

Market effects offset the reciprocation of grooming in free-ranging redfronted lemurs, *Eulemur fulvus rufus*

Markus Port^{a,b,*}, Dagmar Clough^{a,b}, Peter M. Kappeler^{a,b}

^a Department of Behavioral Ecology and Sociobiology, German Primate Center

^b Department of Sociobiology/Anthropology, University of Göttingen

ARTICLE INFO

Article history:

Received 21 May 2008

Initial acceptance 2 July 2008

Final acceptance 29 August 2008

Published online 30 October 2008

MS. number: 08-00337

Keywords:

aggression
biological market
Eulemur fulvus rufus
grooming
reciprocal altruism
redfronted lemur

Social grooming is a commonly observed affiliative behaviour in primates. Grooming has been suggested to represent a service in a biological marketplace, exchanged either for grooming or for other social commodities or services. Accordingly, grooming is predicted to be approximately reciprocated within a dyad when no other services are being exchanged, but it should be more asymmetrical if partners have different quantities of other services to offer. We analysed 412 grooming bouts observed in four groups of free-ranging redfronted lemurs to test this prediction. Grooming in this species seems to take place in a highly reciprocal manner because partners usually alternate in the roles of groomer and gromee within a grooming bout. However, within dyads there were asymmetries in the duration of grooming given and received. In both sexes, more grooming was directed from low-ranking towards high-ranking individuals than vice versa, and in males this asymmetry became more pronounced as the number of subordinates per group increased. Grooming in bisexual dyads was generally skewed in favour of males, but patterns of grooming between the sexes were less clear than within the sexes. In addition, aggression occurred at high frequencies between classes of individuals that were characterized by nonreciprocal grooming, suggesting that grooming may serve as a means to reduce aggression in dyads with a high potential for conflicts. Taken together, our results indicate that a strict reciprocation of grooming can be offset by power differentials between partners, where grooming appears to be traded by subordinates in exchange for the tolerance of dominants.

© 2008 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Cleaning another individual's fur (allogrooming, hereafter grooming) constitutes a common form of affiliative behaviour in primates (Sparks 1967; Goosen 1987), and has also been observed in a number of other mammalian species (e.g. impalas, *Aepyceros Melampus*: Hart & Hart 1992; wood mice, *Apodemus sylvaticus*: Stopka & Macdonald 1999; meerkats, *Suricata suricatta*: Kutsukake & Clutton-Brock 2006). Grooming is beneficial for the recipient as dirt and ectoparasites are removed (Hutchins & Barash 1976; Barton 1985); yet this behaviour is likely to be associated with costs for the individual performing it, for example, in the form of decreased vigilance (Maestriperi 1993; Mooring & Hart 1995) or decreased time available for other activities (Dunbar 1992; Henzi et al. 1997). It has therefore been suggested that grooming represents a form of altruism (Seyfarth & Cheney 1984).

Across primate species, many grooming interactions take place among relatives (Schino 2001), where altruism can be attributed to kin selection (Hamilton 1964). However, grooming also occurs among nonkin. Altruism among nonkin is assumed to be favoured

by natural selection if the altruist later receives a significant benefit from the recipient of the initial altruistic act (reciprocal altruism: Trivers 1971). It has therefore been suggested that grooming within pairs of individuals should be reciprocated over time, or exchanged for other beneficial acts (Hemelrijk & Ek 1991). Because the first theoretical model to predict grooming relationships in primates considered grooming to be the means by which individuals maintain social bonds (Seyfarth 1977), much emphasis concerning an interchange with other forms of altruism has traditionally been laid on support in conflicts (e.g. Seyfarth & Cheney 1984; Hemelrijk 1994). However, whereas several studies revealed that grooming itself is usually reciprocated (e.g. Hemelrijk & Ek 1991; Leinfelder et al. 2001; Ventura et al. 2006), evidence suggesting an exchange for coalitionary support is rare (Henzi & Barrett 1999; but see Schino 2007 for a recent meta-analysis).

