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Making friends in an asymmetric game: the establishment of male-female grooming exchanges in vervet monkeys

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Abstract
Various concepts have been developed to explain cooperation among unrelated individuals, but linking proposed strategies to empirical evidence remains a challenge, especially for variable reciprocal investments. One famous strategy is "raise-the-stakes", proposing low initial investments but a steady increase if the partner matches the other's investments or increases their own investments in a series of exchanges. Contrarily, the "making-friends" strategy predicts high investment between strangers that may either be kept up or downregulated if not fully matched. We tested these predictions on grooming exchanges between wild male-female vervet monkeys, a species with regular male dispersal. Contrary to both predictions, females had a consistently high initial investment and groomed immigrants for longer than was reciprocated, showing no adaptation to the formation of debts. However, females gradually reduced grooming over the first 6 months. Males, on the other hand, did not alter grooming investments over time. Thus, grooming exchanges eventually almost evened out. We present various potential explanations for these results, which are overall more consistent with the "making friends" strategy. Most importantly, this study highlights the complexity of real-life cooperation, emphasizing the need for models that explicitly incorporate life history parameters into cooperative strategies.

Significance statement

This study demonstrates the importance of considering life-history differences between interaction partners when applying theoretical cooperation models to empirical cases. We examined the development of grooming relationships – a behaviour serving both hygiene and social functions in primates – between newly immigrated male and resident female vervet monkeys. We did not observe a slow building up of exchanges, as predicted by a "raise-the-stakes" strategy. Instead, we found that socially established females heavily invest into grooming immigrant males, without receiving matching returns. These results suggest that female core groups compete with neighboring female core groups over males and the services those provide. Our data highlight avenues for future data-informed theoretical models on cooperation.

Main text

Introduction

Although many game theoretical models have been proposed to explain stable cooperation between unrelated individuals [1–4], empiricists face great challenges to apply them to explain levels of cooperation observed in nature. Despite various criticisms [3, 5, 6], the Iterated Prisoner's Dilemma (IPD; [7]) remains a frequently adopted model for explaining cooperation between unrelated individuals. An important aspect to consider when evaluating the usefulness of the IPD is distinguishing between the presence of a PD payoff matrix – where defecting always yields a higher immediate payoff than cooperating, irrespective of the partner's behaviour – and the strategies that have been proposed to yield cooperative solutions to an IPD [5]. For example, early proposed strategies like contrite Tit-for-Tat, generous Tit-for-Tat or Pavlov (see discussion in [8]) may only apply if possible actions are discrete (i.e. to cooperate or to defect is an all-or-nothing decision) and hence have fixed payoff consequences. However, in biological settings, cooperation is rarely "all-or-nothing" [9]: players can alter their level of investment based on certain predictions. If cooperative investment becomes variable, individuals can adjust their behavior and amount of investment based on their partner's previous investment. Various strategies that utilize variable investment within IPD structured games have been proposed and, within a wide parameter space, cooperation is predicted to spread to fixation within the population [10–12].

One of the most famous strategies proposed to yield stable cooperation in a continuous IPD is "raise-the-stakes" (RTS; [12]). When applying the RTS strategy, an individual initially invests little

with a novel partner to avoid being exploited by a cheater ("testing the waters") but gradually increases their investment if the partner matches or exceeds the investment. In other words, players decide on levels of cooperation or investment based on a partner's previous investment. This also implies that RTS does not increase if an investment is not matched by a partner, and cooperation only gradually increases over time when both partners cooperate [12]. Under the model assumptions, the RTS strategy spreads quickly to fixation and cannot be invaded by non-cooperators once established [12]. While the initial model does not specify cost and benefit functions, a follow-up by Killingback & Doebeli [10] shows a similar dynamic when the benefits of investment yield diminishing returns: the evolved cooperative ESS makes individuals start with levels that are below the payoff maximum, and responses to return benefits eventually lead to levels of helping that maximize benefit-to-cost ratios, which allows for no variation within a population.

The models by both Roberts & Sherratt [12] and Killingback & Doebeli [10] propose purely evolutionary strategies, i.e., the initial level of investment and updating rules are genetically coded. Furthermore, it is assumed that all individuals are in equal condition, that there is no partner choice and partner switching, and hence no scope for social bonding (also called "friendships" [13]) and payoff interdependence . At evolutionary equilibrium, all players therefore play the same strategy. These assumptions and outcomes contrast with a recent model by Leimar & Bshary [11], which also assumes that individuals can make variable investments to help someone in need, but does account for the effect of partner choice and individual variability of players, with players learning about other individuals (where learning parameters may evolve according to selection on resulting behaviour). They found that when encountering new group members, players here follow a strategy that may be called "making-friends" (MF) following Trivers [15]: individuals start with high initial investment [11]– opposite to the predictions of the RTS. Individuals can subsequently change their investment based on where they stand with their partner: investment remains high if a partner asking for help has helped more than received, but investment drops if the partner is already in debt. Debts may build up because of chance events but also because lower quality individuals are more likely to need help. What is similar to the previous models is the assumption that interactions take place between unrelated individuals. Although this model is partly based on observations of female vampire bats, it needs further empirical validation across different contexts and species.

