

## Wild female vervet monkeys change grooming patterns and partners when freed from feeding constraints

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Social animals face daily challenges to fulfil feeding, resting and social needs. In vervet monkeys, *Chlorocebus pygerythrus*, females are the core of the social group, in which relationships are mainly established and maintained through grooming. However, social relationships are not necessarily mutual or driven by the same interests. In a complex and diverse social environment, individuals may benefit from the ability to adapt their manoeuvring to different pressures. We experimentally manipulated the activity budget of two adult females (fed subjects) per group in four wild groups to investigate activity budgets, grooming behaviour variation and the implications for possible changes in social interactions. Specifically, we provisioned food to one fed subject at a time for 2 weeks (treatment), evaluated changes in their grooming behaviour before, during and after being fed, and compared their behaviour with that of the remaining adult females in the group (nonfed subjects) over the same period. In the provisioning phase, the fed subjects decreased feeding time, but increased resting and social time. We found that fed subjects increased their grooming strength and ratio of grooming given to received and showed preferences to groom existing partners, kin and adult females. Moreover, we found no carryover effect of provisioning on grooming strength after the treatment terminated. Our results demonstrate rapid social behaviour plasticity following manipulation of ecological conditions for specific female individuals, allowing for flexible shifts in grooming patterns that hint at Machiavellian-like adjustments that may help achieve social benefits through, at least partially, restructuring their social network when experimentally released from daily feeding obligations.

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While living in social groups allows individuals to reduce predation risks and to keep neighbouring groups at bay, it also causes within-group competition for resources (Beauchamp, 2014; Cheney & Seyfarth, 1987; Rubenstein, 1978; van Schaik & van Hooff, 1983). Within-group competition leads to selection on individuals to show behaviours that minimize the costs of conflict, such as showing submissive behaviour to dominants and building alliances for mutual support (Broom et al., 2009; Forkman & Haskell, 2004; Mesterton-Gibbons & Dugatkin, 1995).

It has been proposed that cooperation and conflict between members of a group was a major selective force for the evolution of

complex cognitive processes and more complex brains. The Machiavellian intelligence hypothesis, initially developed to understand primate social behaviour, focuses on cognitive processes (Bshary et al., 2011; Humphrey, 1976; Whiten & Byrne, 1988; Whiten & van Schaik, 2007). Early empirical efforts linked some primate observations on tactical deception, that is, the production of a signal out of its usual context to induce recipients to show context-related behaviour (to their disadvantage and the signaller's advantage) to the presence of theory of mind, that is, the ability to perceive other individuals as agents with their own goals and beliefs (Byrne & Whiten, 1992; Harcourt, 1988). However, tactical deception has been observed in various species that have small brains relative to monkeys and apes, including forest birds, domestic chickens, *Gallus gallus domesticus*, drongos, *Dicrurus*

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*adsimilis*, ravens, *Corvus corax*, wolves, *Canis lupus*, and cleaner fish, *Labroides dimidiatus* (Bugnyar & Kotrschal, 2002; Byrne & Whitten, 1997; Flower et al., 2014; Munn, 1986; Packard, 2012; Soares et al., 2014). Such examples show that, in contrast to the general proposal of the Machiavellian intelligence hypothesis, ecology rather than brain morphology predicts whether animals are capable of manipulating their social environment, suggesting that more empirical studies are needed to clarify the underlying cognitive processes of specific social behaviours (Brosnan & Bshary, 2010; Brosnan et al., 2010; Brosnan et al., 2010).

A more modest approach to the Machiavellian intelligence hypothesis is to focus first on the extent to which animals show strategic sophistication in their social interactions, as a basis for the potential development of experimental paradigms that allow testing of whether the underlying cognitive processes are complex. An estimate of strategic sophistication can be how flexible animals are in their ability to respond to social and environmental information. Behavioural flexibility or plasticity helps avoid rigid adherence to certain behavioural options and instead permits the adoption of flexible behavioural possibilities (Lehmann et al., 2007a, 2007b; Oliveira, 2012; Snell-Rood, 2013; Stamps & Groothuis, 2010; Taborsky & Oliveira, 2012). Flexibility can potentially operate on different timescales, for example within a day, between seasons or even years (Henzi et al., 2009; Sick et al., 2014).

One potential way to test for behavioural flexibility in the context of social manoeuvring is to alter time budget constraints. Given that time is a finite resource, it is important to consider that the time individuals devote to social interactions must be traded off against other relevant activities like feeding or resting (Dunbar, 1992). Meta-analyses show that high demands for foraging and resting limit the time individuals have to socially interact with group peers (Dunbar et al., 2009; Lehmann et al., 2007b). Under natural conditions, all members of a group face similar time budget constraints, which may mask individual competition over access to the most profitable partners within a group. For example, all group members may prefer to interact, cultivate and potentially establish social bonds with the most dominant individuals, as these may provide protection and/or tolerance (Seyfarth, 1977; Wubs et al., 2018). If all group members have time limitations to establish social bonds, it may be difficult to investigate the competitive nature of social interactions. However, reducing time budget constraints of preselected subjects may reveal whether they use the extra time for social manoeuvring or whether they simply rest more.

Here, we experimentally subsidized individual female vervet monkeys, *Chlorocebus pygerythrus*, with high-quality food to test how that manipulation would affect their time budget, and to what extent they would use the reduced need for foraging to improve their social relationships and with whom. We focused on changes in their grooming activities as a key social behaviour. Grooming serves to remove a partner's ectoparasites that are difficult to remove by oneself, but also to build social relationships and to repair them (termed reconciliation; de Waal & van Roosmalen, 1979) not only in primates (Bonnie & de Waal, 2004; Burkett et al., 2016; Dunbar & Shultz, 2010; Engelman & Herrmann, 2016; Fedurek & Dunbar 2009; Preston & de Waal, 2002) but also in a variety of mammals (Feh & de Mazierès, 1993; Mooring et al., 1996; Stieger et al., 2017), birds (referred to as preening; Emery et al., 2007; Fraser & Bugnyar, 2012; Morales Picard et al., 2020) and even in fish (referred to as tactile stimulation; Bshary & Würth, 2001; Soares et al., 2011). Grooming has relaxing effects due to a variety of physiological responses, including the release of beta-endorphins (Dunbar, 2010; Keverne et al., 1989; Machin & Dunbar, 2011) and has also been related to oxytocin levels (Benítez et al., 2018; Carter & Wilkinson, 2015; Crockford et al., 2013; Snowdon et al., 2010) or the reduction of stress hormones

(Brent et al., 2011; Crockford et al., 2008; Seyfarth & Cheney, 2012; Soares et al., 2012; Wittig et al., 2008). Regular grooming partners are more likely to form coalitions during conflicts (Schino & Aureli, 2008; Seyfarth et al., 2010; van Schaik et al., 2006; Young et al., 2014), exchange commodities such as tolerance or support in conflicts (Borgeaud & Bshary, 2015; Schino, 2007; Schino & Aureli, 2008; Tiddi et al., 2011), and share food (Carter & Wilkinson, 2013; Fruteau et al., 2009; Ventura et al., 2006; von Bayern et al., 2007; Wittig et al., 2014). Having strong stable bonds appears to have measurable positive fitness consequences in terms of life expectancy and infant survival (Riehl & Strong, 2018; Silk et al., 2003; Silk et al., 2010). Based on this, we expected that a reduction in foraging time may reveal changes in grooming behaviours that could indicate strategizing, understood as a predilection or selective affinity towards certain group members (van Schaik, 2016).

In four study groups, one high-ranking and one low-ranking adult female received extra food each day during a treatment phase for 2 weeks. Thus, we focused our study on two different categories of females: the experimental individuals we fed during the treatment phase (fed subjects hereafter) and the rest of the adult females (nonfed subjects hereafter). We selected adult females as study subjects because vervet monkeys live in female-bonded groups where they are the philopatric sex (Isbell et al., 1991). Robust female–female associations can enable them to override the potential costs of male aggression (Barrett & Henzi, 2002; Sterck et al., 1997) and assist coordination to solve collective action problems while defending territories and the food sources within them (Willems et al., 2015). The hierarchy of females is rigid and linear whereby dominants have priority of access to food sources, and individuals have precise third party rank relationship knowledge (Borgeaud et al., 2015; Renevey et al., 2013). We conducted our experiment during the dry season when food is scarce, so we expected vervet monkeys across age–sex classes to be experiencing time budget restrictions. Because social interactions determine group structure and the nature of the connections within the group (Hinde, 1976; Whitehead et al., 1999), we used a social network analysis approach for the quantitative analysis of the interactions (edges) between individuals (nodes; Whitehead, 2008) and their underlying causes and consequences (Cantor et al., 2021). Social network analysis allows the assessment of social interactions dynamically by linking social behaviours to time slots, thus permitting the comparison of time intervals and accurately pinpointing changes (Farine, 2018; Hobson et al., 2013; Pinter-Wollman et al., 2014; Waters & Fewell, 2012).

First, we needed to confirm that activity budgets varied during the experimental feeding treatment (confirmatory activity budgets). We predicted that by experimentally inducing a reduction in the need for the fed subjects to allocate time to foraging, our experimental manipulation should lower time budget constraints on resting, which we predicted would increase. If the time allocated to social interactions is normally limited (Dunbar et al., 2009; Lehmann et al., 2007a, 2007b), we also expected fed subjects to spend more time socializing, in particular, to spend more time grooming other individuals. Such a result would yield several follow-up questions. (1) Do changes in the grooming of fed subjects differ from those of nonfed subjects when freed from feeding restrictions, and do fed subjects change their grooming partners differently depending on how much they groom before the treatment? Moreover, does having extra time improve the fed subjects' standing in the group, that is, does their position in the social network become more central through (2) an increase in their number of grooming partners and/or (3) the frequency of interactions? (4) Do other group members reciprocate or groom fed subjects more in return (grooming reciprocity, the ratio of grooming given to grooming received)? Further, how do fed subjects

distribute their extra grooming relative to their partners' attributes: do they focus on (5) existing social partners, (6) high-ranking individuals, (7) relatives or (8) other adult females? (9) If the fed subjects increase their grooming given as part of the activity budget while fed, do they maintain it after the food provisioning is finished? Finally (10) do dominant and subordinate fed subjects adjust grooming in similar ways (increase in grooming given) and (11) do they differ in their grooming reciprocity? Changes in grooming patterns, including grooming with more partners, should, in turn, affect key social network parameters (Brent et al., 2013; Crofoot et al., 2011; Henzi et al., 2009). We used grooming interaction data to calculate the rate of accumulation of grooming partners and the number of interactions over time, which constitute informative measures of the individuals' social investment in the group (Farine & Whitehead, 2015; Krause, James, & Croft, 2010; Sueur et al., 2011). If vervet monkey females strategically compete with other group members over access to profitable partners and/or over central positions within the group's social network, we expected that fed subjects would have more rapidly expanding grooming networks than nonfed subjects. Furthermore, we predicted that fed subjects should opt to preferentially groom adult females and high-ranking individuals because of the benefits that can be gained from socializing with them (Seyfarth, 1977).