Henzi & Barrett (1999) extended the traditional reciprocal altruism approach of social grooming by attributing a more flexible function to this behaviour. Following biological market theory (Noë & Hammerstein 1995), they proposed that grooming represents a service in a biological marketplace, which can be exchanged for grooming (reciprocated) or for other services or commodities in the market. Accordingly, grooming is predicted to be reciprocated in dyads where no other services are being exchanged, but to be

* Correspondence: M. Port, Department of Behavioral Ecology and Sociobiology, German Primate Center, Kellnerweg 4, 37077 Göttingen, Germany.
E-mail address: mport@gwdg.de (M. Port).

asymmetrical if it is traded as a commodity to obtain a different service from the partner. Coalitionary support represents only one possible service; further services or commodities are, for instance, tolerance (Kapsalis & Berman 1996; Kutsukake & Clutton-Brock 2006), food (de Waal 1997) or matings (Gumert 2007a). Thus, individuals can be divided into different trader classes, depending on what they have to offer. The concept of trader classes has found wide application within the biological market framework, not only in the study of grooming behaviour or other forms of intraspecific cooperation, but also in interspecific mutualism (Noë 2001). The exchange of commodities between members of different trader classes is predicted to be influenced by supply and demand in the market, such that individuals offering a rare commodity are expected to increase their demands from trading partners. Asymmetries in supply and demand usually result from different numbers of individuals within classes, for example from different numbers of males and receptive females (Gumert 2007a) or cleaner fish and their clients (Soares et al. 2008), but may also be the consequence of the seasonal appearance of commodities, such as contested food resources (Barrett et al. 2002).

The market model has successfully been applied to explain grooming patterns in both Old World monkeys (e.g. Barrett et al. 1999; Henzi & Barrett 2002; Gumert 2007a, b) and New World monkeys (Lazaro-Perea et al. 2004), but to our knowledge this is the first study to apply it to a group-living strepsirrhine, the redfronted lemur. Like all strepsirrhines, these lemurs use a tooth-comb in the lower jaw for grooming, which, in a sequence of upward movements of the head, is stroked through the partner's fur (Barton 1987). After having performed such an episode of upward movements, the former groomer is then typically groomed by its partner. Afterwards, the roles are reversed again, and several episodes are exchanged this way before one partner terminates the grooming bout. Therefore, redfronted lemurs provide an excellent opportunity to study grooming in a species in which it is always reciprocated within a bout. Hence, our study is not subject to a problem frequently encountered by previous studies, which is the absence of immediate reciprocation (cf. Barrett & Henzi 2001; Schino et al. 2003).

We examined grooming reciprocity in redfronted lemurs by analysing both the number of grooming episodes of each partner and the total duration of grooming exchanged within a bout. As we expected market forces to offset grooming reciprocity in some dyads, we did not predict grooming to be completely reciprocal. Instead, we derived the following predictions.

(1) Among females, we predicted more grooming to be directed from low-ranking females towards high-ranking ones than vice versa. This prediction is based on the observation that the former are often targets of aggression by the latter (Vick & Pereira 1989), often leading to evictions from their groups (see *Methods*). Hence, we predicted grooming to be used by low-ranking females mainly as a currency exchanged for the tolerance of high-ranking females.

(2) Although Henzi & Barrett (1999) originally developed their market model to explain grooming relationships among females, they later argued that grooming is likely to be exchanged for mating opportunities between the sexes (Barrett & Henzi 2001; see also Gumert 2007a). As females are generally the limiting resource for males (Trivers 1972), we predicted grooming to be asymmetric in male–female dyads, with more grooming directed from males to females than vice versa. In addition, we predicted the level of asymmetry to increase when the value of the commodity exchanged was particularly high, that is, during the mating season.

(3) Only a few studies have examined grooming relationships among males (Hemelrijk & Ek 1991), possibly because grooming is relatively rare among males in most species (Goosen 1987; van Hooff & van Schaik 1994). Redfronted lemurs represent an ideal study species to examine this behaviour in males, not only because

it is common (Kappeler 1993a), but also because males in this species can effectively be divided into two trader classes owing to their unique social system (Ostner & Kappeler 1999): in each group one male is clearly dominant over all other males, whereas subordinates cannot be ranked further in a linear hierarchy. We therefore predicted grooming to be reciprocal between subordinates (which can exchange grooming only for itself), whereas more grooming should be directed from subordinates to dominants in exchange for the latter's tolerance, in particular with regard to group membership, but possibly also in the context of mating (see Duffy et al. 2007). In addition, according to the law of supply and demand, we expected dominants to increase their demands if they were given the opportunity to pay off competing subordinates. As a consequence, the level of asymmetry in dominant–subordinate dyads should increase with increasing number of subordinates, in particular as the threat of eviction should also be more pronounced as group size increases.

Finally, we were interested in whether patterns of aggression in redfronted lemurs correspond to patterns of grooming. We therefore analysed aggressive interactions between individuals assigned to the same trader classes as defined in our analysis of grooming.