Testing which decision rules wild animals use when starting a new relationship, and how they adjust levels of reciprocal investments based on the interaction history is challenging, as it requires observing each pairwise interaction from the very beginning. We are not aware of an existing empirical study that contains such data. While translocated cleaner fish *Labroides dimidiatus* show initially high investment to build up new relationships with 'client' reef fish [16], the study system does not fit a key assumption of the models, since the strategic options of cleaners and clients are asymmetric (only cleaners need to decide about levels of investment), rather than symmetric. Another study found no evidence of adult female baboons adjusting grooming efforts to what they had received from the groomee during their last interaction [17], but focal individuals had known each other long before data collection started (females are the philopatric sex in baboons) and were genetically related to varying degrees, therefore not fitting key assumptions of the models [10–12]. Nevertheless, grooming reciprocation among primates remains an often-used empirical system to test theoretical cooperation models, especially when it comes to variable investment. Although grooming can serve both hygienic and (several) social functions, and may be traded for other commodities besides grooming [18–24], it is often used as a proxy for pair bond strength in primates [25]. While little evidence is found for immediate reciprocity, in the long term grooming given generally correlates strongly with grooming received among female primates [26]. Thus, grooming exchanges in primates offer a valuable context for studying cooperative strategies, including how such exchanges develop between newly-met pairs of unrelated individuals over time, if relevant

data can be collected as long as at least one interaction partner has just immigrated into the study group.

Vervet monkeys (*Chlorocebus pygerythrus*) are a suitable system to test variable investment strategies such as RTS and MF. Vervet monkeys live in promiscuous multimale/multifemale groups with regular male dispersal [27] and philopatric females, who form the social core of the group [28–30]. Our study on the development of grooming interaction patterns focuses on male-female pairs of vervet monkeys following male immigration into a new group. We only consider male-female grooming interactions in this study as male-male grooming interactions are rarely observed. Having access to multiple groups habituated to human observers, we could observe males migrating between study groups from their first days in their new groups. This allowed us to observe their grooming interactions with novel, unrelated partners.

Under the assumption of long-term reciprocity, we expect long-term grooming investment to be equal between partners. If both of our parties – males and females – follow the RTS strategy, we expect low initial investment, due to the uncertainty of their partner (the "testing the waters" principle). However, if they follow the MF strategy [11], we expect high initial investment from both partners. For both strategies, the existing models predict that grooming services should be closely matched if parties respond to their partner's investment. However, in our empirical case, there may be an important additional dimension to these two strategies. Interactions between individuals belonging to opposite sexes may affect the course of exchange rates in ways that existing reciprocity models do not consider. Immigrant males might initially invest more in grooming with females, as they are looking for inclusion in the group [31] or are generally looking to increase their centrality, which positively affects survival and reproductive opportunities [32–34]. Females, already being more central in the network [22, 28–30], are likely not to have these direct benefits of relationships with males, or at least to a lesser extent. Alternatively, females may initially groom more than what they receive from males if there is competition between groups of philopatric females to attract males. Indeed, there is evidence that having additional males in a group brings benefits to females in the form of lowered predation risk and assistance in territory defense [35, 36], which may outweigh the costs due to increased feeding competition [37].

In this study we tested how females and newly immigrated male vervet monkeys build up grooming exchanges, while partners are still naïve to each other. We observed initial investment and the build-up of investment between females and immigrants and assessed whether reciprocity between them develops, and compared this with the grooming exchanges between females and already integrated males. Specifically, we tested whether these grooming exchanges and their progression fit the predictions of the RTS or the MF strategy. Observing how these novel partners initiate grooming exchanges, reciprocate grooming investments and how that might differ from already established relationships should shed light on the build-up of cooperative relationships and the applicability of theoretical models to empirical systems.

Results

To determine whether grooming exchanges between immigrant males and adult females followed the "raise-the-stakes" (RTS) or "making-friends" (MF) strategy, we looked at the duration of grooming exchanges between females and immigrants, as well as females and residents. This left us with 18 immigrant males and 22 resident males (Table 1), of which ten males went from immigrant to resident status during our study period, leaving us with 30 unique male individuals and 73 unique females. Over our two-year data collection period, we recorded 405 grooming events involving females and immigrant or resident males (respectively 112 and 293 events). Immigrant males groomed females in 61 recorded instances (mean duration: 93.06 seconds), whereas females groomed immigrants 51 times (mean duration: 158.60 seconds). Similarly, residents groomed

females 142 times (mean duration: 137.42 seconds), while females groomed residents 151 time (mean duration: 157.70 seconds).

Our first model, which analyzed the progression of investment over time as well as different investment levels across all four partner combinations, yielded three significant results. First, females invested significantly more time in grooming immigrants than vice versa (*estimate* = 0.61, *SE* = 0.18, p = 0.004). Second, we found a significant difference in slopes of how much females groom immigrants over time compared to residents over time (*estimate* = -0.43, *SE* = 0.14, p = 0.003). The third significant result was that females significantly decreased their investment over time when grooming immigrants (*estimate* = -0.38, *SE* = 0.12, p = 0.002) (Table 2, Fig. 1). All other analyses were not significant, i.e. immigrant and resident males groomed females for similar durations, and females did not show further variation in how long they groomed males (Table 2, Fig. 1).