## METHODS

### *Study Site and Subjects*

We carried out our experiment at the Inkawu Vervet Project (IVP) research site, in Mawana Game Reserve (28°00.327S, 031°12.348E, Kwazulu Natal, South Africa). The study was conducted with four groups: Kubu (four adult females and 12 individuals in total), Ankhase (three adult females and 22 individuals in total), Noha (six adult females and 29 individuals in total) and Baie Dankie (10 adult females and 44 individuals in total), making a total of 23 adult females that were key in their societies (see Appendix Tables A1–A3; Isbell et al., 1991). Among all adult females of each group, we selected one dominant and one subordinate as experimental fed subjects (subjects hereafter) based on their rank (see Appendix Table A4). We chose the highest-ranking female as the dominant fed subject in each group and the lowest or closest to the lowest-ranking female as the subordinate fed subject. The other adult females were nonfed subjects (see Appendix Table A5 for group composition). All individuals were recognized through identifiable physical traits and observers were considered experienced enough to participate in data collection after 80% of Cohen's kappa agreement between observers was reached.

### *Experimental Design and Data Collection*

Primates living in seasonal environments experience fluctuations in food availability and must adapt their activity budget to this (Henzi et al., 2003; Canteloup et al., 2019; McFarland et al., 2014). When food is scarce primates intensify feeding efforts on lower-quality resources with a low foraging efficiency (Miller et al., 2020) and they also regulate resting time to endure harsh environmental conditions (Dunbar, 1992; Korstjens et al., 2010). This experiment was carried out during the dry season (July–October) when food availability was low as this motivates the monkeys to participate (see Appendix Figs A1–A4). We structured the experiment as follows: (1) 2 weeks to 1 month of a nonfeeding phase (control-before), (2) 4 weeks of treatment (2 weeks feeding the dominant subject and 2 weeks feeding the subordinate subject but not simultaneously) and (3) 2 weeks to 1 month of a nonfeeding phase (control-after; see Appendix and Table A6 for details). Food

provisioning consisted of two feeding sessions per day: the first, early in the morning as the monkeys woke up, consisted of two apples with 40 grains of corn inserted (around 280 kcal); the second, 3 h later, consisted of two apples (around 200 kcal; see Appendix for details). Food provisioning constituted approximately half to a third of the daily caloric intake depending on females' reproductive state (Hess et al., 1979; Seier et al., 2000).

Before the experiment we trained the monkeys to get the food from the apparatus. Food was provided in personalized wooden boxes that we opened with a remote control when the fed subjects touched the box. Personalization consisted of wooden covers with unique colour patterns that individuals learnt to recognize when presented with two boxes placed 2 m apart. We considered subjects to be successful in choosing the right box when they performed the right choice above 75% of the time during training sessions.

We collected systematic focal animal sampling data (Altmann, 1974) on all experimental females, fed subjects and nonfed subjects, throughout the day, to record their activity across study phases: control-before, treatment (dominant fed, subordinate fed) and control-after. The main activities were feeding, resting, moving and social (sitting in contact, mouth-to-mouth, grooming given, grooming received; see Appendix Table A7). Because moving activity is influenced by group behavioural patterns (Montiglio et al., 2018), especially during the dry season when food is sparsely distributed (Janson & van Schaik, 1988), we did not draw conclusions from this activity, since our focus lay on behaviour at the individual level. Our focal data were collected in 20 min bouts, with behaviours (feeding, resting, moving and broad social) entered every 2 min, over three time periods (of the same length spanning sunrise to sunset) on alternate days to cover the entire spectrum of activities, as vervets often nap for long stretches during the hottest part of the day. Altogether, we collected over 17 000 data points during 283 h of focal observations across the 23 experimental females (average  $6.21 \pm 0.1$  h per individual per study phase; see Appendix Tables A8–A10). The same data were used to calculate the grooming-derived parameters for each experimental female's social network.

While our focal observations were focused only on experimental females, grooming partners could belong to any category of individuals. Given that it was not always possible to keep an individual in sight during a focal observation, which caused the loss of some data points, we converted our grooming measurements to rates (Davis et al., 2018; Leu et al., 2016). Our first measure was equivalent to 'degree' in a social network (a measure of the total number of edges connected to a particular focal individual, here the number of grooming partners), which we calculated as the accumulation of grooming partners (i.e. degree divided by observation time) to account for differences in observation time. The second measure was the strength of a female's connections (Farine, 2015), which was calculated as the number of grooming interactions or events detected over the individual's focal observations, divided by the time for which that individual was observed. We calculated social bonds using proximity data collected from focal animal sampling (Altmann, 1974) following Fedurek's method as an indicator of social affinity between female dyads (Borgeaud & Bshary, 2015, 2018; Fedurek et al., 2013; Machanda et al., 2014) which was highest when two individuals were mutual social partners. Accordingly, we refer to mutual social partners as having a social bond. We used agonistic interaction data from ad libitum data to calculate rank scores using the Elo-rating package (Neumann et al., 2011; Sánchez-Tójar et al., 2018) in R (R Core Team, 2008). We included dyadic agonistic interactions that had a clear aggressive (chase, bite, hit, take place, hand on top of the head, stare-attack) and submissive behaviour (retreat, flee, scream, crawl). Finally, we used our 10-year life history database to extract

mother–offspring and siblings' affiliations as a measure of kinship (see Appendix for details).

#### *Effect of Food Supplementation on Activity Budgets*

As a first step, we investigated whether the treatment phase or supplementary feeding induced changes in the activity budgets (feeding, resting, moving and broad social) of the fed subjects. We analysed each activity separately: feeding, resting, broad social (social henceforth) and grooming given. We conducted a series of generalized linear mixed models (GLMMs; Bolker et al., 2009; Zuur et al., 2010) with binomial distribution to evaluate the effect of the treatment (measured as the phase of the study: treatment-dominant fed and treatment-subordinate fed) on the different activities. The response variable in the models was binary to represent whether each activity was displayed or not in each study phase. Thus, we studied the variation of feeding, resting and social behaviours, from which we extracted grooming given behaviours, and we performed GLMMs with each activity as the response variable, study phase as the explanatory variable and the category of individual (fed and nonfed) as another explanatory variable with an interaction between the two. We analysed the change in activities over two study phases: (1) control–before versus treatment (effect of treatment) and (2) treatment versus control–after (carryover effects) separately for fed subjects and nonfed subjects as only fed subjects were exposed to experimental conditions during the treatment phase. Individual identity, group and time of the day were set as random factors in the models. All analyses were performed using the lme4 package (Bates et al., 2015) in R (R Core Team, 2008).

#### *Network Measures of Grooming Given*

To test the impact of food supplementation on grooming behaviours, we calculated the rate of accumulation of grooming partners, grooming strength and grooming reciprocity during each study phase from the focal data, including all age and sex classes of possible grooming partners the females had. The accumulation of grooming partners reflects the number of relationships a given individual accumulated over observation time, while grooming strength refers to the number of grooming interactions over observation time (Clayton, 2017; Farine & Whitehead, 2015; Krause et al., 2007; Kurvers et al., 2014; Whitehead, 2008; Wilson et al., 2014). Both measures are suitable indicators of the social connectivity of the individual within the group and of her social standing (Krause et al., 2007; Whitehead, 2008). We used grooming given to measure the number of grooming partners and strength as a grooming network measure to identify the focal individuals giving grooming to social partners (any individual of the group). As a proxy of grooming reciprocity, we divided each female's grooming given by her grooming received with each social partner (Hemelrijk, 1990).

We studied changes in grooming across study phases to address different questions. Specifically, we tested the following. (1) We assessed the change in grooming partners when individuals were freed from feeding restrictions by dividing number of grooming events given to partners (grooming strength) during the treatment by the number of grooming events given to partners (grooming strength) in the control–before phase. This permitted us to see whether fed and nonfed subjects changed their grooming differently and whether the individuals whose grooming strength was most limited initially expressed a larger increase in grooming given than those whose grooming strength was higher. (2) We investigated whether the supposed extra time that the fed subjects gained thanks to the supplementary feeding influenced their standing in

the network by studying their accumulation of grooming partners through the increase in grooming given and (3) the frequency of grooming for which we used grooming strength between the control–before and treatment phases. (4) We examined to what extent the grooming reciprocity ratio (grooming ratio hereafter) might shift between the control–before and the treatment phases. A positive ratio indicates a subject has a bias towards giving grooming, while a negative one indicates a bias towards receiving grooming. Ratios close to zero reflect evenness in grooming given and received. (5–8) We investigated whether the 'extra grooming', in the form of grooming strength, that we expected fed subjects to perform during the treatment phase preferentially targeted specific individuals as grooming partners relative to the following attributes (all binary): (5) existing social partner, (6) high rank, (7) kin and (8) adult females. A variation in preferences could indicate tactical selection of social partners before engaging in grooming interactions. (9) Because extra food was provided only in the treatment phase, we investigated whether the fed subjects' expected grooming increase during this phase, in the form of grooming strength, was maintained in the control–after phase. This would imply the existence of carryover effects.

Additionally, we evaluated possible grooming differences between dominant and subordinate subjects. We evaluated whether dominant and subordinate fed subjects adjusted their grooming given similarly by looking at their grooming strength and their grooming ratio.

