

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/269771102>

Social preferences influence the short-term exchange of social grooming among male bonobos

Article in *Animal Cognition* · December 2014

DOI: 10.1007/s10071-014-0826-0 · Source: PubMed

CITATIONS

14

READS

216

2 authors, including:



[Martin Surbeck](#)

Harvard University

49 PUBLICATIONS 1,518 CITATIONS

SEE PROFILE

Some of the authors of this publication are also working on these related projects:



Social cognition in chimpanzees and bonobos. [View project](#)

Social preferences influence the short-term exchange of social grooming among male bonobos

Martin Surbeck · Gottfried Hohmann

Received: 22 August 2014/Revised: 31 October 2014/Accepted: 9 December 2014/Published online: 18 December 2014
© Springer-Verlag Berlin Heidelberg 2014

Abstract The emotional mediation hypothesis proposes a mediating role of social bonds in the exchange of services. This model predicts that the form of short-term exchange of services depends on the relationship between the individuals involved. Here, we test this prediction in the exchange of grooming among males in a wild bonobo community for which close relatedness could be excluded. As bonobo males hardly engage in food sharing or agonistic support, grooming is mainly exchanged for grooming. While overall grooming, both given and received, correlates across dyads and within sessions, the form of grooming exchange within a given session differs according to dyadic association preferences. Individuals with a higher tendency to associate, ergo more familiar individuals, exhibit larger time differences and reduced reciprocation in consecutive grooming bouts than less familiar individuals. These results support the idea that emotional components are involved in the exchange of services between unrelated individuals.

Keywords Social bonds · Emotional mediation hypothesis · Reciprocity · Short-term contingency · Tit-for-tat · Grooming · Primates, great apes · *Pan paniscus* · Altruism · Biological market

Introduction

A potential mechanism that underlies cooperation among unrelated individuals is reciprocity, according to which the role of actor and recipient of altruistic behavior is reciprocated over time so that both partners ultimately obtain fitness benefits (Trivers 1971). Models explaining the form of exchange of altruistic behavior can be broadly categorized into partner control and partner choice models. While they relate to different aspects of reciprocal altruism, partner control models focus on mechanisms minimizing the risk of exploitation within a given dyad (e.g., parceling: Connor 1995; raising the stakes: Roberts and Sherratt 1998), and partner choice models emphasize the individuals choice among several potential partners, inducing competition among them (Fruteau et al. 2009). One example is biological market theory, according to which exchange of services follows the law of supply and demand (Noë and Hammerstein 1995). Overall, the primate literature suggests that different altruistic behaviors can be exchanged for each other such as grooming for support (Schino 2007) or grooming for food or tolerance at food source (Barrett et al. 2002; de Waal 1997). Evidence for reciprocation of services is based in most cases on an association of services given and received across dyads over extended time periods (e.g., Jaeggi and Schaik 2011). However, open questions remain concerning the underlying mechanisms of the observed patterns (Clutton-Brock 2009).

De Waal (2000) proposed three proximate mechanisms (ordered by increasing cognitive requirements) involved in the exchange of services between individuals which could explain an overall relationship across dyads between services given and received: Firstly, symmetry-based reciprocity, where exchange between individuals is based on

Electronic supplementary material The online version of this article (doi:10.1007/s10071-014-0826-0) contains supplementary material, which is available to authorized users.

M. Surbeck (✉) · G. Hohmann
Max Planck Institute for Evolutionary Anthropology,
Leipzig, Germany
e-mail: surbeck@eva.mpg.de

symmetrical features such as kinship or mutual associations, making both partners react in a similar way to each other. While this mechanism would lead to an overall relationship between services given and received, its evolutionary stability has been questioned (Schino and Aureli 2010). Secondly, attitudinal reciprocity in which a behavior is influenced by the attitude of partners in the recent past and in which services provided are contingent to a certain degree on preceding behavior. Thirdly, calculated reciprocity based on score-keeping in which individuals account for all exchanged services within dyads.