Regarding our second question on the balance in grooming efforts, initial investments in interactions with immigrant males were highly female-biased, while grooming reciprocity was more balanced with resident males but remained slightly biased towards female investing more (Fig. 2; reciprocity over two-year period with negative values, meaning that females groom more and positive males groom more: *mean* = -0.10, *median* = -0.23). When comparing the slopes of immigrants and residents, we found a marginally non-significant difference between the progression of reciprocity over time of immigrants versus residents (*estimate* = 0.63, *SE* = 0.35, p = 0.07). We found a significant positive slope for immigrants (*estimate* = 0.62, *SE* = 0.30, p = 0.04), but no significant slope for residents (*estimate* = -0.01, *SE* = 0.18, p = 0.93).

Discussion

We examined how grooming exchange patterns between immigrating males and philopatric female vervet monkeys develop over time, to observe which grooming exchange strategies they followed. We found no evidence that vervet monkeys use decision rules that would fit the logic of "raise-the-stakes" [12], since we did not find high initial investment of both partners, nor an escalation of cooperation. Instead, males provided rather constant grooming services to females. Females even showed the highest grooming investment with newly immigrated males, and their investment decreased over months until stabilizing at a level that was quite similar to male grooming investment into females. While the data thus fit to some degree the "making friends" strategy [11], it is clear that additional factors need to be considered in order to explain the initial asymmetries. We therefore need to consider asymmetries between the sexes to explain why females initially groom newly immigrated males for longer, and only lower their investment over several weeks to eventually closely match male investment. We discuss these results in more detail below.

According to the RTS strategy, initial investment of both parties should be low, and investment increases when the partner reciprocates [12]. Neither sex showed any evidence that initial grooming bouts given are short and then slowly increase over time if matched. Instead, grooming bouts either started with a particularly high investment in the beginning with a small decrease over time (females), or were rather stable over time (males). Therefore, the "raise-the-stakes" hypothesis can be refuted despite an important shortcoming in our data: we do not have enough observations to analyze the precise dynamics of the progression of grooming exchanges in specific male-female dyads. Although we corrected for the repeated observations of grooming individuals in our models, we could not test whether receiving a long or short grooming bout is followed by a matching return grooming bout, as would be expected if individuals use a decision-rule that is based on direct reciprocity considerations. Nevertheless, the data suggest that for male-female vervet monkey grooming interactions, new partners are not concerned about their own grooming investments not being returned. In other words, the risk of being cheated does not appear to be of importance for male or female grooming decisions, shown by the absence of an increase in grooming investment of both parties.

The model by Leimar & Bshary [11] predicts that the first act of helping reflects an investment as close to the maximum an individual is willing to give, and that such help is readily given to a new partner as long as this individual is or becomes a group member. The results partly fit the model's predictions in that initial grooming investments are as high or even higher than later grooming investments. As acknowledged before, we lack the detailed dyad-level data necessary to test how individuals respond to a build-up of grooming asymmetries within dyads, as a means to assess whether decision-rules follow the logic of reciprocity. However, we consider it unlikely that the model can explain why there is an initial grooming bias by females and why it eventually disappears and close-to-matching grooming exchanges develop. More precisely, we consider it unlikely that females reduce their initial grooming investment simply because they do not receive adequate matching by the male partners. This is because in that case, females would make systematic and repeated errors when encountering a new male. Such errors should be eradicated by learning or natural selection, leading females to start with lower initial investment when encountering new male partners. In fact, females give newly immigrated males especially long grooming services, longer than what they receive back from these partners. Therefore, other factors need to be considered to explain the initial asymmetry in male – female grooming exchanges.

The grooming bias cannot be explained by differences between the sexes regarding the need to form new social relationships. In vervet monkeys, adult females form the social core of the group, being surrounded by related females with whom they have established social bonds [29]. Such female-female bonds allow females to often dominate males, despite being smaller [42, 43]. Thus, females do not need to form new relationships, while immigrant males do. One could therefore have expected that immigrant males show high initial grooming investment into females in order to better integrate into the group through the formation of social bonds with resident females [28–30]. Apart from improved group inclusion, grooming females could in addition yield increased mating opportunities [31, 44, 45] and support in conflicts as immigrants rise in the male hierarchy [34, 46, 47]. Indeed, immigrant males groom females as much as established males do, fitting the 'making friends' hypothesis. But immigrants do not show extra effort, whereas females do. If the females' effort were limited to the first few days, one could have hypothesized that a likely higher ectoparasitic load in newly immigrated males [48] might have caused females to prolong the grooming of immigrant males as a way to obtain food. However, it seems unlikely that immigrants' parasite loads take months to decline.

Females thus seem to expect long-term benefits from grooming immigrant males, as they start with a higher initial investment and do not get paid back directly in the form of grooming. There are several hypotheses as to why having new males join a group could yield net benefits for females, despite increased feeding competition [49]. Among them are inbreeding avoidance [50, 51], help in territorial defense [18, 35, 52], increased access to resources [53] and a decrease in predation risk [36, 54]. A previous study on vervet monkeys found that newly immigrant males show more antipredator vigilance than females [55], indicating that they immediately contribute to the general safety of the group. Females investing in immigrant males is in line with the hypothesis that additional males bring potential benefits in the form of *services* [36]. On top of that, having a more male-biased adult sex ratio in a vervet group may promote female dominance, as is predicted by DomWorld [43], yielding more power for females to choose their partner [56]. Once males are convinced to stay, females can reduce their investment to "normal" levels.