METHODS

Redfronted Lemurs

Redfronted lemurs are 2 kg, sexually monomorphic, cathemeral Malagasy primates living in groups of 5–16 individuals with an even or male-biased sex ratio (Overdorff et al. 1999; Ostner & Kappeler 2004). Groups usually consist of a core of related females, whereas males migrate, sometimes delaying dispersal beyond sexual maturity (Wimmer & Kappeler 2002). Male dispersal is not usually associated with prior aggression, but male eviction can occasionally occur in unusually large groups (Vick & Pereira 1989; M. Port, personal observation). Females, in contrast, are more frequently evicted as group size increases, typically by members of their own sex. One male per group, the so-called 'central male' (Ostner & Kappeler 1999), clearly dominates all other males, whereas the remaining subordinates cannot be ranked along a linear hierarchy. Central males interact affiliatively with females more frequently than subordinate males (Ostner & Kappeler 1999) and father the majority of offspring born in their groups (Kappeler & Port 2008). Reproduction in redfronted lemurs is highly seasonal. Mating behaviour is largely restricted to a few weeks in May–June (Ostner & Kappeler 2004), during which a female's fertile period is limited to 1–3 days (Boskoff 1978).

Study Population and Data Collection

The study was conducted in Kirindy Forest, a dry deciduous forest located within a forestry concession operated by the Centre Formation Professionnelle Forestière (CFPF), approximately 60 km northeast of Morondava, western Madagascar. For a detailed description of the forest see Sorg et al. (2003). Study animals belonged to one of four groups (A, B, F, J) living in a 60 ha study area (CS7), which is part of the German Primate Center field site. As part of an ongoing long-term study, all individuals were habituated to human presence and have been regularly captured and marked with unique nylon collars (weight 10 g, equivalent to 0.005–0.01% (mean = 0.007%) of an animal's body weight) or radiocollars (Biotrack, Wareham, Dorset, U.K.; weight 32 g, equivalent to 0.015–0.021% (mean = 0.016%) of an animal's body weight). Animals were equipped with the collars during brief anaesthesia (induced by applying 0.2 ml GMII; Rensing 1999) after blow-pipe darting by an experienced Malagasy technician. Individuals are returned to their social groups within 1 h and we have not observed any injuries or

adverse effects on behaviour as a result of the capture procedure or the collars. Our research was approved by the Malagasy Ministère de l'Environnement et des Eaux et Forêts.

Behavioural observations were conducted from March to September 2005 and from April to July in 2006 and 2007. Group compositions in the respective years are presented in Table 1. Focal animal observations were carried out on all adult individuals (>2.5 years) in an alternating order for 3.5 h in the morning (between 0700 and 1100 hours) and 3 h in the afternoon (between 1400 and 1730 hours). For each focal animal, both periods together (i.e. 6.5 h of observation) made up one statistical day. We recorded all affiliative and agonistic interactions of the focal animal following Pereira & Kappeler (1997), noting who initiated and who terminated the interaction. As spontaneous submission (i.e. agonistic interactions in which one animal showed submissive behaviour without prior aggression by its partner) was very rare (see also Kappeler 1993b), this form of agonism was not included in our analysis. Thus, for the present study, an agonistic interaction always consisted of either an aggressive act (cuff, bite, etc.) or signal (certain vocalizations), and was defined as decided if the target showed submissive behaviour, and as not decided if the target showed no perceptible signs of submission. In addition, during focal animal observations one of us (M.P.) recorded grooming behaviour using a handheld computer (PsionWorkabout, Psion PLC, London, U.K.). A grooming bout was defined to begin when one animal initiated the first grooming episode, and to end if either one animal left, or the partners remained in social contact, but did not exchange grooming for at least 5 min. This way, a total of 412 complete grooming bouts between either adult or subadult (1–2.5 years) individuals were recorded. Although subadults were not included in the focal animal observations, they were included in the analysis of grooming reciprocity because the threat of group eviction is most pronounced for this class of individuals. We did not include infants in this analysis, however, as we did not expect infants to possess fully developed grooming skills.

Data Analyses

Each of the 412 grooming bouts was analysed separately, using the Observer software package (Noldus Information Technology, Wageningen, The Netherlands). This way, we obtained both the number of grooming episodes of two interacting animals within a bout as well as the precise duration of grooming exchanged between the partners. In 6% of episodes (accounting for 9% of the total time spent grooming) both partners groomed simultaneously. Because these episodes represented a relatively small fraction of overall grooming and as they were not relevant for assessing the

level of reciprocity, they were excluded from further analyses, which then proceeded at two levels.