Additionally, the emotional mediation hypothesis by Aureli and Schaffner (2002) proposes a mediating role of social bonds in the exchange of services and in partner choice. It states that emotions associated with different social partners allow for bookkeeping of social interactions, and decisions are made on the basis of emotions toward specific partners (Tooby and Cosmides 2008). Due to stronger emotional connections, close individuals are expected to be more tolerant of short-term imbalances in the exchange of services, and therefore, immediate reciprocation is expected to be more common in dyads having weaker social associations (Jaeggi et al. 2013; Schino and Aureli 2009). Some indications for this phenomenon come from a study of captive chimpanzees where food getting success upon grooming a partner was more pronounced in dyads where overall little grooming occurred (de Waal 1997), from a study of captive brown capuchins where spontaneous altruism increased with social closeness (de Waal et al. 2008) and from the finding that short-term reciprocation is stronger in less closely bonded dyads among baboons (Cheney et al. 2010). Overall, data on the link between the relationship of unrelated individuals and their form of short-term exchange in the wild are rare.

The aim of this study was to test for the proposed link between the form of short-term reciprocation and social relationship quality across different unrelated dyads by measuring the exchange of grooming between wild male philopatric bonobos (*Pan paniscus*). Grooming is regarded as a service given by one individual which confers benefits to the recipient in terms of hygiene and possible calming effects (de Waal 1997). While affiliative behaviors are more frequent among female–female and mixed-sex dyads (Hohmann et al. 1999), there are reasons why grooming between bonobo males are well suited for this undertaking: Firstly, they neither support each other regularly in agonistic conflicts, nor do they share food or engage in other behaviors that have been shown to be exchanged for grooming in other species (Ihobe 1992). Consequently although rare events between males, grooming is likely exchanged mainly for grooming. Secondly, while many studies have investigated the overall reciprocation of grooming across dyads (e.g., Schino and Aureli 2008),

bonobos engage in grooming sessions in which partners often take turns, allowing for the study of short-term exchanges.

First, we test for an overall correlation between grooming, both given and received. This we do both on an overall level across dyads of unrelated males using all grooming sessions and at the level of single sessions where both participants take turns. Second, we test the prediction of the emotional mediation hypothesis that the relationship between participants, as assessed by association patterns, is linked to the short-term exchanges within all grooming sessions.

Methods

Ethics statement

Permits to conduct research at LuiKotale in Salonga National Park, Democratic Republic of Congo were granted by the Institut Congolais pour la Conservation de la Nature in Kinshasa, Democratic Republic of Congo.

Behavioral data

Behavioral data were collected during party follows from May 2007 to July 2009 at LuiKotale near Salonga National Park, DRC. During this time, 5 adult and 4 subadult males, 11 parous and up to five nulliparous immigrant females resided in the habituated Bompusa bonobo community. For all but two male dyads, it could be excluded that they were siblings, half-siblings or parent–offspring (Schubert et al. 2013). For the remaining two dyads, maternal relatedness could be confirmed in one case and is strongly suspected in the other case due to their very strong association pattern.

We preferentially followed parties containing males and recorded the identity of the bonobos within each 1-h segment (Hashimoto et al. 2001). While following parties, grooming between individuals was recorded ad libitum. Whenever the start of a dyadic grooming interaction was observed, all switches and mutual grooming events were recorded. Because grooming often happens in several dyads at the same time and we only focused on a single dyad, the observed grooming frequencies are underestimating the actual occurrence frequency of this behavior. A grooming session was defined as a dyadic grooming interaction, which ended when neither of the two partners groomed the other for 5 min. A unidirectional grooming session was scored if no switches between groomer and groomee occurred within one session, while a bidirectional session consisted of both partners grooming the other during one session. A bout was defined as the part of a grooming session consisting of continuous grooming given

from one individual and ended if this individual's hand lost contact with the partner for 15 s.

Behavioral measures

Dyadic association

In fission–fusion societies, social preferences of individuals can be reflected in the grouping patterns among the individuals (Langergraber et al. 2007). In order to quantify the strength of association between individuals, we calculated a pairwise affinity index (PAI) based on the preferences of individuals to range in the same party. We calculated the PAI for male dyads based on the hourly party compositions according to Langergraber et al. (2007): we first calculated the observed simple ratio index of a given dyad (SRI_{obs}) and then subtracted the expected simple ratio value of this dyad (SRI_{exp}) as derived by randomization considering individual differences in gregariousness and observation time. We z-transformed the values to a mean of 0 and a standard deviation of 1.