In conclusion, our results do not support the "raise-the-stakes" strategy [12]. While the "making friends" strategy [11] fits the data better, the differences between female and male grooming patterns highlight the importance of considering initial asymmetries within cooperative exchanges when developing such models. Cooperation is rarely symmetrical in its payoffs in empirical settings whenever both partners might hold different social statuses, positions in hierarchy, embody differing life-history traits, or may offer different resources. Basing new models on empirical data will yield ever more realistic concepts.

Methods

We used observational data collected at the iNkawu Vervet Project (IVP) field site, Mawana Game Reserve (MGR), South Africa. MGR is a private game reserve, approximately 11 000 ha in size and located in the northern parts of the KwaZulu-Natal province. IVP data are collected year-round by trained field assistants who undergo monkey's identification tests and interobserver reliability tests with the onsite scientific manager before collecting data. Over a period of two years (June 2022 to June 2024), observers conducted three 20-minute continuous focal samples on each adult individual in a given 10-day period, though never twice on the same day or during the same time block (morning, noon and afternoon). Within focal observations, a grooming interaction was considered as such when the same two partners performed interactive behaviours with each other (excluding the duration of "behavioral gaps", such as a bout of self-scratching, lasting less than 60s), when both partners did not interact with a third party in the meantime and when neither partner moved significantly between behaviors. The durations of these interactions were considered in seconds for assessing the duration females groom males and vice versa. We used data from seven neighboring groups of vervet monkeys (namely AK, BD, CR, IF, KB, LT and NH). Because not all groups have been followed since the start of IVP in 2010 and habituation levels differs between the groups, group identity was considered in our analysis.

To compare grooming interactions of immigrant males with females to the ones of males that have been in a group for longer, we created two categories of males with an equal length in days. We chose to compare newly immigrated males to males that have already been present in a group for at least a year, to make sure they are sufficiently familiar with their female partners. The number of days a male was considered as an immigrant was based on a breakpoint model – a statistical method used to identify points of abrupt change [38, 39]. The breakpoint of abrupt change (if any) was therefore classified as the point in time where there was a significant change in grooming behavior between partners. After visual inspection of the progression of the duration of grooming exchanges where females groom males and vice versa, we could identify no clear breakpoints. Visual inspection of the progression of reciprocity over time did yield a potential breakpoint. We therefore applied our breakpoint model to the progression of reciprocity over time. Reciprocity was mathematically determined as a spectrum ranging from -1 to +1, where 0 indicates equal grooming efforts. A positive score reflects a bias toward male grooming effort, while a negative score reflects greater female grooming effort. We calculated the proportion of time (in seconds) a female groomed a male versus the time a male groomed a female using the formula:

$$\frac{(Duration\ male\ grooming\ female) - (duration\ female\ grooming\ male)}{(Duration\ male\ grooming\ female) + (duration\ female\ grooming\ male)} = reciprocity$$

We considered the first year of a male's presence to determine our breakpoint, since we are interested in finding the point where new males are no longer "novel" and partners are no longer naïve to each other. Analysis of our breakpoint model found that the best fit was at day 171, meaning that there was a significant change in behavior during these grooming exchanges, which was in line with our expectations after visual inspection. We therefore defined immigrant males as males from day 0 to 171 of their residence. Because male vervet monkeys disperse multiple times during their adult life [27], we had ample opportunity to assess their integration into a new group. Long-term records were used to identify males that dispersed into the same group twice; these were excluded from the dataset. Because some males dispersed into our population from unknown groups, and were therefore unhabituated, the "habituation level" (i.e., habituated vs. unhabituated) was considered for immigrant males. If a male was born in our population or had spent time in a habituated group previously, he was marked as habituated. If he was not, he was marked as unhabituated and excluded from the dataset, to ensure accurate data collection on grooming duration. To guarantee that resident males had established themselves in a group and had had the

opportunity to create social bonds with females, we defined resident males as males on day 365 to (365 + 171 =) day 536 of their residence. All residents were considered habituated.

After defining the breakpoint in our model, we compared initial investments of females to immigrants and vice versa by comparing the duration of grooming bouts between both partners. We compared these initial investments with later investment, i.e., investment (grooming duration) between females and residents. This data should inform us about the levels of initial investment as well as show any differences between strategies or partners. Lastly, we considered the progression of grooming duration in all four partner combinations (female-immigrant male, immigrant male-female, female-resident male and resident male-female).

All data were analyzed using R version 4.2.2. We performed a negative binomial generalized linear mixed model to compare duration of grooming interactions between the different partner combinations. A generalized linear mixed model with a binomial family was performed to understand the development of social exchanges (i.e., reciprocity) through time. A table of all models can be found in the supplementary materials S1.

To test the progression of investment over time as well as different investment levels across all four partner combinations, we used a triple interaction between the sex of the groomer (male or female), the status of the male (resident or immigrant) and the number of days the male has been in his status over the duration of the grooming interaction. Due to the seasonality of male-female primate relationships [40, 41], we also expected season to have a potential effect on male-female grooming duration. We therefore included 'season', as well as the variable 'group', as fixed effects. Since both the mating season as well as potentially lactating females are known to influence male-female relationships, we divided the year into four seasons: the baby season (the three months when most births occur), the mating season (three months when most mounts occur) and two three-month periods in between (defined here as winter and summer, distinguished by their contrasting food availability). In all our models, the male and the female identity were included as random effects to account for repeated measures within individual females and males, as well as the date of the interaction. These models were used to test the progression of investment over time by considering the slopes from the interaction term and differences in investment from the results of the status or sex term.