First, to determine whether grooming was reciprocated within bouts, we were interested in whether the animals performed and received the same number of episodes, and whether both partners groomed for approximately the same total duration. We used linear mixed-effects models, in which the performance of an animal (i.e. either episodes or duration) was regressed against the performance of its partner. For each bout, the performances of the grooming partners were randomly assigned as the response and explanatory variable in the regression model (i.e. grooming received and grooming given). Thus, each dyad, which represents the independent unit in studies of social behaviour, could yield two 'clusters' (cf. Manson et al. 2004): bouts in which the performance of animal A was assigned the response and the performance of animal B the explanatory variable, and vice versa. To avoid pseudoreplication of clusters containing the same animals, 'cluster' (as defined above) was included in the model as a random effect. The model was fitted using maximum likelihood estimation. To allow for a direct comparison between the number of episodes exchanged and the duration of grooming, both measures were standardized using *z* transformation. Owing to a right-tailed skew in the distribution of grooming durations, we used a Box-Cox transformation (Box & Cox 1964) to achieve normality before the data were standardized. For further comparisons, we report the deviance ($D = -2 \log$ likelihood of the fitted model) of each model.

Second, to test whether power asymmetries between partners are responsible for grooming asymmetries within dyads, we calculated an index of reciprocity *R* (Payne et al. 2003; see Löttker et al. 2007 for a similar approach):

$$R = \frac{(G_A - G_B)}{(G_A + G_B)}$$

in which G_A is the amount (episodes or time) animal A, and G_B the amount animal B, spent grooming. The *R* index can range from –1 to 1, where a value of 0 represents complete reciprocity, negative values indicate that individual A received more grooming than it gave, and positive values indicate that individual B received more grooming than it gave. Note that, in contrast to the regression analysis, partners within a dyad were assigned the roles of A or B according to the trader classes to which they belonged in the lemurs' grooming market, rather than randomly (Table 2).

We calculated *R* indices for all available grooming bouts, but as most dyads were observed in more than one bout, means across bouts were calculated within each dyad. We then assigned dyads to one of eight categories, according to the different trader classes to

Table 1
Compositions of the four study groups

Group	Year	Adult males	Subadult males	Adult females	Subadult females	Infants
A	2005	3	0	2	2	1
	2006	3	0	2	1	0
	2007	4	0	2	1	2
B	2005	6	1	2	0	2
	2006	4	1	3	0	0
	2007	4	1	3	0	3
F	2005	2	0	1	2	1
	2006	2	0	3	0	0
	2007	3	0	3	0	0
J	2005	3	1	2	0	1
	2006	4	0	2	0	0
	2007	2	0	2	0	1

Adults: > 2.5 years; subadults: 1–2.5 years; infants: < 1 year. If group compositions changed within years, compositions that prevailed over most of the time are presented.

Table 2

Categories to which dyads of redfronted lemurs were assigned according to their membership in different 'trader' classes, and the number of dyads obtained in each category

Category	Role A	Role B	Dyads
CI	Central males	Immigrant subordinates	6
CN	Central males	Natal subordinates	9
SS	Subordinates*	Subordinates*	14
FC	Females	Central males	13
FRP	Females	Reproductive subordinates†	22
FRL	Females	Relatives‡	9
HH	High-ranking females*	High-ranking females*	4
HL	High-ranking females	Low-ranking females	6

* No further distinctions were made within these classes; roles were assigned randomly but consistently within dyads.

† Subordinates that were not or distantly related to the female with which they groomed; generally immigrants, but also a few natal subordinates.

‡ Subordinates that were closely related (brothers, sons) to the female with which they groomed. Relatedness for all dyads relevant to this study could be derived from pedigrees.

which each animal belonged (Table 2). We defined three categories of male–male dyads, three categories of male–female dyads and two categories of female–female dyads. In male–male dyads, males were classified as either central or subordinate male (see Introduction), and subordinates were further divided into natal subordinates and immigrants. In male–female dyads, males were also classified as central and subordinate male, but in this case subordinates were further divided into reproductive males (i.e. subordinates not or distantly related to their female dyadic partner) and relatives (i.e. close relatives of their female dyadic partner). Note that the classification of subordinates within male–male dyads does not match the classification of subordinates within male–female dyads. Although immigrants could be classified as reproductive males without exception, some subordinates were observed mating with females of their natal groups (e.g. their aunts or cousins); these natal males were therefore classified as reproductive males in male–female dyads. Finally, females were ranked based on decided agonistic interactions (see above): however, each group contained two females that almost never interacted agonistically and which we therefore both classified as high ranking. If groups consisted of more than two females, the remaining females regularly received aggression from, and showed submission to, either one or both of the high-ranking females and could therefore be classified as low ranking. A dyad of low-ranking females existed only once (group A, 2005), but as these individuals were not included in the focal animal observations during that time, no grooming was observed in this dyad.

