61–71.
- Kaburu, S. S. K., & Newton-Fisher, N. E. (2015b). Trading or coercion? Variation in male mating strategies between two communities of East African chimpanzees. *Behavioral Ecology and Sociobiology*, 69(6), 1039–1052.
- Kaburu, S. S. K., & Newton-Fisher, N. E. (2016a). Bystanders, parcelling, and an absence of trust in the grooming interactions of wild male chimpanzees. *Scientific Reports*, 6, 20634.
- Kaburu, S. S. K., & Newton-Fisher, N. E. (2016b). Markets misinterpreted? A comment on Sanchez-Amaro and Amici (2015). *Animal Behaviour*, 119, E1–E5.
- Kitchen, D. M., Cheney, D. L., & Seyfarth, R. M. (2005). Contextual factors mediating contests between male chacma baboons in Botswana: Effects of food, friends and females. *International Journal of Primatology*, 26(1), 105–125.
- Kutsukake, N., & Clutton-Brock, T. H. (2010). Grooming and the value of social relationships in cooperatively breeding meerkats. *Animal Behaviour*, 79(2), 271–279.
- Langergraber, K. E., Mitani, J. C., & Vigilant, L. (2007). The limited impact of kinship on cooperation in wild chimpanzees. *Proceedings of the National Academy of Sciences of the United States of America*, 104(19), 7786–7790.
- Machanda, Z. P., Gilby, I. C., & Wrangham, R. W. (2014). Mutual grooming among adult male chimpanzees: The immediate investment hypothesis. *Animal Behaviour*, 87, 165–174.
- Maestriperri, D. (1993). Vigilance costs of allogrooming in macaque mothers. *American Naturalist*, 141(5), 744–753.
- Manson, J. H., Navarrete, C. D., Silk, J. B., & Perry, S. (2004). Time-matched grooming in female primates? New analyses from two species. *Animal Behaviour*, 67(3), 493–500.
- McFarland, R., Henzi, S., Barrett, L., Wanigaratne, A., Coetzee, E., Fuller, A., et al. (2015). Thermal consequences of increased pelt loft infer an additional utilitarian function for grooming. *American Journal of Primatology*, 78(4), 456–461.
- Mitani, J. C. (2009a). Cooperation and competition in Chimpanzees: Current understanding and future challenges. *Evolutionary Anthropology*, 18(5), 215–227.
- Mitani, J. C. (2009b). Male chimpanzees form enduring and equitable social bonds. *Animal Behaviour*, 77(3), 633–640.
- Mitani, J. C., & Nishida, T. (1993). Contexts and social correlates of long-distance calling by male chimpanzees. *Animal Behaviour*, 45, 735–746.
- Mooring, M. S., & Blumstein, D. T. (2004). The evolution of parasite-defence grooming in ungulates. *Biological Journal of the Linnean Society*, 81, 17–37.
- Mooring, M. S., & Hart, B. L. (1995). Costs of allogrooming in impala: Distraction from vigilance. *Animal Behaviour*, 49(5), 1414–1416.
- Mulder, R. A., & Langmore, N. E. (1993). Dominant males punish helpers for temporary defection in superb fairy-wrens. *Animal Behaviour*, 45(4), 830–833.
- Muller, M. N., & Wrangham, R. W. (2004). Dominance, cortisol and stress in wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behavioral Ecology and Sociobiology*, 55(4), 332–340.
- Murray, C. M., Gilby, I. C., Mane, S. V., & Pusey, A. E. (2008). Adult male chimpanzees inherit maternal ranging patterns. *Current Biology*, 18(1), 20–24.
- Nakamura, M. (2000). Is human conversation more efficient than chimpanzee grooming? Comparison of clique sizes. *Human Nature*, 11(3), 281–297.
- Neumann, C., Dubocq, J., Dubuc, C., Ginting, A., Irwan, A. M., Agil, M., et al. (2011). Assessing dominance hierarchies: Validation and advantages of progressive evaluation with elo-rating. *Animal Behaviour*, 82(4), 911–921.
- Newton-Fisher, N. E. (n.d.) [Data set of social interactions among Sonso community chimpanzees]. Unpublished raw data.
- Newton-Fisher, N. E. (1997). *Tactical behaviour and decision making in wild chimpanzees* [PhD thesis]. Cambridge, U.K.: University of Cambridge.
- Newton-Fisher, N. E. (1999). Association by male chimpanzees: A social tactic? *Behaviour*, 136, 705–730.