We calculated $SRI_{obs} = Pa(AB)/(Pa(A) + Pa(B) - Pa(AB))$, with $Pa(AB)$ = number of parties containing both A and B, $Pa(A)$ = number of parties containing A, and $Pa(B)$ = number of parties containing B.

The randomization procedure assigned for each observation of a given individual the observed number of party members by randomly drawing individuals with a probability corresponding to their overall frequency of appearance in the whole data set. Such a randomization keeps both the gregariousness of a given individual and its observation frequency constant. The results of this randomization procedure are highly correlated with the results from another randomization which keeps constant both the total duration and temporal autocorrelation in an individual's party attendance and the frequency distribution of the duration of its party attendances. The dyadic SRI_{exp} was the mean SRI value of 1,000 of such randomizations (for further details, see Surbeck et al. 2011).

Association patterns can change over time, but because PAIs calculated separately for the first and the second half of the study period strongly correlated (Mantel test with Spearman rho as test statistics: $\rho = 0.81$, $N = 9$, $p < 0.001$), we used a PAI calculated from the overall study period.

Form of grooming exchange within sessions

Overall, we consider each grooming session a 'natural experiment' of exchange for any given dyad. In order to quantify the exchange of grooming, we used the absolute time difference between consecutive grooming bouts. We calculated the mean absolute time differences between

consecutive grooming bouts within a session with alternating groomers and averaged these differences over all sessions for a given dyad (mean difference between bouts, MDE). The higher this value, the larger the time difference between consecutive bouts of giving and receiving for an individual within a given dyad. Mutual grooming was considered as simultaneous grooming by both partners and has no influence on the time difference between given and received during a grooming session.

To test for a possible function of grooming as a reconciliatory behavior, we correlated dyadic grooming and aggression frequencies using Spearman's rank correlation.

Data analysis using generalized linear mixed models (GLMM)

Test for an overall correlation between grooming given and received across dyads

To analyze whether overall grooming given correlates with grooming received across dyads, we ran a GLMM on all completely recorded grooming sessions between males. We used the total grooming received within a dyad as a response variable. As test variable, we included grooming given within a dyad. To account for individual differences, we controlled for identity of both partners within a dyad (individual A and individual B) by including them separately as random effects. Since individual A and individual B were randomly chosen within a dyad, we ran the model 1,000 times while randomly assigning the individuals within a dyad to be either individual A or B, and averaged the results. To control for the possibility that some dyads contributed more to the data set than others due to opportunistic sampling, we divided the grooming given by the number of grooming sessions (to control for possible bias in the test variable) and included the number of grooming sessions as an offset variable (to control for possible bias in the response variable). The model was fitted in R using the package lme4 with a Poisson error distribution and loglink as the link function. We tested for model stability by excluding dyads one by one. This revealed robust results (See electronic supplementary material).

Test for within-session correlation between grooming given and received

To analyze whether grooming given within bidirectional sessions correlates with grooming received, we ran a GLMM with the grooming given within a bout as response variable and grooming received in the preceding bout as test variable. In order to be able to distinguish whether a within-session correlation of grooming given and received was due to the effects of a correlation between consecutive

bouts (tit-for-tat) or to an overall relationship between the averages of bouts given and received within a session, we did within-subject centering of the test variable (van de Pol and Wright 2009). Thus, we included the test variable grooming received in two different terms: once as the means of grooming received per bout within a session and secondly as the difference of the previous bout from the mean of all bouts except the last within a given session. We controlled for the identity of the giver and the receiver, as well as for the dyad by including them as random effects. The control for giver and receiver was done in a way accounting for random slopes of both test variables (Barr et al. 2013). The model was fitted in R using the package lme4 with a Poisson error distribution and loglink as the link function. To test for model stability, we excluded levels of random effects one by one. This revealed robust results (See electronic supplementary material).