We defined grooming to be nonreciprocal if the 95% confidence intervals of the mean R values within categories did not include 0; in addition, we tested for differences between categories using analysis of variance (ANOVA). In the case of grooming between females, we used nonparametric statistics because of the low number of available dyads.

Frequencies of aggressive interactions across categories were compared using chi-square tests; by calculating the expected frequencies we took into account both the different numbers of dyads within categories and the different observation times of individuals within dyads. The analysis of aggressive interactions did not include the mating season, as the dominance relationships between males can temporarily collapse during this time (Ostner & Kappeler 1999). Statistical analyses were performed with R version 2.5.1 (R Foundation for Statistical Computing, Vienna, Austria). All tests were two tailed.

RESULTS

Grooming Reciprocity within Bouts

The linear mixed-effects model for the number of episodes exchanged within a bout revealed a highly significant relationship between the number of episodes redfronted lemurs spent grooming their partners and the number of episodes they were groomed by them ($F_{1,254} = 2228.94$, $P < 0.001$). The overall slope of the regression was positive, and close to 1 ($b \pm SE = 0.91 \pm 0.02$), that is, close to the predicted relationship if grooming was completely reciprocal (Fig. 1a). The same analysis performed on the total duration of grooming exchanged within a bout, revealed an apparently similar result. The amount of time the animals spent grooming their partners was significantly related to the amount of time they received grooming ($F_{1,254} = 261.56$, $P < 0.001$); hence, grooming was time matched within bouts. However, in contrast to the analysis of episodes, the slope of the regression strongly deviated from perfect reciprocity ($b \pm SE = 0.62 \pm 0.04$; Fig. 1b), indicating that factors other than strict reciprocity affected the distribution of grooming duration within a bout. Moreover, the deviance of the model containing grooming durations was much

higher ($D = 950.35$) than the deviance of the model containing episodes ($D = 385.37$).

In summary, grooming appeared to be highly reciprocal with regard to an exchange of episodes, but reciprocity was much weaker for the time both partners spent grooming. We therefore restricted the following analyses of possible market effects on the symmetry of grooming to the analysis of grooming durations.

Grooming Reciprocity, Aggression and Trader Class

Male–male dyads

Grooming among male redfronted lemurs was only reciprocal in dyads consisting of subordinates (mean $R \pm 95\%$ confidence interval = 0.03 ± 0.1), whereas central males received more grooming from both immigrants and natal males than they gave in return (mean $R \pm 95\%$ confidence interval = -0.26 ± 0.21 and -0.29 ± 0.13 , respectively; Fig. 2). The symmetry of grooming was different across the three male categories (one-way ANOVA: $F_{2,26} = 11.14$, $P < 0.001$), where dyads consisting of subordinates differed significantly from both other categories (Scheffé test: SS versus CI: $P = 0.009$; SS versus CN: $P = 0.001$; see Table 2 for categories). Moreover, throughout the study 10 subordinates were observed grooming with both a central male and another

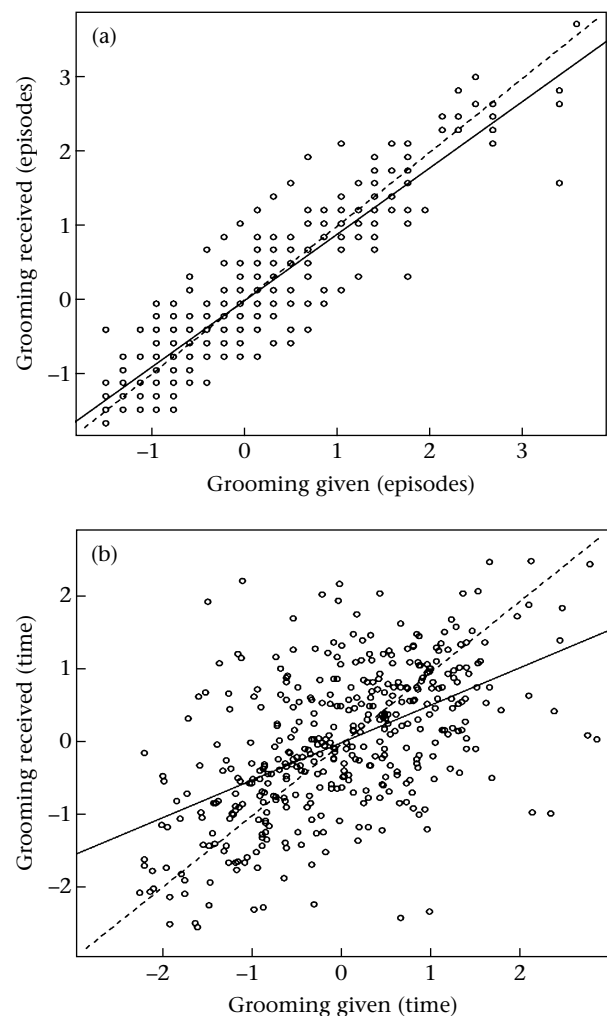


Figure 1. Grooming reciprocity within bouts. (a) Number of episodes each animal performed grooming within a bout. (b) Total grooming durations. The solid lines indicate the estimated slope of the regression; the dashed lines represent the lines of complete reciprocity. Both measures are standardized (z transformed); grooming durations were Box-Cox transformed before standardization.