Secondly, to analyze the progression of grooming reciprocation, we fitted a generalized linear mixed-effects model with a binomial distribution, with grooming interactions between dyads over a day that had a positive reciprocity (the male groomed more than the female) score considered as 1, and interactions with a negative score considered as 0 (the female groomed more than the male). Interactions in which partners groomed each other for exactly the same duration were excluded from this analysis. The response variable, *reciprocity*, was modelled as a function of the status of the male (either immigrant or resident) in an interaction with the number of days the male has been in his status as a predictor variable. When comparing the AIC scores of a model with and without group and seasonal effects, we found that the model without group and season had a lower score and therefore decided to leave the group and season effect out. Unfortunately, data here didn't support the inclusion of the female identity as a random effect as it explained too little variation in the data. Only the male identity was therefore included as a random effect.

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References

1. S. A. West, A. S. Griffin, A. Gardner, Evolutionary Explanations for Cooperation. *Curr. Biol.* **17**, R661–R672 (2007).

2. R. Bshary, R. Bergmüller, Distinguishing four fundamental approaches to the evolution of helping. *J. Evol. Biol.* **21**, 405–420 (2008).

3. R. C. Connor, Cooperation beyond the dyad: on simple models and a complex society. *Philos. Trans. R. Soc. B Biol. Sci.* **365**, 2687–2697 (2010).

4. J. M. McNamara, O. Leimar, Variation and the response to variation as a basis for successful cooperation. *Philos. Trans. R. Soc. B Biol. Sci.* **365**, 2627–2633 (2010).

5. N. J. Raihani, R. Bshary, Resolving the iterated prisoner's dilemma: theory and reality: Resolvings the IPD. *J. Evol. Biol.* **24**, 1628–1639 (2011).

6. J. R. Stevens, F. A. Cushman, M. D. Hauser, Evolving the Psychological Mechanisms for Cooperation. *Annu. Rev. Ecol. Evol. Syst.* **36**, 499–518 (2005).

7. R. Axelrod, W. D. Hamilton, The Evolution of Cooperation. *Science* **211**, 1390–1396 (1981).

8. L. A. Dugatkin, The Evolution of Cooperation. *Oxf. Univ. Press USA* **47**, 355–362 (1997).

9. L. Keller, H. K. Reeve, Familiarity breeds cooperation. *Nature* **394**, 121–122 (1998).

10. T. Killingback, M. Doebeli, The Continuous Prisoner's Dilemma and the Evolution of Cooperation through Reciprocal Altruism with Variable Investment. *Am. Nat.* **160**, 421–438 (2002).

11. O. Leimar, R. Bshary, Social bond dynamics and the evolution of helping. *Proc. Natl. Acad. Sci.* **121** (2024).

12. G. Roberts, T. N. Sherratt, Development of cooperative relationships through increasing investment. *Nature* **394**, 175–179 (1998).

13. J. Silk, Using the 'F'-word in primatology. *Behaviour* **139**, 421–446 (2002).

14. G. Roberts, Cooperation through interdependence. *Anim. Behav.* **70**, 901–908 (2005).

15. R. L. Trivers, The Evolution of Reciprocal Altruism. *Q. Rev. Biol.* **46**, 35–57 (1971).

16. R. Bshary, Building up relationships in asymmetric co-operation games between the cleaner wrasse Labroides dimidiatus and client reef fish. *Behav. Ecol. Sociobiol.* **52**, 365–371 (2002).

17. L. Barrett, S. P. Henzi, T. Weingrill, J. E. Lycett, R. A. Hill, Female baboons do not raise the stakes but they give as good as they get. *Anim. Behav.* **59**, 763–770 (2000).

18. T. J. M. Arseneau-Robar, *et al.*, Female monkeys use both the carrot and the stick to promote male participation in intergroup fights. *Proc. R. Soc. B Biol. Sci.* **283**, 20161817 (2016).

19. K. N. Balasubramaniam, C. M. Berman, Grooming interchange for resource tolerance: biological markets principles within a group of free-ranging rhesus macaques. *Behaviour* **154**, 1145–1176 (2017).

20. L. Barrett, S. P. Henzi, T. Weingrill, J. E. Lycett, R. A. Hill, Market forces predict grooming reciprocity in female baboons. *Proc. R. Soc. Lond. B Biol. Sci.* **266**, 665–670 (1999).

21. C. Borgeaud, R. Bshary, Wild Vervet Monkeys Trade Tolerance and Specific Coalitionary Support for Grooming in Experimentally Induced Conflicts. *Curr. Biol.* **25**, 3011–3016 (2015).

22. M. Gareta García, D. Lemieux, R. Bshary, Factors affecting tolerance persistence after grooming interactions in wild female vervet monkeys, Chlorocebus pygerythrus. *Anim. Behav.* **177**, 135–145 (2021).

23. R. M. Seyfarth, A Model of Social Grooming Among Female Monkeys. *J. Theor. Biol.* **65**, 671–698 (1977).

24. B. Tiddi, F. Aureli, G. Schino, Grooming Up the Hierarchy: The Exchange of Grooming and Rank-Related Benefits in a New World Primate. *PLoS ONE* **7**, e36641 (2012).

25. J. Silk, D. Cheney, R. Seyfarth, A practical guide to the study of social relationships. *Evol. Anthropol. Issues News Rev.* **22**, 213–225 (2013).