Test for a relationship between exchange of grooming within sessions and the PAI

To investigate the form of short-term exchange of grooming within dyads, we first considered both unidirectional and bidirectional grooming sessions. Because short unidirectional sessions often result from interruptions by other individuals and therefore do not reflect short-term exchanges within a given dyad, we then only analyzed the subset of dyads which engaged in bidirectional grooming sessions. We feel that although reducing the sample size, these criteria improve the explanatory power of the results by likely removing noise from the data. To analyze the relationship between the PAI and the grooming exchange within a session, we ran a GLMMs with the dyadic MDE as a response variable. As test variable, we included the dyadic PAI. We controlled for rank differences within a dyad (included as a fixed effects) and identity of the individuals (random effects) in the model. We ran the models 1,000 times while randomly assigning the individuals within a dyad to be either individual A or B, and averaged the results. To exclude that differences in the MDE were not a byproduct of shorter bout lengths in the grooming of certain dyads, we ran the model for MDE including mean bout length as a further control variable. The model was fitted in R using the package lme4, with a Gaussian error distribution and identity link as the link function. To rule out that the significant effects are artifacts of small samples especially if we only consider bidirectional grooming bouts (which are more likely to reveal strong effects by chance alone), we bootstrapped confidence intervals for all fixed effects. Also, these were based on 1,000 random assignments of subject to the two random effects (individual A and B) whereby we ran 1,000 bootstraps for each of the 1,000 assignments and then averaged the upper (97.5 %)

and lower (2.5 %) confidence limits obtained from each of the 1,000 random selections (See electronic supplementary material).

As the data are not independent (many individuals in several dyads), our analysis had to control for individual identities within the dyads and therefore using GLMM was the only choice. We ran all analysis in R (version 3.0.2, Baayen 2009) using the functions lmer and glmer of the R package lme4 (Bates et al. 2013). For data used for analysis, see electronic supplementary material.

Results

A total of 387 complete grooming sessions including a male were recorded, out of which 91 (24 %) were between males and 56 (15 %) between males for which relatedness in terms of brothers, half-brothers or father–son could be excluded. These grooming sessions were distributed among 22 dyads, lasted on average 14 min (range 0.5–42 min) and consisted on average of 3.3 bouts (range 1–10 bouts). From those grooming sessions, 36 (64 %) were bidirectional. These were distributed among 17 dyads, lasted on average 16 min (range 2–42 min) and consisted on average of 4.6 bouts (range 2–10 bouts). The 20 unidirectional grooming sessions lasted on average only 1.5 min (median, range 0.5–25 min). Mutual grooming was observed for 49 min (8.5 % of duration of bidirectional grooming sessions). Overall grooming frequency within male dyads did not correlate with aggression frequencies (Spearman's rank correlation: $\rho = -0.07$, $N = 36$, $p = 0.69$).

Overall relationship between grooming given and received across dyads and within sessions

The total amount of grooming received was significantly correlated with the amount of grooming given across male dyads (GLMM: Intercept = 1.03; Estimate \pm SE = 0.52 ± 0.12 ; $p < 0.01$; Table 1). Hence, individuals receive more grooming during a session from individuals whom they give more grooming. While we did not find a correlation between grooming given in one bout and the grooming received in the preceding bout within bidirectional grooming sessions (tit-for-tat; GLMM: Intercept = 0.38; Estimate \pm SE = 0.00 ± 0.01 ; $p = 0.91$;

Table 1 Results from GLMM with overall grooming given as response variable

	Estimate	SE	Z value	<i>p</i>
Intercept	1.04	0.35		
Mean grooming received per session	0.52	0.12	4.21	>0.01

Table 2 Results from a GLMM with the grooming given in a bout as response variable

	Estimate	SE	Z value	<i>p</i>
Intercept	0.38	0.09		
Mean bout duration within session	0.231	0.02	9.96	<0.001
Preceding bout deviation from mean bout duration within session (tit-for-tat)	−0.001	0.01	−0.11	0.912

Table 3 Results from the GLMM with the mean differences between consecutive grooming bouts (MDE) as the response variable