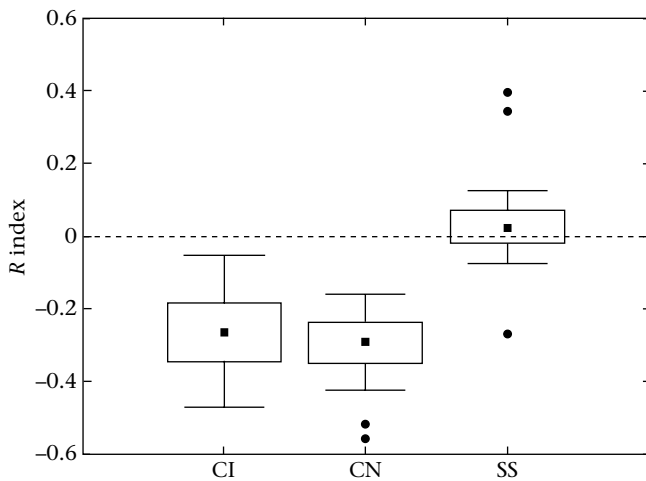


Figure 2. Mean \pm SE (boxes) R indices within the three male categories. Whiskers indicate the 95% confidence interval of the means; outliers are given as dots. The dashed line indicates complete reciprocity. CI: dyads consisting of central males and immigrants; CN: dyads consisting of central males and natal males; SS: dyads consisting of subordinates only.

subordinate. These subordinates spent on average more time grooming the central male (mean $R \pm$ 95% confidence interval = -0.29 ± 0.14) than they spent grooming the subordinate (mean $R \pm$ 95% confidence interval = -0.06 ± 0.13). This difference was statistically significant (paired t test: $t_9 = -2.54$, $P = 0.03$).

Because no difference in grooming reciprocity was found between dyads consisting of central males and immigrants and dyads consisting of central males and natal males (Scheffé test: CI versus CN: $P = 0.95$), we pooled the data from both categories and analysed whether the level of reciprocity changed as a function of male group size. Data were split into different study periods (years) if male group composition changed between years. We found a negative correlation between the level of reciprocity and the number of subordinates ($r_{14} = -0.67$, $P = 0.005$), indicating that central males received most grooming from subordinates when the number of competing subordinates was highest. One dyad entered the analysis twice: the central male of group B was observed grooming with the same subordinate in 2005 and in 2006. Removing either data point from the correlation did not alter the results, however.

Aggressive interactions outside the mating season occurred at a rate of 0.43, 0.16 and 0.21 events per statistical day between central males and immigrants, central males and natal males, and among subordinates, respectively. Central males initiated all agonistic interactions with both immigrants and natal males, and won 55% of encounters ($N = 53$) with immigrants and 94% of encounters ($N = 16$) with natal males. The remaining conflicts were undecided; generally, central males displayed aggressive behaviour towards subordinates but the latter showed no perceptible reaction. In no case did a subordinate win an agonistic interaction with the central male. The frequencies of aggression were not equally distributed across the three male categories ($\chi^2_2 = 37.36$, $P < 0.001$). Central males directed significantly more aggression towards immigrants ($\chi^2_1 = 23.29$, $P < 0.001$), whereas aggression was less frequent than expected among subordinates ($\chi^2_1 = 14.02$, $P < 0.001$).