26. G. Schino, F. Aureli, Grooming reciprocation among female primates: a meta-analysis. *Biol. Lett.* **4**, 9–11 (2008).

27. S. P. Henzi, J. W. Lucas, Observations on the Inter-Troop Movement of Adult Vervet Monkeys (Cercopithecus aethiops). *Folia Primatol* **33**, 220–235 (1980).

28. C. Borgeaud, S. Sosa, R. Bshary, C. Sueur, E. Van De Waal, Intergroup Variation of Social Relationships in Wild Vervet Monkeys: A Dynamic Network Approach. *Front. Psychol.* **7** (2016).

29. D. L. Cheney, R. M. Seyfarth, The representation of social relations by monkeys. *Cognition* **37**, 167–196 (1990).

30. R. M. Seyfarth, D. L. Cheney, Social Awareness in Monkeys. *Am. Zool.* **40**, 902–909 (2000).

31. B. Smuts, *Sex and Friendships in Baboons* (Routledge, 2017).

32. E. A. Archie, J. Tung, M. Clark, J. Altmann, S. C. Alberts, Social affiliation matters: both same-sex and opposite-sex relationships predict survival in wild female baboons. *Proc. R. Soc. B Biol. Sci.* **281**, 20141261 (2014).

33. J. Ostner, O. Schülke, "Linking Sociality to Fitness in Primates: A Call for Mechanisms" in *Advances in the Study of Behavior*, (Elsevier, 2018), pp. 127–175.

34. J. B. Silk, *et al.*, Strong and Consistent Social Bonds Enhance the Longevity of Female Baboons. *Curr. Biol.* **20**, 1359–1361 (2010).

35. R. Bshary, X.-Y. L. Richter, C. Van Schaik, Male services during between-group conflict: the 'hired gun' hypothesis revisited. *Philos. Trans. R. Soc. B Biol. Sci.* **377**, 20210150 (2022).

36. C. P. Van Schaik, R. Bshary, G. Wagner, F. Cunha, Male anti-predation services in primates as costly signalling? A comparative analysis and review. *Ethology* **128**, 1–14 (2022).

37. C. H. Janson, M. L. Goldsmith, Predicting group size in primates: foraging costs and predation risks. *Behav. Ecol.* **6**, 326–336 (1995).

38. S. T. Iqbal, B. P. Bailey, Understanding and developing models for detecting and differentiating breakpoints during interactive tasks in *Proc SIGCHI Conf Hum Factor Comput Syst*, (ACM, 2007), pp. 697–706.

39. J. H. Tomal, J. J. H. Ciborowski, Ecological models for estimating breakpoints and prediction intervals. *Ecol. Evol.* **10**, 13500–13517 (2020).

40. A. Baniel, G. Cowlishaw, E. Huchard, Stability and strength of male-female associations in a promiscuous primate society. *Behav. Ecol. Sociobiol.* **70**, 761–775 (2016).

41. J. B. Silk, *et al.*, The benefits of social capital: close social bonds among female baboons enhance offspring survival. *Proc. R. Soc. B Biol. Sci.* **276**, 3099–3104 (2009).

42. C. K. Hemelrijk, J. Wantia, K. Isler, Female Dominance over Males in Primates: Self-Organisation and Sexual Dimorphism. *PLoS ONE* **3**, e2678 (2008).

43. T. Saccà, G. Gort, E. Van De Waal, C. K. Hemelrijk, Male intrasexual aggression and partial dominance of females over males in vervet monkeys. *Front. Ecol. Evol.* **10**, 930266 (2022).

44. K. E. Langergraber, J. C. Mitani, D. P. Watts, L. Vigilant, Male–female socio-spatial relationships and reproduction in wild chimpanzees. *Behav. Ecol. Sociobiol.* **67**, 861–873 (2013).

45. O. Schülke, J. Bhagavatula, L. Vigilant, J. Ostner, Social Bonds Enhance Reproductive Success in Male Macaques. *Curr. Biol.* **20**, 2207–2210 (2010).

46. C. Young, R. McFarland, L. Barrett, S. P. Henzi, Formidable females and the power trajectories of socially integrated male vervet monkeys. *Anim. Behav.* **125**, 61–67 (2017).

47. S. Shultz, R. Dunbar, Bondedness and sociality. *Behaviour* **147**, 775–803 (2010).

48. D. van Vuren, Ectoparasites, Fitness and Social Behaviour of Yellow-Bellied Marmots. *Ethology* **102**, 686–694 (1996).

49. R. W. Wrangham, An Ecological Model of Female-Bonded Primate Groups. *Behaviour* **75**, 262–300 (1980).

50. A. A. Galezo, *et al.*, Mechanisms of inbreeding avoidance in a wild primate. *Curr. Biol.* **32**, 1607-1615.e4 (2022).

51. E. M. Tennenhouse, Inbreeding Avoidance in Male Primates: A Response to Female Mate Choice? *Ethology* **120**, 111–119 (2014).

52. L. A. Isbell, D. L. Cheney, R. M. Seyfarth, Costs and benefits of home range shifts among vervet monkeys (Cercopithecus aethiops) in Amboseli National Park, Kenya. *Behav. Ecol. Sociobiol.* **27**, 351–358 (1990).