To calculate the significance of the change in grooming, we used null model hypothesis testing (Croft et al., 2011; Farine, 2017; Farine & Whitehead, 2015). Since we were interested in understanding how food provisioning influenced our observed focal data (how fed and nonfed subjects changed their grooming rates) and whether subjects showed possible tactical preferences to direct grooming to specific partner' attributes and grooming reciprocity, we designed a permutation test in which we randomized the study phase variable within each individual. This test is similar to node permutations, but instead of randomizing identity we randomized the study phase corresponding to each individual's social metric (social network measures of accumulation of grooming partners, strength, grooming ratio). We calculated the observed effect by subtracting the mean change in the category subjects from the mean change in the category nonsubjects, thus obtaining the test statistic representing the difference in the response between individuals according to treatments. We repeated this calculation on the permuted data 1000 times. We evaluated the significance of the differences by comparing the observed test statistic to the distribution of the randomized test statistic values, where an observed value is significantly different if it is greater or smaller than 95% of the randomized data (Farine, 2017). Therefore, we interpreted both upper and lower significance thresholds following the criterion: 'the result is significant at  $\Prand = 0.05$  if 2.5% of the random values are greater than or equal to the observed value, or if more than 97.5% of the random values are greater than or equal to the observed value' (Farine, 2017, p. 1311); here we refer to the significance value generated from the permutation test as  $\Prand$  (see scheme representing the different steps of the study details in Appendix Fig. A1).

#### *Ethical Note*

Ethical permission for the study was granted by the Ezemvelo Wildlife Board (KwaZulu-Natal, South Africa), the University of Cape Town and the van der Walt family, owners of Mawana Game Reserve. The study adhered to the ASAB/ABS Guidelines for the Treatment of Animals in Behavioural Research. All individuals were habituated to the feeding boxes without direct human–monkey interaction. We attracted fed subject adult females to the box set-

up by clicking the tongue, a sound they learned to associate with the feeding sessions. Fed subjects approached their boxes voluntarily and had no dependent infants during the study. The experimental set-up did not cause dominant females to attack subordinate counterparts, and hence no wounds were caused by our experiment. Corn and apples were cleaned beforehand and handled with gloves to avoid the possible transmission of diseases. Similar training has been conducted on vervet monkeys by other researchers at the IVP study site without appearing to affect the wellbeing of the individuals (Arseneau-Robar et al., 2016; Bono et al., 2018; Borgeaud & Bshary, 2015; Borgeaud et al., 2017; Canteloup et al., 2020).

## RESULTS

### *Effect of Food Supplementation on Activity Budgets*

We found that the fed subjects significantly decreased their feeding from the control-before to the treatment phase by around 22% and subsequently increased it by approximately 16% from the treatment phase to the control-after phase (Tables 1, 2, Fig. 1). In contrast, nonfed subjects increased feeding time by about 6% during the treatment phase relative to the control-before phase, and decreased it by 14% during the control-after phase (Tables 1, 2, Fig. 1). Fed subjects significantly increased their resting during the treatment, by almost 16%, compared to the control-before phase, and decreased during the control-after phase by almost 8% (Tables 1, 2, Fig. 1). Nonfed subjects maintained their resting levels from the control-before to the treatment phase but increased them almost twofold during the control-after phase (Tables 1, 2, Fig. 1).

Regarding broad social behaviours, the fed subjects significantly increased these by almost 10% from the control-before to the treatment phase and decreased them in the control-after phase by around 11% (Tables 1, 2, Fig. 1). Nonfed subjects maintained their broad social behaviours across all three phases (Tables 1, 2, Fig. 1), therefore not changing their sociality significantly (as a consequence, grooming given remained unchanged too). Fed subjects significantly changed their allocation to grooming given across study phases: during the treatment phase they increased their grooming given by almost 7% compared to the control-before phase, and reduced it afterwards by 6.5% (Tables 1, 2, Fig. 1). Nonfed subjects decreased their grooming given from the control-

before to the treatment phase, with a nonsignificant increase in the control-after phase relative to the treatment phase (Tables 1, 2, Fig. 1). Fed subjects did not significantly change their moving activity from the control-before to the treatment phase but they did change from the treatment to the control-after phase (Tables 1, 2, Fig. 1). Nonfed subjects significantly decreased their moving activity by 4% between the control-before and the treatment phase and increasing it by almost 6% between the treatment and control-after phase (Tables 1, 2, Fig. 1).

### *Changes in Grooming Partners*

The permutation analysis revealed that the fed subjects ( $N = 8$  individuals) changed their grooming partners differently than nonfed subjects ( $N = 15$  individuals) between the control-before and the treatment phase (Table 3, Test A), as they increased their network more than nonfed subjects (mean difference subjects versus mean difference nonfed subjects) that did not undergo a relevant change (slope in Appendix Fig. A5). Moreover, the fed subjects' negative slope suggests that those that had lower grooming in the control-before phase increased it more (larger ratio between treatment and control-before phases). Thus, individuals that groomed least during the control-before phase (left side of  $x$ -axis, Appendix Fig. A5) added more grooming partners to their network (per unit of observation time) during the treatment phase, as the grooming in the treatment phase was disproportionately larger than the grooming in the control-before phase.

### *Changes in Grooming Given*

For all analyses involving comparisons between fed subjects and nonfed subjects sample sizes were eight and 15 individuals, respectively. Permutation tests revealed that fed subjects increased the rate of accumulation of grooming partners between the control-before and treatment phase (Table 3, Test B, Fig. 2) 1.21 times and nonfed subjects 0.57 times. Moreover, subjects increased their grooming strength significantly compared to nonfed subjects (Table 3, Test C), as they increased it 2.43 times in the treatment compared to the control-before phase whereas nonfed subjects decreased it by 0.79 times. Fed subjects increased their grooming given proportionately more than the grooming they received from other group members; their grooming ratio increased 3.7 times

**Table 1**  
Summary of GLMMs showing the effect of study phase on the different activities

Dependent variable	Category	Explanatory variable Study phase	Estimate	SE	<i>P</i>
Feeding	Fed subjects	Treatment vs Control-before	-0.972	0.081	<0.001
		Control-after vs Treatment	0.720	0.078	<0.001
	Nonfed subjects	Treatment vs Control-before	0.278	0.055	<0.001
		Control-after vs Treatment	-0.621	0.053	<0.001
Resting	Fed subjects	Treatment vs Control-before	0.884	0.098	<0.001
		Control-after vs Treatment	-0.423	0.087	<0.001
	Nonfed subjects	Treatment vs Control-before	-0.088	0.085	0.294
		Control-after vs Treatment	0.661	0.071	<0.001
Social	Fed subjects	Treatment vs Control-before	0.662	0.107	<0.001
		Control-after vs Treatment	-0.839	0.110	<0.001
	Nonfed subjects	Treatment vs Control-before	-0.100	0.076	0.387
		Control-after vs Treatment	0.053	0.075	0.763
Grooming given	Fed subjects	Treatment vs Control-before	0.942	0.158	<0.001
		Control-after VS Treatment	-0.843	0.149	<0.001
	Nonfed subjects	Treatment vs Control-before	-0.275	0.102	0.019
		Control-after vs Treatment	0.184	0.103	0.172
Moving	Fed subjects	Treatment vs Control-before	-0.259	0.127	0.102
		Control-after vs Treatment	0.319	0.122	0.025
	Nonfed subjects	Treatment vs Control-before	-0.490	0.087	<0.001
		Control-after vs Treatment	0.647	0.081	<0.001

**Table 2**  
Summary of the activity budget GLMMs for the different activities

Dependent variable	Explanatory variables	$\chi^2$	df	P
Feeding	Study phase	38.650	2	<0.001
	Category of individual	40.767	1	<0.001
	Study phase * Category of individual	214.167	2	<0.001
Resting	Study phase	55.339	2	<0.001
	Category of individual	38.411	1	<0.001
	Study phase * Category of individual	119.583	2	<0.001
Social	Study phase	16.003	2	<0.001
	Category of individual	7.660	1	0.0056
	Study phase * Category of individual	63.717	2	<0.001
Grooming given	Study phase	3.705	2	0.157
	Category of individual	6.042	1	0.014
	Study phase * Category of individual	61.512	2	<0.001
Moving	Study phase	79.337	2	<0.001
	Category of individual	0.247	1	0.619
	Study phase * Category of individual	5.609	2	0.061

Study phase: control-before, treatment, control-after; category of individual: fed subjects, nonfed subjects.

from not skewed during the control-before phase to being more biased towards giving grooming (Table 3, Test D), while nonfed subjects decreased it 0.19 times in the treatment compared to the control-before phase.

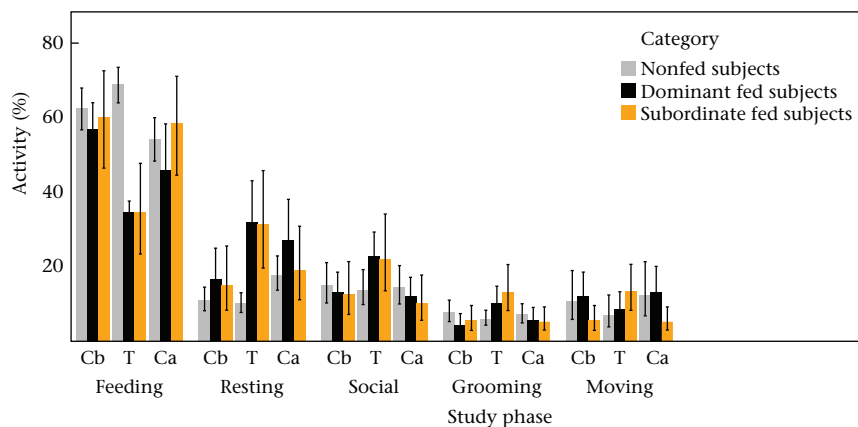
Fed subjects increased their grooming strength significantly to their existing social partners 4.3 times (nonfed subjects decreased it 0.66), their kin 1.51 times (nonfed subjects decreased it 0.68), and to other adult females 5.5 times (nonfed subjects decreased it 0.83; Table 3, Test E, G, H), while their increase in grooming strength to high-ranked individuals (1.66 times) was close to significant (Table 3, Test F; nonfed subjects decreased it 0.86 times). Regarding a possible carryover effect, fed subjects decreased their grooming strength significantly 0.45 times in the control-after phase and did not maintain the increase recorded from the control-before to the treatment phase (Table 3, Test I) while nonfed subjects increased it 1.19 times from the treatment to the control-after phase. Summarizing, fed subjects changed their grooming measures positively more than nonfed subjects, except in the carryover of strength which decreased after the treatment phase.