- Newton-Fisher, N. E. (2000). Male core areas: Ranging by Budongo forest chimpanzees. *Pan Africa News*, 7(1), 10–12.
- Newton-Fisher, N. E. (2002a). Ranging patterns of male chimpanzees in the Budongo forest: Range structure and individual differences. In C. S. Harcourt, & B. R. Sherwood (Eds.), *New perspectives in primate evolution and behaviour* (pp. 287–308). Otley, U.K.: Westbury Scientific Publishing.
- Newton-Fisher, N. E. (2002b). Relationships of male chimpanzees in the Budongo Forest, Uganda. In C. Boesch, G. Hohmann, & L. F. Marchant (Eds.), *Behavioural diversity in chimpanzees and bonobos* (pp. 124–137). Cambridge, U.K.: Cambridge University Press.
- Newton-Fisher, N. E. (2004). Hierarchy and social status in Budongo chimpanzees. *Primates; Journal of Primatology*, 45, 81–87.
- Newton-Fisher, N. E. (2014). Roving females and patient males: A new perspective on the mating strategies of chimpanzees. *Biological Reviews of the Cambridge Philosophical Society*, 89(2), 356–374.
- Newton-Fisher, N. E. (2017). Modelling social dominance: Elo-ratings, prior history, and the intensity of aggression. *International Journal of Primatology*. <http://dx.doi.org/10.1007/s10764-017-9952-2>.
- Newton-Fisher, N. E., Emery-Thompson, M., Reynolds, V., Boesch, C., & Vigilant, L. (2010). Paternity and social rank in wild chimpanzees (*Pan troglodytes*) from the Budongo forest, Uganda. *American Journal of Physical Anthropology*, 142(3), 417–428.
- Newton-Fisher, N. E., & Lee, P. C. (2011). Grooming reciprocity in wild male chimpanzees. *Animal Behaviour*, 81(2), 439–446.
- Nishida, T. (1988). Development of social grooming between mother and offspring in wild chimpanzees. *Folia Primatologica*, 50, 109–123.
- Nishida, T. (2011). *Chimpanzees of the Lakeshore*. Cambridge, U.K.: Cambridge University Press.
- Nishida, T., & Hosaka, K. (1996). Coalition strategies among adult male chimpanzees of the Mahale Mountains, Tanzania. In W. C. McGrew, L. F. Marchant, & T. Nishida (Eds.), *Great ape societies* (pp. 114–134). Cambridge, U.K.: Cambridge University Press.
- Noë, R., & Hammerstein, P. (1994). Biological markets: Supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behavioral Ecology and Sociobiology*, 35(1), 1–11.
- Noë, R., & Hammerstein, P. (1995). Biological markets. *Trends in Ecology & Evolution*, 10(8), 336–340.
- Noë, R., van Schaik, C. P., & van Hooft, J. A. R. A. M. (1991). The market effect: An explanation for pay-off asymmetries among collaborating animals. *Ethology*, 87(1–2), 97–118.
- Perry, S., Manson, J. H., Muniz, L., Gros-Louis, J., & Vigilant, L. (2008). Kin-biased social behaviour in wild adult female white-faced capuchins, *Cebus capucinus*. *Animal Behaviour*, 76(1), 187–199.
- Radford, A. N. (2012). Post-allogrooming reductions in self-directed behaviour are affected by role and status in the green woodhoopoe. *Biology Letters*, 8, 24–27.
- Reynolds, V. (2005). *The Chimpanzees of the Budongo Forest*. Oxford, U.K.: Oxford University Press.
- Roberts, G., & Sherratt, T. N. (1998). Development of cooperative relationships through increasing investment. *Nature*, 394(6689), 175–179.
- Russell, Y. I., & Phelps, S. (2013). How do you measure pleasure? A discussion about intrinsic costs and benefits in primate allogrooming. *Biology & Philosophy*, 28(6), 1005–1020.
- Sanchez-Amaro, A., & Amici, F. (2015). Are primates out of the market? *Animal Behaviour*, 110, 51–60.
- Schino, G. (2006). Grooming and agonistic support: A meta-analysis of primate reciprocal altruism. *Behavioral Ecology*, 18(1), 115–120.
- Schino, G., & Alessandrini, A. (2015). Short-term costs and benefits of grooming in Japanese macaques. *Primates*, 56(3), 253–257.
- Seyfarth, R. M. (1977). A model of social grooming among female monkeys. *Journal of Theoretical Biology*, 65(4), 671–698.

- Seyfarth, R. M. (1980). The distribution of grooming and related behaviours among adult female vervet monkeys. *Animal Behaviour*, 28(3), 798–813.