53. P. M. Kappeler, V. Mass, M. Port, Even adult sex ratios in lemurs: Potential costs and benefits of subordinate males in Verreaux's sifaka (*Propithecus verreauxi*) in the Kirindy Forest CFPF, Madagascar. *Am. J. Phys. Anthropol.* **140**, 487–497 (2009).

54. C. P. van Schaik, M. Hörstermann, Predation risk and the number of adult males in a primate group: a comparative test. *Behav. Ecol. Sociobiol.* **35**, 261–272 (1994).

55. M. Baldellou, S. Peter Henzi, Vigilance, predator detection and the presence of supernumerary males in vervet monkey troops. *Anim. Behav.* **43**, 451–461 (1992).

56. C. K. Hemelrijk, M. Wubs, G. Gort, J. Botting, E. Van De Waal, Dynamics of Intersexual Dominance and Adult Sex- Ratio in Wild Vervet Monkeys. *Front. Psychol.* **11**, 839 (2020).

Figures and Tables

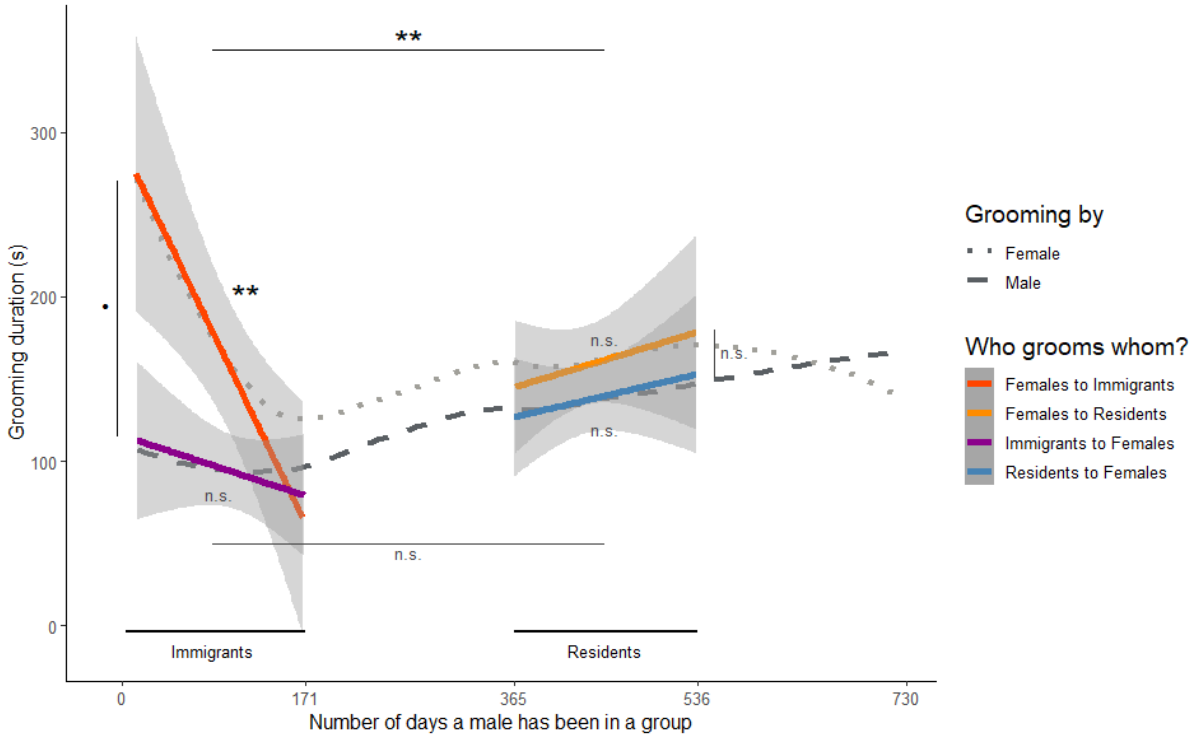

Figure 1: Grooming duration between females and males in relation to the male's status. The dotted gray lines represent the overall trends for grooming duration, with the smaller dots for females and larger dots for males. The colored lines show model trends for different grooming interactions: females grooming immigrant males (dark orange), females grooming resident males (yellow), immigrant males grooming females (purple), and resident males grooming females (blue). The decrease in grooming duration by females grooming immigrant males is significant (*indicated with* $**$). Females also changed their grooming duration significantly different over time for immigrants than they do for residents (*indicated with* $**$). There was a marginally non-significant difference between the change in grooming duration over time between immigrants and females (*indicated with* •); the overall mean difference in grooming investment between immigrants and females was significant (not indicated in figure).