There was no significant difference between dominants ( $N = 4$  individuals, one per group) and subordinates ( $N = 4$  individuals, one per group) in how much they increased their grooming efforts between the control-before and treatment phase (Table 3, Test J, Fig. 3a); dominant subjects increased their grooming given 2.33 times and subordinate subjects 2.46 times. Regarding the grooming ratio, dominants and subordinates gave more than they received at

the dyadic level (Table 3, Test K, Fig. 3b), although both dominant and subordinate subjects groomed more while fed, dominants increasing from a negative ratio, more grooming received than given, to a positive ratio, while subordinates simply increased their positive grooming ratio (see Appendix Fig. A6).

## DISCUSSION

In this experiment, we investigated whether provisioning food to selected adult female vervet monkeys for 2 weeks would change their activity budget, grooming behaviour and resulting social connectivity in the group. In comparison to the other adult females, fed subjects significantly changed their activity budget; notably they decreased feeding and increased resting, social and grooming behaviours while being fed (treatment phase) compared to the preceding and following phases. Fed subjects significantly increased allocation to social behaviours and grooming given during the treatment phase, independently of their hierarchy status. Finally, they not only groomed more, but also increased the rate at which they accumulated grooming partners over time (close to significance) and their grooming strength. Importantly, the subjects' increase in grooming activities during the treatment phase was not distributed equally among other group members but preferentially targeted females with specific nonmutually exclusive attributes: kin, existing partners, high-ranking and adult females. Thus, both high- and low-ranking subjects used the period of reduced time budget



**Figure 1.** Changes in activity budgets across phases. The percentage of each activity in the activity budgets of nonfed, dominant fed and subordinate fed subjects is shown for the control-before (Cb), treatment (T) and control-after (Ca) phases. Confidence intervals show the upper and lower limits of the means for each activity. More statistical output details are provided in Tables 1 and 2.

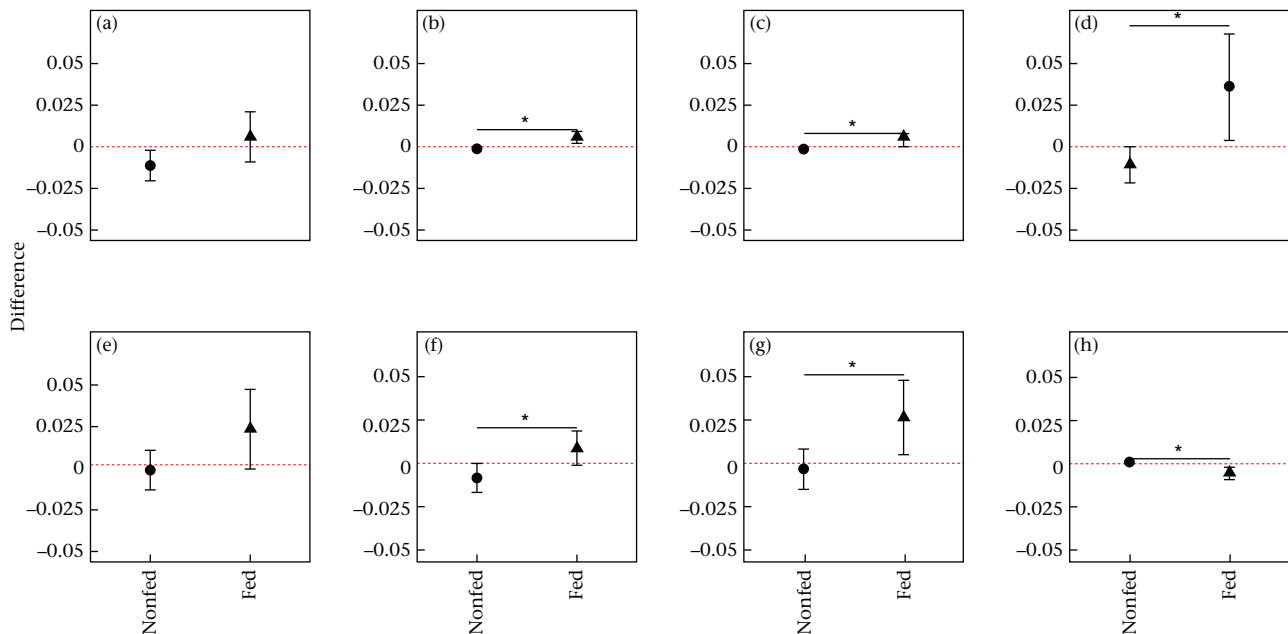
**Table 3**  
Results of null model analysis for the different grooming measures (A-K)

Test	Grooming variable	Fed subjects		Nonfed subjects		Observed value	Permutation quantiles		Prand
		Mean difference	change	Mean difference	change		2.5% threshold	97.5% threshold	
A	Change in grooming partners	-209.6	NA	-84.53	NA	-125.07	-141.8	31.79	0.055
B	Accumulation of grooming partners	0.005	1.21	-0.011	0.57	0.016	-0.0071	0.018	0.958
C	Strength	0.006	2.43	-0.001	0.79	0.007	-0.001	0.003	1*
D	Grooming ratio	0.004	-3.7	-0.0017	0.19	0.006	-0.001	0.004	0.992*
E	Strength to bonded partners	0.035	4.36	-0.011	0.66	0.046	-0.015	0.035	1*
F	Strength to rank	0.02	1.66	-0.004	0.86	0.024	-0.012	0.027	0.951
G	Strength to kin	0.008	1.51	-0.008	0.68	0.016	-0.008	0.016	0.981*
H	Strength to adult females	0.027	5.5	-0.004	0.83	0.031	-0.009	0.025	0.988*
I	Carryover effect (strength)	-0.005	0.45	0.0007	1.19	-0.003	-0.006	0.003	0.001*
J	Grooming given (activity budget)	6.06	2.33	8.38	2.46	-2.32	-4.50	11.93	0.366
K	Grooming ratio	30.50	-0.11	22.21	3.66	8.28	-21.47	55.53	0.586

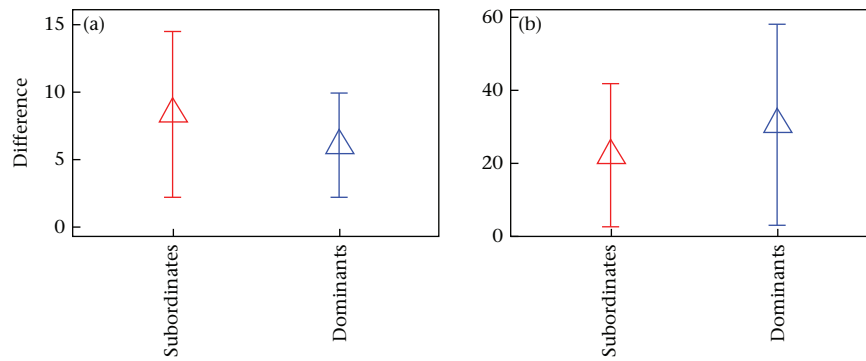
Mean difference illustrates the difference between fed and nonfed subjects between treatment and control-before phases (except for carryover, which is calculated between control-after and treatment phases). Change calculates the variation that fed subjects and nonfed subjects experienced between phases by dividing the treatment values by the control-before values (except in carryover, dividing control-after by treatment), so values below 1 represent decreases and values higher than 1 represent a positive increase. Observed and Prand are based on the difference in the means of fed and nonfed subjects between phases. In test A the calculation of % of change is not possible as it involves both phases (grooming partners during treatment/grooming partners during control-before). Test B corresponds to the accumulation of grooming partners. Tests A-I compare fed and nonfed subjects. Tests J and K compare the two fed subject subcategories (dominants and subordinates). Permutation quantiles represent the upper and lower thresholds for significance, corresponding to the upper 97.5% and lower 2.5% quantiles of the test statistics estimated from the permuted data. Prand values are shown with an asterisk when significant at the upper or lower tail ( $P < 0.025$  or  $P > 0.975$ ). Negative results in tests D and K (grooming ratio) are caused by a negative value in the control-before phase (see Appendix Table A11).

constraints to improve their social standing with key group members. In the absence of knowledge of the underlying mechanisms, we consider these strategic adjustments in their social behaviour 'Machiavellian-like'. Nevertheless, the fact that subjects used more of their free time for resting than for social activities warrants further investigation. Only the collection of similar data on other species may reveal whether our results should be interpreted as 'vervets are not particularly Machiavellian in their social behaviour' or whether being the only one with spare time often prevented subjects from finding interaction partners, making resting the default alternative.

Our experimental manipulation worked as expected, with fed subjects freeing 22% of their feeding time despite supplementary feeding ending around 1000 to 1100 each day while data collection continued until sunset (around 1800). Dominant and subordinate individuals adjusted their time budgets in remarkably similar ways, suggesting that individuals experience time budget trade-offs rather independently of their rank. Although these changes were elicited via food provisioning, our results support the hypothesis that animals under stark seasonality contrasts can behave flexibly to adjust time budgets to challenging contexts (Henzi et al., 2003;



**Figure 2.** Grooming measures of nonfed and fed subjects across study phases. Differences between the control-before and treatment phases are shown in (a-g) and between treatment and control-after phases in (h). (a) Difference in the accumulation of grooming partners, (b) difference in grooming strength, (c) difference in grooming ratio, (d) difference in grooming strength to bonded partners, (e) difference in grooming strength to high-ranking partners, (f) difference in grooming strength to kin partners, (g) difference in grooming strength to adult females and (h) grooming strength carryover. Error bars show the 2.5 and 95% quantiles of the differences between phases. As each value was calculated accounting for the time of observation as the exact time each individual was observed in each study phase, the changes in values are all close to 0, even though effect sizes can be large (see text). Histograms showing permuted and observed values are shown in Fig. A7 in the Appendix. Red dashed lines at zero separate increases (above dashed line) and decreases (below the dashed line). \* $P < 0.05$ .



**Figure 3.** Observed values for subordinate fed subjects and dominant fed subjects. Differences represent changes in grooming behaviour between the control-before and the treatment phases. (a) Difference in grooming given (as a percentage of the activity budget) and (b) difference in grooming ratio calculated from grooming strengths between the control-before and treatment phases.

Canteloup et al., 2019; Dunbar et al., 2009; Herbers, 1981; McFarland et al., 2014; Pollard & Blumstein, 2008).