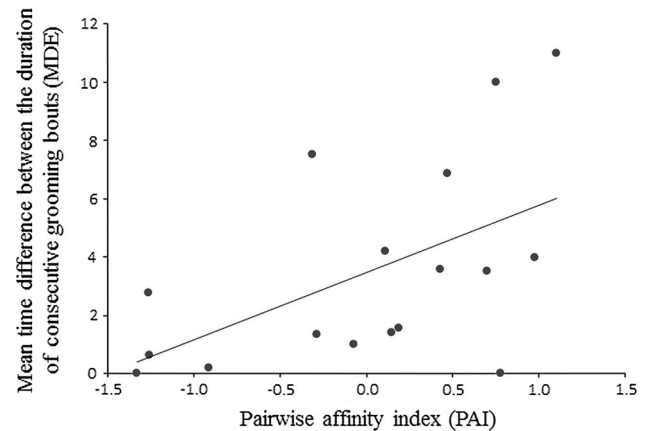
	Estimate	SE	<i>T</i> value	<i>p</i>
A				
Intercept	1.35	0.11		
Bout length	0.62	0.07	8.98	<0.01
Pairwise affinity (PAI)	0.16	0.07	2.26	0.08
Rank differences	−0.03	0.08	−0.39	0.65
B				
Intercept	1.25	0.13		
Bout length	0.49	0.10	4.99	<0.01
Pairwise affinity (PAI)	0.34	0.10	3.49	0.02
Rank differences	−0.11	0.11	−0.96	0.39

A including all grooming sessions, B including only bidirectional grooming sessions

Table 2), there was a significant correlation of total grooming given and received within these sessions (GLMM: Intercept = 0.38; Estimate ± SE = 0.23 ± 0.02; $p < 0.001$; Table 2). Thus, while grooming is generally not immediately reciprocated from one bout to the next within a given bidirectional grooming session, it is generally reciprocated over the whole session.

Relationship between exchange of grooming within sessions and PAI

Association patterns within given dyads were correlated with the exchange of grooming within a session. Dyads with higher dyadic association indices tend to exhibit larger differences between consecutive grooming bouts within a session (GLMM: Intercept = 1.35; Estimate ± SE = 0.16 ± 0.07; $p = 0.07$; Table 3) than dyads with lower association indices. If we consider only bidirectional sessions, this result is significant (Fig. 1; GLMM: Intercept = 1.25; Estimate ± SE = 0.34 ± 0.10; $p = 0.02$; Table 3). Accordingly, dyads which are more frequently associated have larger time differences from one bout to the next within a grooming session than dyads that are less often associated. These results were not artifacts of small sample

**Fig. 1** The relationship between short-term exchange of grooming (measured as mean time difference between the duration of consecutive bouts) and the pairwise affinity index (PAI) in bidirectional grooming sessions

sizes as indicated by confidence intervals not encompassing zero (see electronic supplementary material).

Furthermore, rank differences within a dyad had no influence on the exchange of grooming within a dyad (GLMMs: $p = 0.39$ – 0.65 ; Table 3). The PAI of male dyads which have been observed grooming bidirectional ranges from -1.3 to 1.1 and is similar to the range of PAI of all possible male dyads for which relatedness in terms of brothers, half-brothers or father–son could be excluded (-1.6 to 1.1).

Discussion

In this study of grooming exchange among male bonobos, we found that while overall grooming given and received was correlated across dyads and within bidirectional grooming sessions, the form of grooming exchange within a given session differed according to dyadic association preferences. Individuals with a higher tendency to associate, ergo more familiar individuals, exhibited larger time differences and reduced reciprocation in consecutive grooming bouts within a session. Consequently, close associates seemed more generous toward each other in providing grooming independent of the preceding received grooming. Without actually measuring emotions involved, this finding supports predictions by the emotional mediation hypothesis. This hypothesis proposes a mediating role of social bonds in the exchange of services and predicts that the emotions associated with close individuals are a factor allowing for more tolerance of short-term imbalances in services exchanged and a lesser degree of immediate reciprocation (Schino and Aureli 2009).