Female–male dyads

Opposite to the direction expected under the grooming for sex scenario, females groomed both central males and reproductive subordinates longer than vice versa (Fig. 3). The level of asymmetry was strongest in the central male category (mean $R \pm$ 95% confidence

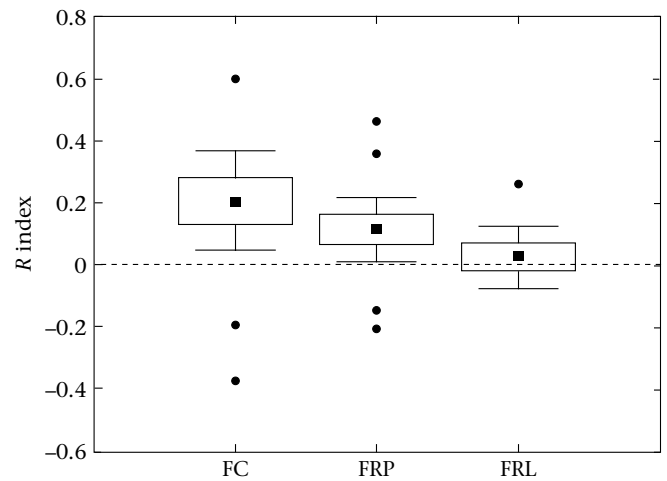


Figure 3. Mean \pm SE (boxes) R indices within the three female–male categories. Whiskers indicate the 95% confidence interval of the means; outliers are given as dots. The dashed line indicates complete reciprocity. FC: dyads consisting of females and central males; FRP: dyads consisting of females and reproductive subordinates; FRL: dyads consisting of females and males to which they were closely related.

interval = 0.3 ± 0.12), but grooming was also slightly biased in favour of males in the reproductive subordinate category (mean $R \pm$ 95% confidence interval = 0.11 ± 0.1). In contrast, grooming was reciprocal between females and males that were closely related to them (mean $R \pm$ 95% confidence interval = 0.03 ± 0.1). However, the level of symmetry did not differ significantly between categories (one-way ANOVA: $F_{2,41} = 1.74$, $P = 0.19$). To check for the possibility that the direction of grooming was reversed during the mating season, we performed a repeated measures ANOVA for the subset of dyads ($N = 14$) with both central and reproductive males for which repeated measures during and outside the mating season were available. Male class was included in the model as the between-subject factor. We did not find any significant effect in this model (season: $F_{1,12} = 0.22$, $P = 0.65$; season*category: $F_{1,12} = 0.66$, $P = 0.43$), indicating that neither central males nor reproductive males increased their grooming effort during the mating season.

Conflicts between females and males occurred at a rate of 0.2, 0.36 and 0.1 events per statistical day with central males, reproductive subordinates and relatives, respectively. Aggression was generally initiated by males, who also won the vast majority of encounters. Females showed submission to central males in 92% ($N = 64$), to reproductive subordinates in 71% ($N = 74$) and to relatives in 74% ($N = 23$) of encounters. Females won agonistic interactions with males in 8% of encounters with reproductive males, and in 4% of encounters with relatives, but they were never observed winning a conflict against a central male. Aggression was not equally distributed across the three female–male categories ($\chi^2_2 = 11.96$, $P = 0.002$), but only central males and females interacted aggressively more often than expected ($\chi^2_1 = 8.0$, $P = 0.005$).

Female–female dyads

In dyads of high-ranking females, both partners spent approximately the same amount of time grooming each other. Within the category of high-ranking females R indices ranged from 0.12 to -0.15 (median = 0). In contrast, a very high asymmetry of grooming was found in dyads consisting of high- and low-ranking females: R indices within this category ranged from -0.23 to -0.58 (median = -0.41), indicating that low-ranking females groomed higher-ranking females longer than vice versa. The level of symmetry was significantly different between the two categories (Mann–Whitney U test: $U = 0$, $N_1 = 4$, $N_2 = 6$, $P = 0.01$, Fig. 4). The bias in favour of high-ranking females in dyads consisting of

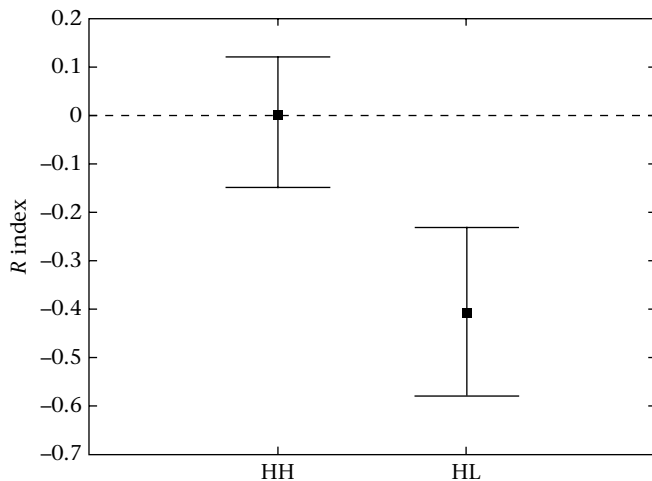


Figure 4. Medians of R indices within the two female categories. Whiskers indicate the overall data range (minimum–maximum). The dashed line represents the line of complete reciprocity. HH: dyads consisting of high-ranking females; HL: dyads consisting of high- and low-ranking females.

high- and low-ranking females represents the strongest asymmetry in grooming observed across all eight categories.