Despite grooming serving important hygienic purposes (Hutchins & Barash, 1976) we interpret the subjects' increase in grooming given during the treatment as evidence of social responsiveness to a motivation to interact more socially and with more partners, which brought about a rewiring in their social networks (Farine, 2021; Kurvers et al., 2014) that may also promote cooperation (Fehl et al., 2011; Ohtsuki et al., 2006; Rand et al., 2011; Wang et al., 2012). We highlight that the dominant subjects increased their grooming ratio slightly above zero, which contrasts with their grooming ratio before the treatment when they received more than they gave. Indeed, dominants are normally perceived as high-quality grooming partners by the rest of the group and hence receive more grooming than they give, partly in exchange for tolerance and coalitionary support (Borgeaud & Bshary, 2015; Renevey et al., 2013; Schino, 2001; Seyfarth, 1977; Snyder-Mackler et al., 2016; Wrangham, 1980; Wubs et al., 2018). Our results demonstrate that even dominants may shift their social priorities when having spare time, increasing their grooming efforts and their social network.

If there had been no benefit to increasing grooming effort, subjects may have been better off by dedicating the surplus time gained from decreasing foraging exclusively to resting (Korstjens et al., 2010), which did not happen. The Machiavellian intelligence hypothesis presupposes that sophisticated tactical behaviours evolved due to the daily challenges of social life (Bshary et al., 2011; Byrne & Whitten, 1997; Harcourt, 1988). Two results are in line with the hypothesis that subjects were indeed strategic in their grooming adjustments: the characteristics of the targets of increased grooming and the increase in the grooming network. Regarding the targets, a selective increase in grooming kin is likely to yield indirect fitness benefits (Hamilton, 1964a, 1964b), while selectively increasing grooming with partners with strong social bonds should yield direct fitness benefits due to interdependency (Roberts, 2005). The selective increase in grooming high-ranking individuals fits the concept of trading services for increased tolerance and support (Seyfarth, 1977; Wubs et al., 2018). Finally, adult females form the core of vervet monkey groups due to female philopatry (Isbell et al., 1990; Renevey et al., 2013; Sterck et al., 1997), and intensifying female–female grooming networks may yield benefits against male aggression (Barrett & Henzi, 2002; Sterck et al., 1997) or enemy groups (Willems et al., 2015). Therefore, while our study did not quantify any potential benefits of the subjects' increased grooming activities, the changes in grooming patterns fit predictions based on well-established concepts of altruism and cooperation. It is known that vervet monkeys can distinguish other individuals' ranks, matriline and relationships

accurately (Borgeaud et al., 2015; Cheney, 2011), and our results indicate the applied value of having such knowledge. Also, the increase in the grooming network suggests that animals living in complex societies can behave tactically, and consequently restructure their networks (Farine, 2021; Flack, Girvan, de Waal, & Krakauer, 2006). Such tactical displays could enable the fulfilment of personal gains by promoting integration in the social network, perhaps by enhancing the bonding (the emotional closeness) with their grooming partners, which requires substantial time and effort (Chang et al., 2013; Roberts et al., 2009; Sutcliffe et al., 2012). Such bonding is adaptive as it can favour help during conflicts (Hemelrijk, 1994; Schino et al., 2007; Seyfarth, 1977) and conflict resolution (de Waal & van Roosmalen, 1979; McFarland & Majolo, 2011) or pave the road for future cooperative interactions (Berghänel et al., 2011; Schülke et al., 2010; Cheney, 2011). In conclusion, there are many potential benefits of unilaterally 'raising the stakes' (Roberts & Sherratt, 1998) when food is supplemented even if the grooming is not reciprocated in kind.

Overall, our experimental manipulation of subjects' feeding conditions offers insights into animals' capacity to exhibit grooming plasticity and network rewiring in interesting ways. Subjects varied several grooming metrics within relatively short time frames, revealing that network structures are not static entities but the outcomes of individuals making tactical decisions according to the specifics of their situation (Sih, Hanser, & McHugh, 2009; Wilson et al., 2014). This flexibility is a key aspect of the Machiavellian intelligence hypothesis, which proposes that primates evolved complex cognitive abilities to cope with a complex social environment (Byrne & Whitten, 1997; Harcourt, 1988). However, we note that our study only identified strategic behaviour in vervet monkeys, without identifying the underlying cognitive machinery. The identification of Machiavellian-like strategic social behaviour in vervet monkeys opens at least the possibility that advanced cognitive processes, like components of a theory of mind (Premack & Woodruff, 1978; Seyfarth & Cheney, 2013) are at play. A second major challenge for future research is to identify the potential benefits of a unilateral increase in grooming. While most potential benefits are likely to be direct, such as the recipient being more tolerant or supportive, there is also the possibility that individual decision rules have cascading effects on group interaction patterns and as a consequence group performance, which would affect the fitness of all group members.

#### Author Contributions

R.B. and M.G.G. conceived the experiment. M.G.G., Cl.Br. and Ch.Bo. collected the data. M.G.G. and D.R.F. conceptualized data analysis, and M.G.G. conducted the analysis and wrote the drafts of



the manuscript that were further edited in a collaborative effort between R.B., M.G.G. and D.R.F.

### Data Availability

All relevant data are available on Figshare at [https://figshare.com/authors/MIGUEL\\_GARETA\\_GARCIA/10749438](https://figshare.com/authors/MIGUEL_GARETA_GARCIA/10749438).

### Declaration of Interest

The authors do not have any competing interests.

### Acknowledgments

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## Appendix

### Data collection

We collected data on all the female individuals (fed and nonfed subjects, see [Tables A1–A3](#)) during all study phases. We left a minimum of 40 min between consecutive focal observations on a given individual to avoid overrepresentation of individuals. When the dominant or subordinate fed subjects were not fed during a treatment phase (for the dominant, when the subordinate was fed; for the subordinate, when the dominant was fed), their grooming behaviour was still counted when they were giving grooming to another female whose grooming was recorded in the focal data as grooming received. If, in contrast, fed subjects that were not being fed received grooming from any other adult female in the group, it was their partner whose grooming behaviour was recorded as grooming given. Likewise, any behavioural data collected on the fed subjects while they were not fed was not used for activity budgets except in the cases mentioned above. Because nonfed subjects were never fed, the data collected during the treatment phases of dominant and subordinate fed subjects were merged into a single treatment phase for the analysis. Focal observations consisted of a sequence of 10 data points collected every 2 min while following an individual in three periods during the day, each of ca. 4 h. The start and end of these periods depended on sunrise and sunset hours.

Focal observations were only included in the models when at least eight of the possible 10 points were collected. Focal data collection was organized to have all individuals sampled evenly across different periods, in all phases.

### Elo-rating

Only agonistic interactions in which both individuals displayed aggressive/submissive behaviours (see Methods) were considered and we excluded data if third parties were involved. Hierarchy calculation was based on ad libitum data collected during the 6 months before the experiment using the Elo-rating package (Neumann, Duboscq, Dubuc, & Ginting, 2011). After the values were calculated (see [Table A4](#) and Data Availability), they were converted to binary (0,1), so high-ranking individuals would be those within the top third of all individuals in the group. In the permutation analysis, we studied whether dominant and subordinate subjects groomed high-ranking individuals more than nonfed subjects. High-ranking individuals were those with an assigned ranking value of 1, while lower-ranking ones were assigned values of 0.

### Social bonds

Bond index calculation was based on ad libitum data collected during the 6 months before the experiment and followed Fedurek (2013). This method determines whether two individuals are preferred social partners using different types of data such as individuals being in the same party, being within 5 m of one another or being nearest neighbours. A bond could be bidirectional (mutual social partners) or unidirectional or could be absent between two individuals. Of these, bidirectional bonds are expected to be strongest and were assigned the value 1; we assigned the value 0 to all remaining dyad combinations so in our analysis social bonds were a binary factor. Note that two individuals being mutual social partners does not preclude one individual having other mutual social partners.

### Kinship

Kinship affiliation information was based on data the IVP has gathered over 10 years of uninterrupted work in the four study groups. We therefore knew from our life history files the mother–offspring and sibling relationships (assigned the value 1), and we excluded other more distant affiliations like cousins or aunt–niece. Thus, family relationships were binary where dyads with no family or more distant family than mother–offspring and siblings had the value 0.

### Food provisioning

The mix of food aimed to offer fast-burning energy through the apple and slower burning carbohydrate-based energy of the corn. Individuals took longer to ingest the apple with corn than apple alone, so we excluded corn in the second feeding to avoid other individuals interfering with the fed subject at a time when group activity was high. The first feeding session offered more time to feed since the monkeys were either still awakening or grooming at the sleeping site. Each session lasted only 10–15 min to avoid fed subjects becoming isolated if they could not catch up with the group after the session. However, this was never the case. We

ensured other individuals were not watching the feeding session to avoid provoking undesired behaviour of third parties (see Figs A2, A3 and A4).

*Activity budget model*

We provide here an example of the model structure that we used for the different activity budgets.

```
feeding <- glmer(feed ~ PhaseNew*Category + (1|individual) + (1|Group) + (1|TP), family = binomial, data=act1).
```

PhaseNew: phase of study (control-before, treatment, control-after).

Category: category of individuals, i.e. fed and nonfed (within fed there are two subcategories of individuals: dominants and subordinates).

Individual: the identity of each individual in the study, subjects and nonfed subjects.

Group: identity of the four groups: AK, BD, KB and NH.

TP: time period; days were split into three periods of equal duration covering all hours of daylight when data collection was conducted.

(The same model structure was used to evaluate resting, social, grooming given and moving).

*Null model hypothesis testing: randomization algorithm*

We used a series of null model hypothesis approach and generated data sets based on randomizations to compare the observed difference in grooming behaviours between the fed and nonfed subjects between phases with the randomized data set (Croft et al., 2011; Farine & Whitehead, 2015). Observed data for each grooming parameter were obtained by subtracting the grooming during the treatment phase from that during the control-before phase for fed and nonfed subjects. For the parameter

'accumulation of grooming partners' (accum. gr partners) we obtained the following:

a1 = accum. gr partners (study phase = control-before & category = fed subjects)

a2 = accum. gr partners (study phase = treatment & category = fed subjects)

b1 = accum. gr partners (study phase = control before & category = nonfed subjects)

b2 = accum. gr partners (study phase = treatment & category = nonfed subjects)

We then calculated the difference in the means of the observed data of each grooming parameter for fed s and nonfed subjects:

$$a = a2 - a1 \text{ (fed subjects)} \quad b = b2 - b1 \text{ (nonfed subjects)}$$

$$t = \text{mean} (a) - \text{mean} (b) \text{ (Observed)} \quad (\text{Prand} <- \text{sum}(\text{ran} <= \text{obs}) / \text{perms}) \text{ (Permuted)}$$

where ran = randomized data, obs = observed data and perms = permuted data.