Although we did not find evidence of a contingency of grooming given in one bout on the grooming received in

the previous one (tit-for-tat), the time differences between consecutive bouts were smaller among individuals of low affinity than among individuals with high affinity. This indicates that short-term contingency might be more likely to be found in relationships with one-time interactions (Schino and Aureli 2010). Since males are philopatric in bonobos, all males have a long-standing history of social relationships and such a scenario is unlikely to be found in this species. Overall, it seems that different mechanisms of reciprocation might be followed depending on the partner (Cheney et al. 2010).

While partner choice is an important mechanism in the exchange of services between individuals and also reflects establishments of close social bonds which can benefit the individuals (Schülke et al. 2010; Silk et al. 2003), the collected data do not allow for questions concerning partner choice to be addressed and therefore is not appropriate for testing the predictions of biological market models.

Because agonistic support and food sharing among male bonobos is very rare, this study used spatial association patterns to characterize the relationships among the males. We incorporate this measurement in a continuous way in order to prevent subjective categorization. Still, spatial association patterns are a rather broad measurement of social relationships that can be the sum of divers interactions. At this stage, we cannot say whether or not individuals perceive relationships with high or low pairwise affinity indices differently. However, individuals with higher association scores seem to groom each other more often (Surbeck et al. in prep) which indicates that the frequency of exchanges over longer time frames influences the form of exchange on a shorter time frame. Emotions are a physiological pathway, which shapes memory, likely interferes with cognitive process (Aureli and Schaffner 2002), and are shown to be involved in altruistic behavior in humans in the form of gratitude (McCullough et al. 2008). Measuring physiological changes related to interactions with different social partners would be a way to directly test whether individuals perceive others differently. Especially, oxytocin might be a candidate to be involved, as grooming of bond partners in chimpanzees (*Pan troglodytes*) leads to higher levels of this neuropeptide in urine than grooming with non-bond partners (Crockford et al. 2013).

While grooming among male bonobos is not exchanged for agonistic support or food, it could theoretically be exchanged for feeding tolerance. In this case, one would expect low-ranking males to trade one-sided grooming with high-ranking males for feeding tolerance, and consequently, more short-term balanced grooming would occur in dyads of similar rank. However, in our data set, rank differences within dyads neither influenced the duration differences nor the reciprocity index of consecutive grooming bouts, making grooming-for-tolerance exchange

an unlikely explanation. Furthermore, grooming might be used as reconciliatory behavior, but first results indicate that grooming and aggression frequencies within dyads do not correlate.

Because the focus of this study was collecting grooming information of many different dyads, the sample size of actual grooming events is rather small. Furthermore, because grooming often happens simultaneously in several dyads, our study underestimates the frequency of male–male grooming. The more frequent male–female grooming does not meet the requirement for this study that it is likely exchanged only for itself. Male–female grooming is likely involved in male reproductive strategies such as mate guarding and furthermore do males and females more frequently form coalitions (Surbeck and Hohmann 2013).

Nevertheless, using observation of short-term exchanges of grooming among 22 different male dyads, more than available in most captive setups, indicates the importance of considering dyadic relationships when analyzing short-term exchanges. Restricting the analyses to bidirectional grooming sessions where we can be sure that both partners were motivated to interact and were not interrupted at the start of the session (reflected in average longer bout duration in bidirectional grooming sessions), this pattern becomes even clearer. In this reduced data set of 17 dyads with association indices covering most of the range of all possible male dyads, we find significant differences in the form of grooming exchange; model stability analyses and bootstrapping confirm the robustness of this main result.

Further studies will have to address how the exchange of grooming changes over the course of many grooming interaction within the same dyad and how it responds to changes in social relationships.

Acknowledgments We thank the members of the LuiKotale Bonobo Project, ICCN and Barbara Fruth for support through various stages of the project. We furthermore thank Roger Mundry for statistical support, Catherine Crockford, Mimi Arandjelovic, Sarah Till Boysen and two anonymous reviewers for their helpful comments on the manuscript.