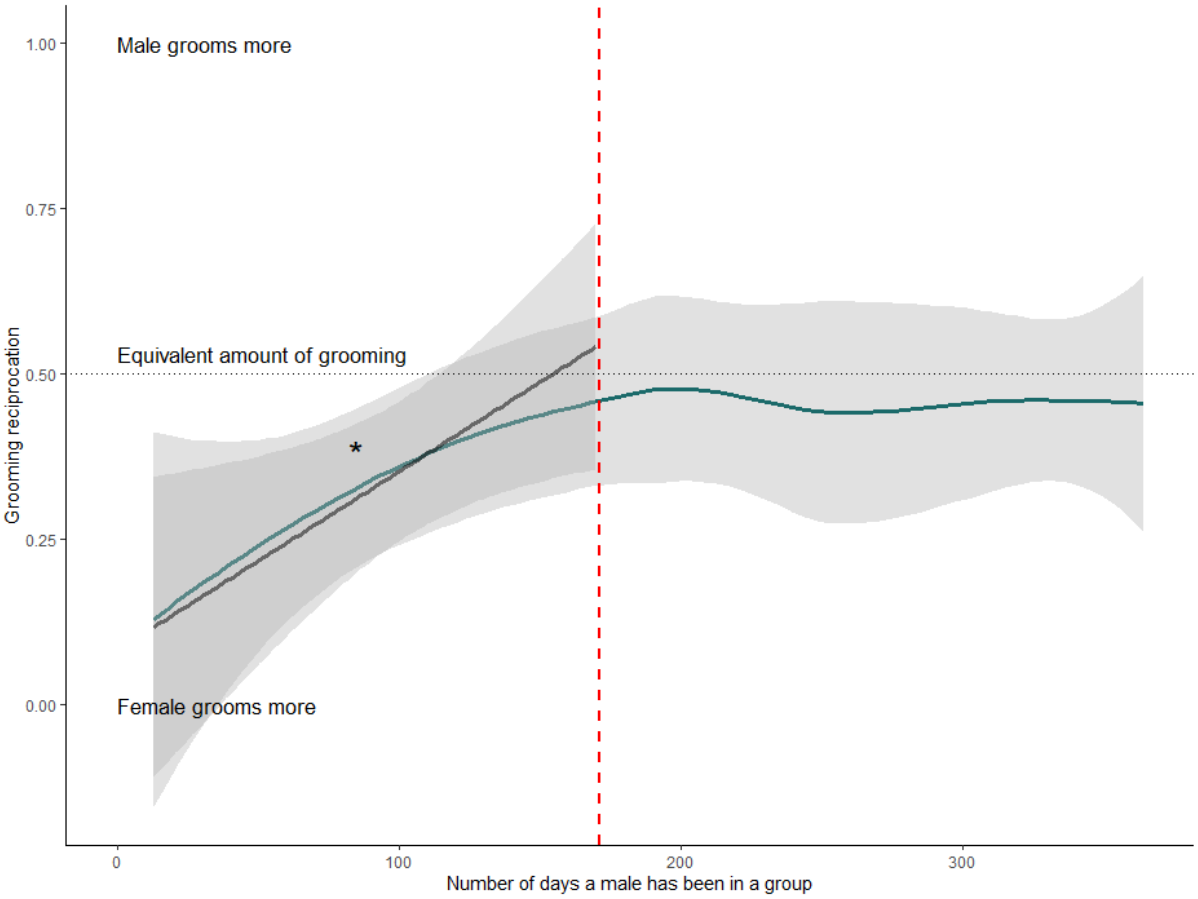

Figure 2: Grooming reciprocation rates between males and females over the first year of a male's tenure. Positive values indicate males investing more and negative values females investing more. The red dotted line shows the breakpoint found by the breakpoint model. Therefore, any interactions with a male to the right of this line is qualified as an interaction with an immigrant. Reciprocity increases significantly for these interactions (*indicated with* $*$).

Table 1: overview of each male category and from which day they are considered to be in a certain category

Male category	Day of residence	n males	n female partners
Immigrant	0 – 171	18	39
Resident	365 – 536	22	61

*Table 2: Overview of the main results from the analysis of grooming behaviour in relation to sex, male status (immigrant or resident), and time (DayStatus). The table provides estimates, standard errors (SE), p-values, and significance levels for comparisons of grooming duration and changes over time across different groups. Significant results (p < 0.05) are marked with "**," marginally significant results (p < 0.1) are marked with ".", and non-significant results are marked with "n.s."*

Comparison	Estimate	SE	p-value	Significance
Females grooming immigrants vs. immigrants grooming females	0.61	0.18	0.004	**
Females grooming residents vs. residents grooming females	0.21	0.1	0.18	n.s.
Females grooming residents vs. immigrants	0.05	0.16	0.99	n.s.
Immigrants grooming females vs. residents grooming females	-0.35	0.17	0.17	n.s.
Females grooming immigrants over time	-0.38	0.12	0.002	**
Females grooming residents over time	0.05	0.1	0.63	n.s.
Immigrants grooming females over time	-0.11	0.14	0.42	n.s.
Residents grooming females over time	0.03	0.1	0.76	n.s.
Females grooming immigrants vs. residents over time	-0.43	0.14	0.003	**
Immigrants grooming females vs. residents over time	-0.14	0.15	0.37	n.s.
Females grooming immigrants vs. immigrants grooming females over time	-0.27	0.16	0.08	.
Females grooming residents vs. residents grooming females over time	0.02	0.1	0.86	n.s.

Appendix

Table S1: statistical models applied to different datasets

Topic	Model	Response variable transformations
Grooming duration	*glmer.nb(*Duration ~ Sex * DayStatus * StatusMale + Group + Season+ *(1|MaleID)* + *(1|FemaleID)*	NA
Reciprocity	*glmer*(BinomialReciprocity ~ DayStatus * Status + *(1| MaleID)*	BinomialReciprocity: *if Reciprocity > 0, 1, otherwise if Reciprocity < 0, 0.*

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The authors do not have any competing interest.

Data availability

All relevant data and code are available on GitHub: https://github.com/mariagranell/establishment_grooming_exchanges/tree/main.

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