**Table A1**  
Number of adult females and total individuals in each study group

Group	KB	AK	BD	NH
Adult females	5	4	11	6
Total individuals	12	23	46	33

**Table A2**  
The selected dominant and subordinate fed and the nonfed subjects in each group

Group	Dominants	Subordinates	Nonfed
AK	Gugu	Nkosikasi	Ndonsa, Mamoobi*
KB	Yenissei	Nessie	Aare, Amur, Mara*
BD	Oulik	Mielies	Asis, Engel, Gesels, Heerlik, Numbies, Pannekoekie, Prinses, Rissiepit, Snorretjie*
NH	Geneva	Pretoria	Gaya, Reva, Roma, Uppsala

\* Females for which we could not collect data due to injuries or shyness. Despite this, whenever our focal individuals interacted with them, they still counted as adult females in our grooming analysis.

**Table A3**  
Females for which focal data collection was unfeasible

Group	Discarded individual	Reason
KB	Mara	Too shy and peripheral for focal data collection
AK	Mamoobi	Badly injured (possibly due to predation) during the study period, she did not manage to keep up with the group during most of the study period
BD	Snorretjie	Too shy and peripheral for focal data collection

**Table A4**  
Elo-rating scores of all adult females

Group	Individual	Rank (Elo score)
AK	<b>Gugu</b>	<b>0.688</b>
	Nkos	0.433
	<b>Ndon</b>	<b>0.221</b>
	Mamo*	0.037
BD	<b>Ouli</b>	<b>0.844</b>
	Asis	0.671
	Prin	0.475
	Heer	0.392
	Snor*	0.378
	Gese	0.349
	Enge	0.326
	Numb	0.270
	Pann	0.033
	<b>Miel</b>	<b>0.009</b>
	Riss	0.000
KB	<b>Yeni</b>	<b>0.600</b>
	Amur	0.436
	Aare	0.327
	Mara*	0.305
NH	<b>Ness</b>	<b>0.216</b>
	<b>Gene</b>	<b>1.000</b>
	Gaya	0.875
	Upps	0.729
	<b>Pret</b>	<b>0.466</b>
	Reva	0.125
	Roma	0.117

Bold indicates fed subjects.

\* Individuals that were excluded from the study because of an injury which prevented the individual keeping up with the group (Mamoobi) or shyness which made it difficult to observe the individual (Mara and Snorretjie).

**Table A5**  
Group composition including all individuals in all groups of study

Group	Name	Age	Sex	Group	Name	Age	Sex
BD	Neuchâtel	Adult	Male	AK	Hlokoloza	Juvenile	Male
BD	Chernobyl	Adult	Male	AK	Heyi	Juvenile	Male
BD	Madagascar	Adult	Male	AK	Nyoni	Juvenile	Male
BD	Mvula	Adult	Male	AK	Ginqika	Juvenile	Female
BD	Hwahwa	Adult	Male	AK	Ghida	Juvenile	Female
BD	Ububhibhi	Adult	Male	AK	Gubha	Juvenile	Female
BD	Oulik	Adult	Female	AK	Humusha	Juvenile	Male
BD	Prinses	Adult	Female	AK	Hluhlwe	Juvenile	Male
BD	Pannekoekie	Adult	Female	AK	Nyanga	Juvenile	Female
BD	Asis	Adult	Female	AK	Ndiza	Juvenile	Male
BD	Heerlik	Adult	Female	AK	Mathimula	Juvenile	Male
BD	Mieles	Adult	Female	AK	Ndawonya	Baby	Female
BD	Snorretjie	Adult	Female	KB	Liffey	Adult	Male
BD	Gesels	Adult	Female	KB	Yenissei	Adult	Female
BD	Numbies	Adult	Female	KB	Mara	Adult	Female
BD	Rissiepit	Adult	Female	KB	Amur	Adult	Female
BD	Engel	Adult	Female	KB	Nessie	Adult	Female
BD	Little blind	Juvenile	Female	KB	Aare	Adult	Female
BD	Rooikat	Juvenile	Male	KB	Yalu	Juvenile	Female
BD	Vakie	Juvenile	Male	KB	Yangtze	Juvenile	Male
BD	Pieperig	Juvenile	Female	KB	Avon	Juvenile	Male
BD	Hippie	Juvenile	Female	KB	Mississippi	Juvenile	Male
BD	Siele	Juvenile	Female	KB	Arno	Juvenile	Male
BD	Nurks	Juvenile	Female	KB	Malawi	Juvenile	Male
BD	Rakker	Juvenile	Male	NH	Govu	Adult	Male
BD	Wurm	Juvenile	Male	NH	Tweed	Adult	Male
BD	Bullebak	Juvenile	Male	NH	Uppsala	Adult	Female
BD	Vulkaan	Juvenile	Male	NH	Geneva	Adult	Female
BD	Aapie	Juvenile	Female	NH	Gaya	Adult	Female
BD	Potjie	Juvenile	Female	NH	Pretoria	Adult	Female
BD	Obelisk	Juvenile	Male	NH	Roma	Adult	Female
BD	Asseblief	Juvenile	Female	NH	Reva	Adult	Female
BD	Heilweis	Juvenile	Male	NH	Xian	Juvenile	Female

**Table A5** (continued)

Group	Name	Age	Sex	Group	Name	Age	Sex
BD	Meerkat	Juvenile	Male	NH	Tirroan	Juvenile	Male
BD	Safari	Juvenile	Female	NH	Rheban	Juvenile	Male
BD	Gaaf	Juvenile	Male	NH	Uji	Juvenile	Male
BD	Nooiens	Juvenile	Female	NH	Glastonberry	Juvenile	Male
BD	Redelik	Juvenile	Female	NH	Xalapa	Juvenile	Female
BD	Eina	Juvenile	Female	NH	Praia	Juvenile	Female
BD	Ooetjies	Baby	Female	NH	Zanzibar	Juvenile	Male
BD	Adder	Baby	Male	NH	Boston	Juvenile	Male
BD	Hasie	Baby	Female	NH	Jixi	Juvenile	Male
BD	Ratel	Baby	Male	NH	Rennes	Juvenile	Female
BD	Puolka	Baby	Female	NH	Umtata	Juvenile	Male
AK	Cancun	Adult	Male	NH	Granada	Juvenile	Male
AK	Wolfie	Adult	Male	NH	Propiano	Juvenile	Male
AK	Atitlan	Adult	Male	NH	Bela-Bela	Juvenile	Female
AK	Gugu	Adult	Female	NH	Jeddah	Juvenile	Male
AK	Nkosikasi	Adult	Female	NH	Lima	Juvenile	Female
AK	Ndonsa	Adult	Female	NH	Ulaanbaatar	Baby	Male
AK	Mamoobi	Adult	Female	NH	Pruszkow	Baby	Male
AK	Geleza	Juvenile	Female	NH	Roslin	Baby	Male
AK	Unwabo	Juvenile	Male	NH	Reykjavik	Baby	Male

**Table A6**

Schedule of phases for each fed subject (dominants and subordinates) for each study group

Group	Control-before	Treatment phase Dominant fed	Treatment phase Subordinate fed	Control-after
AK	2-28 July	1-12 August	16-26 August	6-29 September
KB	1-28 July	16-26 August	2-13 August	6-30 September
BD	1-18 August	29 August-10 September	12-24 September	5-27 October
NH	1-26 August	12-24 September	29 August-10 September	4-25 August

**Table A7**

The main behaviours collected in the focal sampling

Activity	Behaviour
Feeding	Reaching, bite chewing, searching, lick, drink
Resting	Sleeping, resting, self-scratching, autogrooming, vigilant
Social	Affiliative behaviours: grooming, being groomed, mouth to mouth, lip smacking, infant handling, play, nurse infant Agonistic behaviours: stare-attack, take place, steal food, chase, grab, bite, steal baby, hand on top of head Sexual behaviours: present, inspect sexual parts, mounting, masturbating, homosexual mounting
Moving	Walking, jumping, hopping, galloping, climbing, descending

**Table A8**

Sampling effort: data gathered during each phase

Phase	No. of focal observations per individual per period	Total no. of focal observations (over all three periods)	Time observed (min)
Control before	4	12	120
Treatment dominant subject fed	8	24	240
Treatment subordinate subject fed	8	24	240
Control after	4	12	120
Total	24	72	720

Focal observations could include 8–10 focal points; thus, the resulting focal points varied between individuals as explained in the text.

**Table A9**  
Data collection (data points) during the different phases for each adult female

Group	Individual	Category of individual 1	Category of individual 2	Control-before	Treatment	Control-after
AK	Gugu	Fed Subject_Dominant	Fed Subject	122	257	146
AK	Ndon	Nonfed subject	Nonfed subject	118	495	149
AK	Nkos	Fed Subject_Subordinate	Fed Subject	142	236	148
KB	Aare	Nonfed subject	Nonfed subject	107	502	150
KB	Amur	Nonfed subject	Nonfed subject	124	475	135
KB	Ness	Fed Subject_Subordinate	Fed Subject	127	287	156
KB	Yeni	Fed Subject_Dominant	Fed Subject	127	287	156
NH	Gaya	Nonfed subject	Nonfed subject	114	499	116
NH	Gene	Fed Subject_Dominant	Fed Subject	118	235	118
NH	Pret	Fed Subject_Subordinate	Fed Subject	117	236	120
NH	Reva	Nonfed subject	Nonfed subject	129	489	115
NH	Roma	Nonfed subject	Nonfed subject	110	472	108
NH	Upps	Nonfed subject	Nonfed subject	120	488	128
BD	Asis	Nonfed subject	Nonfed subject	110	539	120
BD	Enge	Nonfed subject	Nonfed subject	127	503	127
BD	Gese	Nonfed subject	Nonfed subject	117	522	120
BD	Heer	Nonfed subject	Nonfed subject	128	500	130
BD	Miel	Fed Subject_Subordinate	Fed Subject	129	249	119
BD	Numb	Nonfed subject	Nonfed subject	113	512	120
BD	Ouli	Fed Subject_Dominant	Fed Subject	120	247	118
BD	Pann	Nonfed subject	Nonfed subject	107	478	119
BD	Prin	Nonfed subject	Nonfed subject	112	482	119
BD	Riss	Nonfed subject	Nonfed subject	125	496	130