References

- Aureli F, Schaffner CM (2002) Relationship assessment through emotional mediation. *Behaviour* 139:393–420. doi:[10.2307/4535928](https://doi.org/10.2307/4535928)
- Baayen RH (2009) languageR: Data sets and functions with “Analyzing Linguistic Data: A practical introduction to statistics”, R package version 0.955. <http://CRAN.R-project.org/package=languageR>
- Barr DJ, Levy R, Scheepers C, Tily HJ (2013) Random effects structure for confirmatory hypothesis testing: keep it maximal. *J Mem Lang* 68:255–278. doi:[10.1016/j.jml.2012.11.001](https://doi.org/10.1016/j.jml.2012.11.001)
- Barrett L, Gaynor D, Henzi SP (2002) A dynamic interaction between aggression and grooming reciprocity among female chacma

- baboons. *Anim Behav* 63:1047–1053. doi:[10.1006/anbe.2002.3008](https://doi.org/10.1006/anbe.2002.3008)
- Bates D, Maechler M, Bolker B, Walker S (2013) lme4: Linear mixed-effects models using Eigen and S4. R package version 1.0–5. <http://CRAN.R-project.org/package=lme4>
- Cheney DL, Moscovice LR, Heesen M, Mundry R, Seyfarth RM (2010) Contingent cooperation between wild female baboons. *Proc Natl Acad Sci* 107:9562–9566. doi:[10.1073/pnas.1001862107](https://doi.org/10.1073/pnas.1001862107)
- Clutton-Brock T (2009) Cooperation between non-kin in animal societies. *Nature* 462:51–57
- Connor RC (1995) Impala allogrooming and the parcelling model of reciprocity. *Anim Behav* 49:528–530
- Crockford C, Wittig RM, Langergraber K, Ziegler TE, Zuberbühler K, Deschner T (2013) Urinary oxytocin and social bonding in related and unrelated wild chimpanzees. *Proc R Soc B: Biol Sci* 280 doi:[10.1098/rspb.2012.2765](https://doi.org/10.1098/rspb.2012.2765)
- de Waal FBM (1997) The Chimpanzee's service economy: food for grooming. *Evol Hum Behav* 18:375–386. doi:[10.1016/S1090-5138\(97\)00085-8](https://doi.org/10.1016/S1090-5138(97)00085-8)
- de Waal FBM (2000) Attitudinal reciprocity in food sharing among brown capuchin monkeys. *Anim Behav* 60:253–261. doi:[10.1006/anbe.2000.1471](https://doi.org/10.1006/anbe.2000.1471)
- de Waal FBM, Leimgruber K, Greenberg AR (2008) Giving is self-rewarding for monkeys. *Proc Natl Acad Sci* 105:13685–13689. doi:[10.1073/pnas.0807060105](https://doi.org/10.1073/pnas.0807060105)
- Fruteau C, Voelkl B, van Damme E, Noë R (2009) Supply and demand determine the market value of food providers in wild vervet monkeys. *Proc Natl Acad Sci* 106:12007–12012. doi:[10.1073/pnas.0812280106](https://doi.org/10.1073/pnas.0812280106)
- Hashimoto C, Furuichi T, Tashiro Y (2001) What factors affect the size of chimpanzee parties in the Kalinzu Forest, Uganda?: examination of fruit abundance and number of estrous females. *Int J Primatol* 22:947–959
- Hohmann G, Gerloff U, Tautz D, Fruth B (1999) Social bonds and genetic ties: kinship association and affiliation in a community of bonobos (*Pan paniscus*). *Behaviour* 136:1219–1235
- Ihobe H (1992) Male–Male relationships among wild bonobos (*pan-paniscus*) at Wamba, Republic-of-Zaire. *Primates* 33:163–179
- Jaeggi A, Schaik C (2011) The evolution of food sharing in primates. *Behav Ecol Sociobiol* 65:2125–2140. doi:[10.1007/s00265-011-1221-3](https://doi.org/10.1007/s00265-011-1221-3)