- Shutt, K., MacLarnon, A., Heistermann, M., & Semple, S. (2007). Grooming in Barbary macaques: Better to give than to receive? *Biology Letters*, 3(3), 231–233.
- Silk, J. B. (1999). Male bonnet macaques use information about third-party rank relationships to recruit allies. *Animal Behaviour*, 58(1), 45–51.
- Silk, J. B., Alberts, S. C., & Altmann, J. (2003). Social bonds of female baboons enhance infant survival. *Science*, 302(5648), 1231–1234.
- Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., et al. (2010). Female chacma baboons form strong, equitable, and enduring social bonds. *Behavioral Ecology and Sociobiology*, 64(11), 1733–1747.
- Silk, J., Cheney, D., & Seyfarth, R. (2013). A practical guide to the study of social relationships. *Evolutionary Anthropology*, 22(5), 213–225.
- Simpson, M. J. A. (1973). The social grooming of male chimpanzees. In R. P. Michael, & J. H. Crook (Eds.), *Comparative ecology and behavior of primates* (pp. 411–506). London, U.K.: Academic Press.
- Slocombe, K. E., & Zuberbuehler, K. (2007). Chimpanzees modify recruitment screams as a function of audience composition. *Proceedings of the National Academy of Sciences of the United States of America*, 104(43), 17228–17233.
- Smith, J. E., Memenis, S. K., & Holekamp, K. E. (2007). Rank-related partner choice in the fission-fusion society of the spotted hyena (*Crocuta crocuta*). *Behavioral Ecology and Sociobiology*, 61(5), 753–765.
- Stopka, P., & Macdonald, D. W. (1999). The market effect in the wood mouse, *Apodemus sylvaticus*: Selling information on reproductive status. *Ethology*, 105(11), 969–982.
- Tiddi, B., Aureli, F., di Sorrentino, E. P., & Janson, C. H. (2011). Grooming for tolerance? Two mechanisms of exchange in wild tufted capuchin monkeys. *Behavioral Ecology*, 22, 663–669.
- Vigilant, L., Hofreiter, M., Siedel, H., & Boesch, C. (2001). Paternity and relatedness in wild chimpanzee communities. *Proceedings of the National Academy of Sciences of the United States of America*, 98(23), 12890–12895.
- de Waal, F. B. M. (1982). *Chimpanzee politics*. New York, NY: Harper and Row.
- de Waal, F. B. M. (1996). *Good natured*. Cambridge, MA: Harvard University Press.
- de Waal, F. B. M. (1997). The chimpanzee's service economy: Food for grooming. *Evolution and Human Behavior*, 18(6), 375–386.
- Watts, D. P. (2000). Grooming between male chimpanzees at Ngogo, Kibale National Park. I. Partner number and diversity and grooming reciprocity. *International Journal of Primatology*, 21(2), 189–210.
- Watts, D. P. (2002). Reciprocity and interchange in the social relationships of wild male chimpanzees. *Behaviour*, 139(2), 343–370.
- Wei, W., Qi, X.-G., Guo, S.-T., Zhao, D.-P., Zhang, P., Huang, K., et al. (2012). Market powers predict reciprocal grooming in golden snub-nosed monkeys (*Rhinopithecus roxellana*). *PLoS One*, 7(5), e36802.
- West, S. A., & Gardner, A. (2013). Adaptation and inclusive fitness. *Current Biology*, 23(13), R577–R584.
- West, S. A., Griffin, A. S., & Gardner, A. (2007). Evolutionary explanations for cooperation. *Current Biology*, 17(16), R661–R672.
- Wrangham, R. W., & Smuts, B. B. (1980). Sex differences in the behavioural ecology of chimpanzees in the Gombe National Park, Tanzania. *Journal of Reproduction and Fertility, Supplement*, 28, 13–31.
- Wroblewski, E. E., Murray, C. M., Keele, B. F., Schumacher-Stankey, J. C., Hahn, B. H., & Pusey, A. E. (2009). Male dominance rank and reproductive success in chimpanzees, *Pan troglodytes schweinfurthii*. *Animal Behaviour*, 77(4), 873–885.
- Wubs, M., Bshary, R., & Lehmann, L. (2016). Coevolution between positive reciprocity, punishment, and partner switching in repeated interactions. *Proceedings of the Royal Society of London Series B- Biological Sciences*, 283(1832), 20160488.
- Zamma, K. (2002). Grooming site preferences determined by lice infection among Japanese Macaques in Arashiyama. *Primates*, 43(1), 41–49.