**Table A10**  
Data available for the activity budget analysis

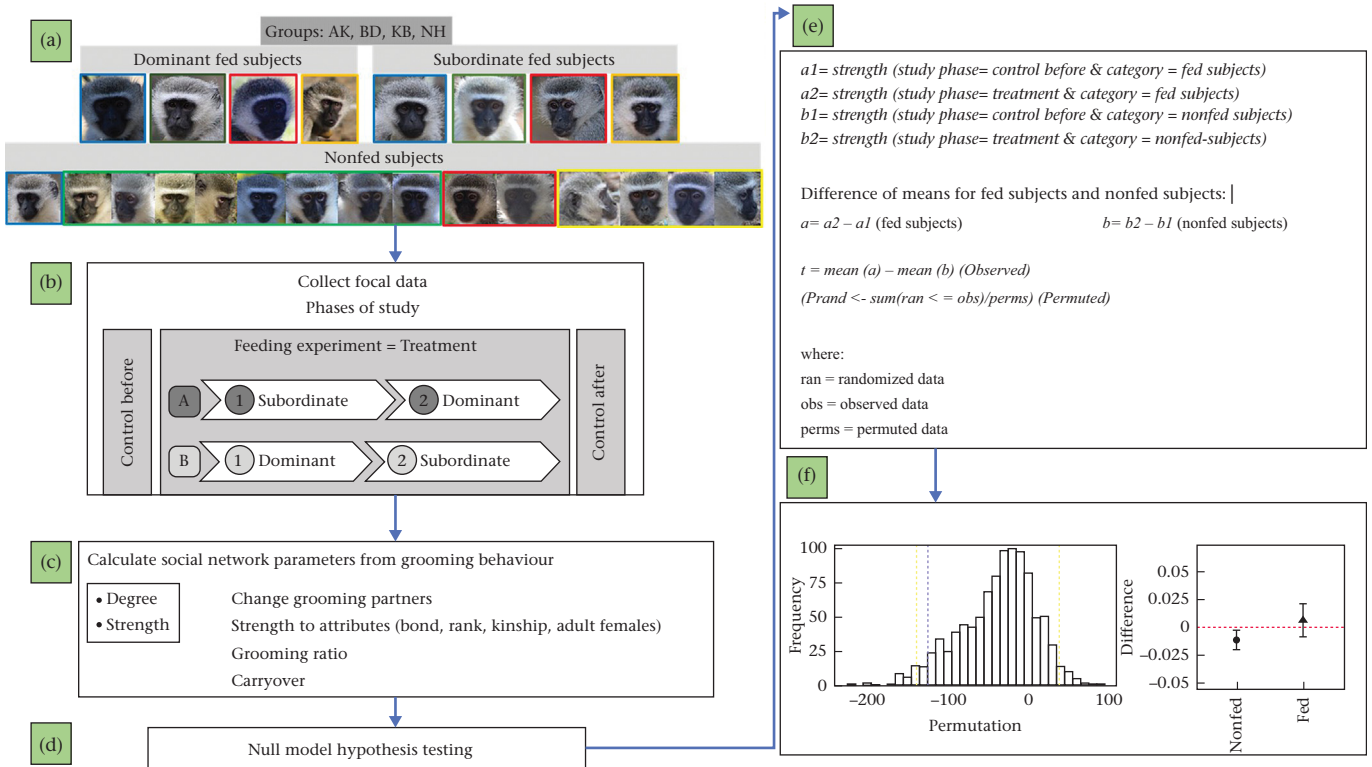
Category	No. of individuals	Phase	Activity			
			Feeding	Moving	Resting	Social
Dominant (fed subjects)	4	Control-before	575	102	160	107
	4	Treatment	354	95	339	234
	4	Control-after	571	147	225	92
Subordinate (fed subjects)	4	Control-before	619	117	127	143
	4	Treatment	352	90	334	232
	4	Control-after	674	65	170	106
Other (nonfed subjects)	15	Control-before	1098	208	198	257
	15	Treatment	5102	575	774	1001
	15	Control-after	1020	258	345	263

**Table A11**  
Control-before and treatment average observed values for fed and nonfed subjects

Test	Grooming variable	Control-before		Treatment	
		Fed	Nonfed	Fed	Nonfed
A	Change in grooming partners	NA	NA	NA	NA
B	Accumulation of grooming partners	0.02682	0.02649	0.03236	0.01509
C	Strength	0.00411	0.00495	0.00998	0.00391
D	Grooming ratio	-0.0008	0.00170	0.00304	0.00032
E	Strength to bonded partner	0.01065	0.03237	0.04649	0.02147
F	Strength to rank	0.02969	0.02790	0.04924	0.02403
G	Strength to kin	0.01678	0.02596	0.02532	0.01774
H	Strength to adult females	0.00592	0.01868	0.03257	0.01543
I	Carryover effect (strength)	0.00999	0.00392	0.00451	0.00468
J	Grooming given (activity budget)	4.56307	5.74594	10.6214	14.12580
K	Grooming ratio	-27.472	8.34759	3.02379	30.56143

Average observed values were computed by dividing the treatment value by the control-before value of each category of individual to reflect the values of change in Table 1. Tests A-I compare fed subjects and nonfed subjects. Tests J and K compare the two fed subject subcategories (dominants and subordinates). NA: not available.

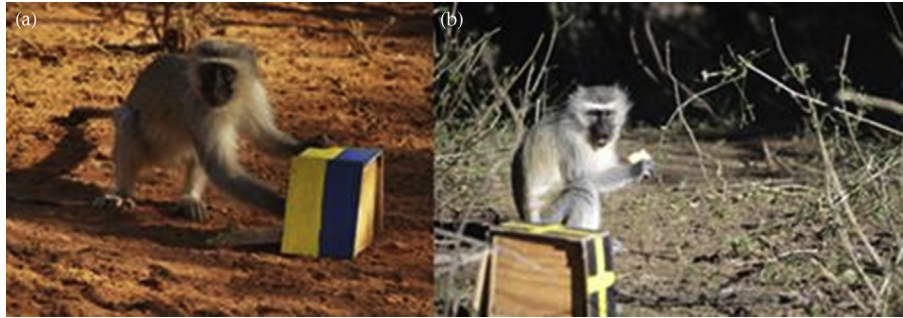




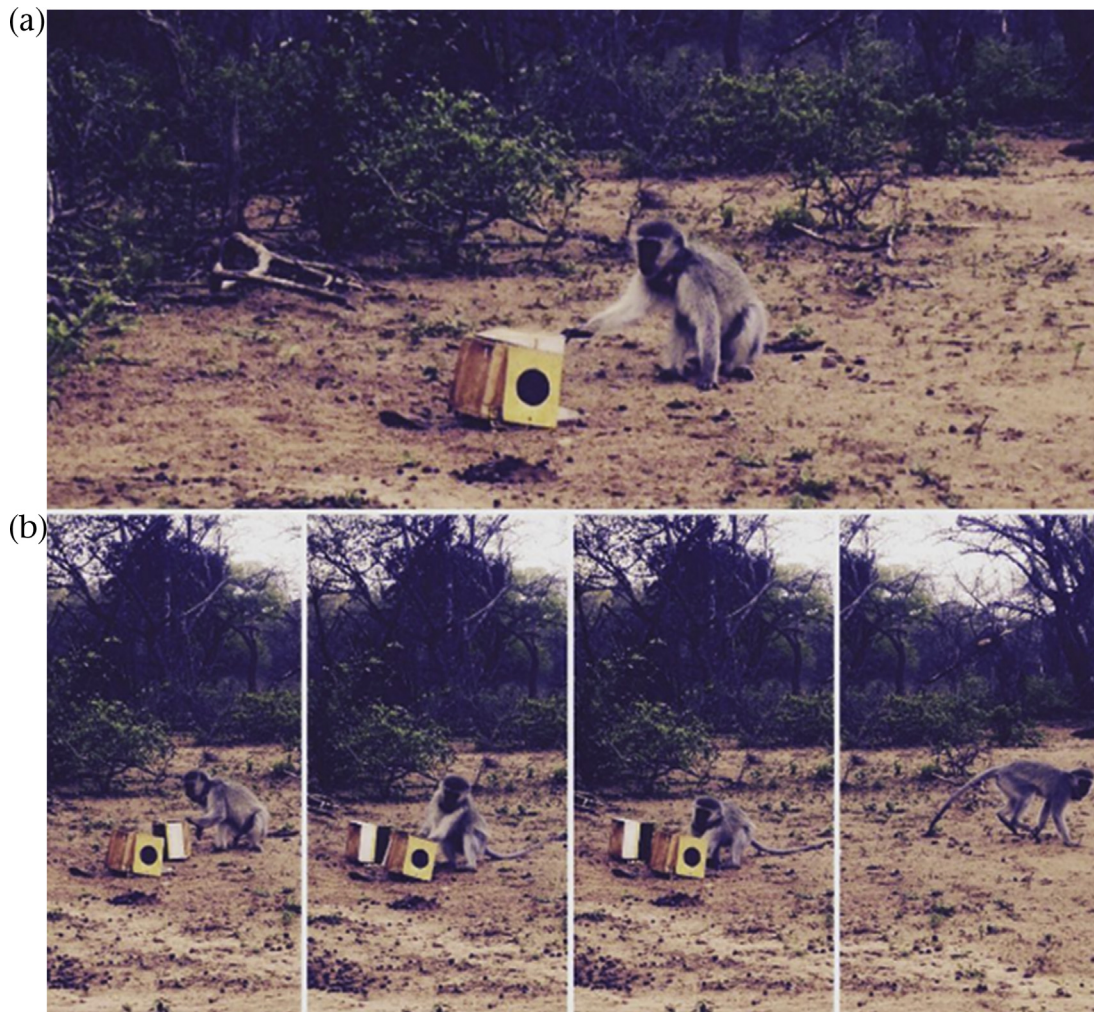
**Figure A1.** Scheme representing the main steps of the study, from data collection to data analysis. (a) The fed (dominants and subordinates) and nonfed females that were part of the focal data collection. Individuals framed in blue, green, red and yellow correspond to the different study groups AK, BD, KB and NH. (b) Data collection based on focal animal sampling across the different study phases: 1 = control-before, 2 and 3 = treatment organized into first subordinate fed, dominant fed later (A) or first dominant fed, subordinate fed later (B) and 4 = control-after. (c) Social network measures calculated from focal data (see Methods for details). (d) Null model hypothesis testing following Farine (2017). (e) Example of the permutation code for the null model hypothesis testing where observed and permuted data were calculated using the different social network measures (see below and the Appendix for further details). (f) Graphical representation of permutation calculations. The histogram and vertical dotted orange lines represent the distribution range of permuted data and the vertical dotted blue line represents the observed data (Farine, 2017). Also shown is the difference in accumulation of grooming partners between the treatment and control-before phases for nonfed and fed subjects. Error bars show the 2.5 and 95% quantiles of the differences between phases.