- Jaeggi AV, De Groot E, Stevens JMG, Van Schaik CP (2013) Mechanisms of reciprocity in primates: testing for short-term contingency of grooming and food sharing in bonobos and chimpanzees. *Evol Hum Behav* 34:69–77. doi:[10.1016/j.evolhumbehav.2012.09.005](https://doi.org/10.1016/j.evolhumbehav.2012.09.005)
- Langergraber KE, Mitani JC, Vigilant L (2007) The limited impact of kinship on cooperation in wild chimpanzees. *Proc Natl Acad Sci USA* 104:7786–7790
- McCullough ME, Kimeldorf MB, Cohen AD (2008) An adaptation for altruism: the social causes, social effects, and social evolution of gratitude. *Curr Dir Psychol Sci* 17:281–285. doi:[10.1111/j.1467-8721.2008.00590.x](https://doi.org/10.1111/j.1467-8721.2008.00590.x)
- Noë R, Hammerstein P (1995) Biological markets. *Trends Ecol Evol* 10:336–339. doi:[10.1016/S0169-5347\(00\)89123-5](https://doi.org/10.1016/S0169-5347(00)89123-5)
- Roberts G, Sherratt TN (1998) Development of cooperative relationships through increasing investment. *Nature* 394:175–179
- Schino G (2007) Grooming and agonistic support: a meta-analysis of primate reciprocal altruism. *Behav Ecol* 18:115–120. doi:[10.1093/beheco/arl045](https://doi.org/10.1093/beheco/arl045)
- Schino G, Aureli F (2008) Grooming reciprocation among female primates: a meta-analysis. *Biol Lett* 4:9–11. doi:[10.1098/rsbl.2007.0506](https://doi.org/10.1098/rsbl.2007.0506)
- Schino G, Aureli F (2009) Reciprocal altruism in primates: partner choice, cognition, and emotions. In: Jane Brockmann H, Leigh WS (eds) *Advances in the study of behavior*, vol 39. Academic Press, Nancy pp 45–69. doi:[10.1016/S0065-3454\(09\)39002-6](https://doi.org/10.1016/S0065-3454(09)39002-6)
- Schino G, Aureli F (2010) Primate reciprocity and its cognitive requirements. *Evol Anthropol* 19:130–135. doi:[10.1002/evan.20270](https://doi.org/10.1002/evan.20270)
- Schubert G et al (2013) Co-residence between males and their mothers and grandmothers is more frequent in bonobos than chimpanzees. *PLoS One* 8:e83870. doi:[10.1371/journal.pone.0083870](https://doi.org/10.1371/journal.pone.0083870)
- Schülke O, Bhagavatula J, Vigilant L, Ostner J (2010) Social bonds enhance reproductive success in male macaques. *Curr Biol* 20(24):2207–2210
- Silk J, Alberts S, Altmann J (2003) Social bonds of female baboons enhance infant survival. *Science* 302(5648):1231–1234
- Surbeck M, Hohmann G (2013) Intersexual dominance relationships and the influence of leverage on the outcome of conflicts in wild bonobos (*Pan paniscus*). *Behav Ecol Sociobiol* 67:1767–1780. doi:[10.1007/s00265-013-1584-8](https://doi.org/10.1007/s00265-013-1584-8)
- Surbeck M, Mundry R, Hohmann G (2011) Mothers matter! Maternal support, dominance status and mating success in male bonobos (*Pan paniscus*). *Proc R Soc B: Biol Sci* 278:590–598. doi:[10.1098/rspb.2010.1572](https://doi.org/10.1098/rspb.2010.1572)
- Tooby J, Cosmides L (2008) The evolutionary psychology of the emotions and their relationship to internal regulatory variables. In: Lewis M, Haviland-Jones JM, Barrett LF (eds) *Handbook of emotions*, 3rd edn. Guilford Press, New York, pp 114–137
- Trivers RL (1971) The evolution of reciprocal altruism. *Q Rev Biol* 46:35–57
- van de Pol MV, Wright J (2009) A simple method for distinguishing within- versus between-subject effects using mixed models. *Anim Behav* 77:753–758. doi:[10.1016/j.anbehav.2008.11.006](https://doi.org/10.1016/j.anbehav.2008.11.006)