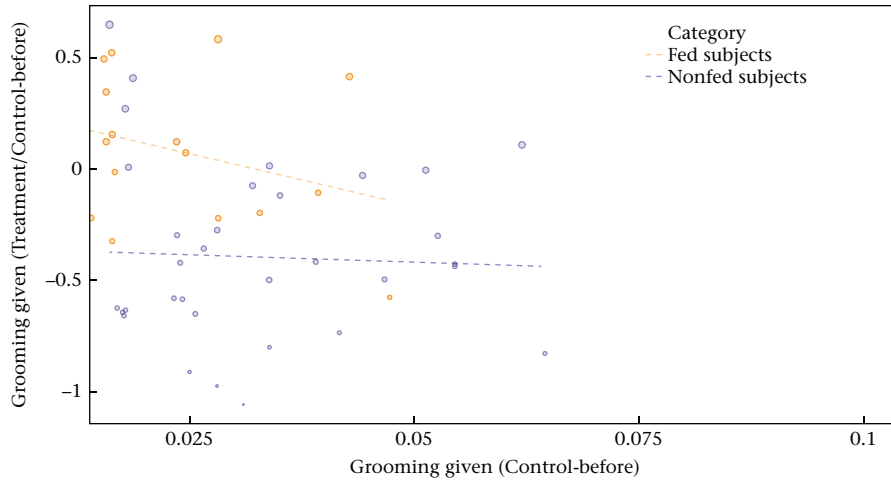
**Figure A2.** Remote-opening box with the personal cover of the dominant adult female Yeni from Kubu group (KB) before the food (an apple with corn inserted into it) was put in the box.



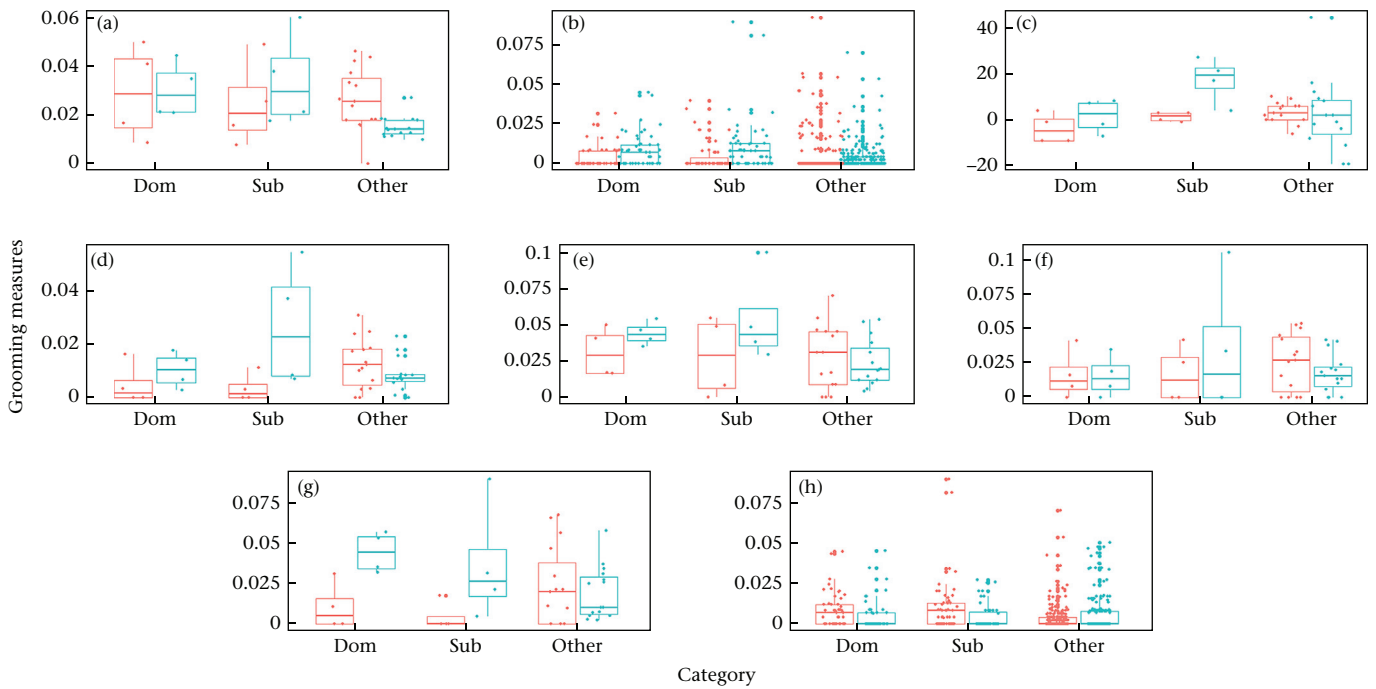
**Figure A3.** Example of feeding sessions. Subordinate adult fed females during a feeding session having access to their box containing a high-quality food: (a) Mieles from BD group and (b) Nessie from KB group.



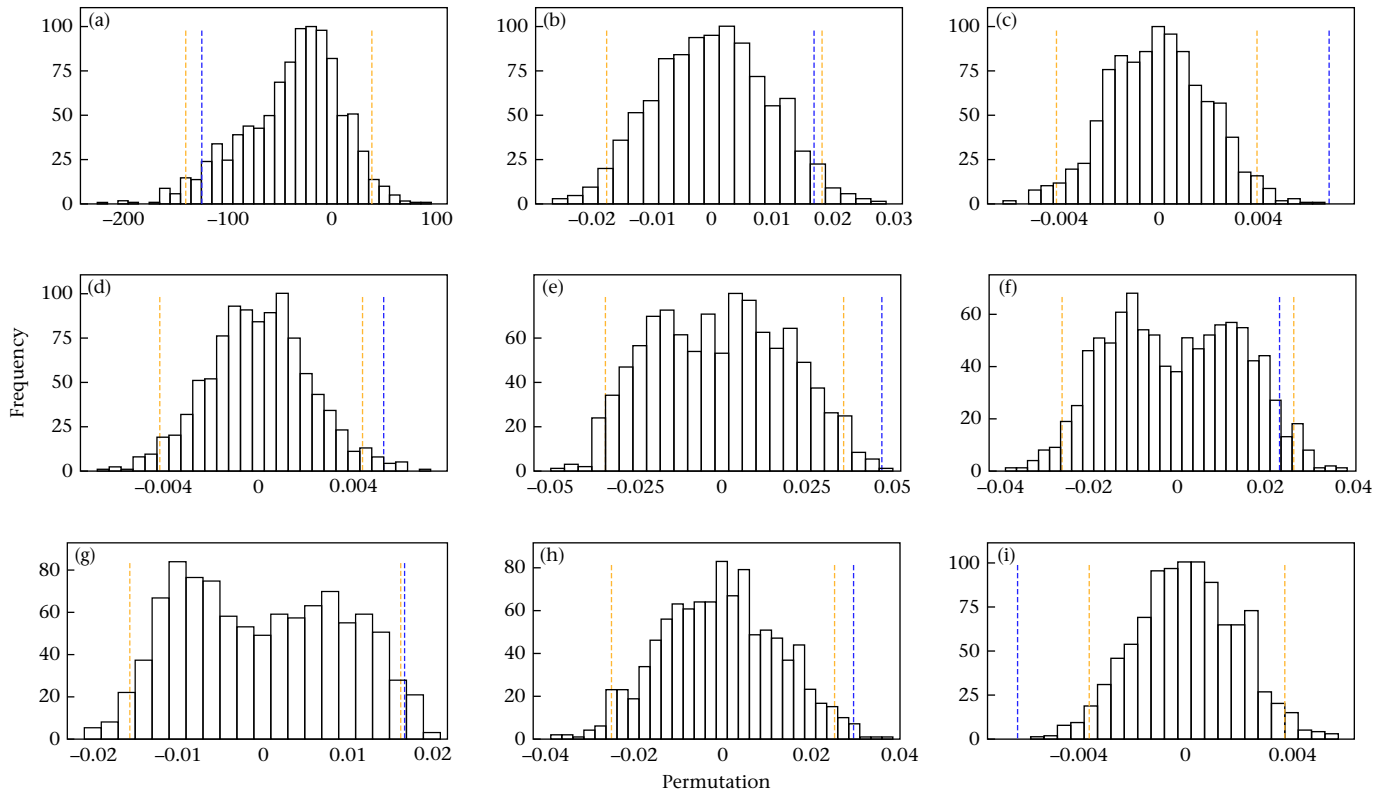
**Figure A4.** Training period. (a) The subject was first trained with one box. (b) The subject was then exposed to two alternative options, her box and a different one (which changed in different trials).



**Figure A5.** Change in grooming social network of fed and nonfed subjects between treatment and control-before phases. The log ratio of grooming given to partners during the treatment and control-before phases is shown in relation to the grooming given during the control-before phase. The size of the circles represents the grooming given strength.



**Figure A6.** Grooming representations of the different aspects of the study: (a) accumulation of grooming partners, (b) grooming strength, (c) grooming ratio, (d) grooming to bond partners, (e) grooming to high-ranking partners, (f) grooming to kin partners, (g) grooming to adult female partners and (h) grooming carryover. (a–g) Comparison of the control-before (red) and the treatment phase (blue). (h) Comparison of the treatment phase (red) and the control-after phase (blue). Each female is represented as a dot. Dom (dominant) and sub (subordinate): fed subjects; other: nonfed subjects. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers.



**Figure A7.** Histograms showing the range of distribution of random and observed values of the different grooming measures. (a) Change in grooming partners, (b) accumulation of grooming partners, (c) grooming strength, (d) grooming ratio, (e) grooming to bonded partners, (f) grooming to high-ranking partners, (g) grooming to kin partners, (h) grooming to adult female partners and (i) grooming carryover. Vertical dotted orange lines indicate the 2.5–97.5% distribution range of the permuted values, and the vertical dotted blue line shows the observed value (difference of the means of fed subjects minus difference of the means of nonfed subjects, with the difference calculated between the control-before and treatment phases; for further details see Methods and the Appendix).