Agonistic interactions between high-ranking females occurred at a very low rate. In 923 h of focal animal observations we could only observe four such conflicts. In contrast, aggression between high- and low-ranking females occurred at the highest rate observed across categories (0.66 encounters per statistical day). Consequently, the frequencies of aggression differed significantly between the two female categories ($\chi^2_1 = 59.48$, $P < 0.001$). Except for two cases, aggression was always initiated by high-ranking females, who also won the majority (86%, $N = 58$) of conflicts with low-ranking females.

DISCUSSION

Grooming and Social Power

Our analyses revealed that grooming between redfronted lemurs was highly reciprocal if the exchange of roles between partners within a grooming bout was considered, but that reciprocity was less pronounced with respect to the total duration that members of a dyad spent grooming each other. Instead, power differentials between grooming partners belonging to different trader classes in a biological marketplace seemed to offset the strict reciprocation of grooming in some dyads. As predicted, grooming was reciprocal in dyads of animals belonging to the same trader class, namely among subordinate males and among high-ranking females, which had no other services or commodities but grooming to offer each other. In contrast, in both sexes, grooming was directed up the social hierarchy, that is, more grooming was given by low-ranking individuals towards high-ranking ones than vice versa. These patterns of grooming are comparable to results obtained in a number of studies on Old World monkeys (e.g. Barrett et al. 2002; Schino et al. 2003; Ventura et al. 2006; but see Leinfelder et al. 2001) and a cooperatively breeding carnivore, the meerkat (Kutsukake & Clutton-Brock 2006). In redfronted lemurs, low-ranking females, the individuals most threatened by eviction from their groups, gave the largest amount of grooming relative to what they received. Similar results were obtained in meerkats (Kutsukake & Clutton-Brock 2006), suggesting that in both species subordinates exchange grooming for the tolerance of dominants.

The patterns of agonistic interactions between different classes of individuals corresponded to the patterns of grooming in that a pronounced level of grooming asymmetry was associated with high rates of agonism. A notable exception was found in males: central males directed significantly more aggression than expected towards immigrants, but not towards natal males, even though the level of grooming asymmetry did not differ between the two subordinate classes. In contrast, the patterns of grooming between the sexes were in accordance with the aforementioned trend: adult males were generally dominant over females, directed more aggression towards females than vice versa, and also received more grooming from females than they gave in return. Moreover, in the female–male category in which grooming was most asymmetric, namely in dyads with central males, the frequencies of aggression were also higher than expected. However, even though more grooming was directed by females towards males, its mean duration was not significantly different between the three female–male categories. We cannot therefore unequivocally explain the functional significance of grooming between the sexes, but as grooming in dyads of females and males unrelated to them was consistently skewed in favour of the latter, both across dyads and over time, we can reject the prediction that males trade grooming for future mating opportunities. Given the fact that males won most agonistic interactions with females, it is possible, but remains to be examined in more detail, that females may trade grooming for access to resources.

A positive relationship between grooming and the level of aggression was also found in chacma baboons, *Papio hamadryas ursinus* (Barrett et al. 2002), Japanese macaques, *Macaca fuscata* (Schino et al. 2005) and meerkats (Kutsukake & Clutton-Brock 2006). It could be argued that it appears to be maladaptive that individuals directing more grooming to others are ‘rewarded’ with higher levels of aggression. Such an argument, however, would imply a causal relationship between aggression and grooming, with higher levels of grooming resulting in reduced aggression, but causality in this relationship could also be the other way around: aggression could result in a higher investment in grooming by subordinates to appease potential aggressors (Silk 1982; Schino et al. 2005). A clear distinction between the two processes becomes difficult as they are likely to operate simultaneously (Schino et al. 2005). Neither relationship would weaken the assumption that grooming is exchanged for the tolerance of higher-ranking individuals, but the adaptive significance of this behaviour can hardly be estimated without a baseline rate of aggression (i.e. the level of aggression in the absence of grooming). The fact, however, that in three primate species and one social carnivore grooming was found to be more reciprocal when aggression was low, but asymmetrical when aggression was common, together with the tension-reducing function of this behaviour (Schino et al. 1988; Aureli et al. 1999) strengthens the suggestion that it serves as a means to reduce aggression in dyads with a high potential for conflicts.

Alternative Explanations

The first theoretical model to examine grooming relationships in primates (Seyfarth 1977) already predicted grooming to be skewed in favour of dominants, hence basically in the direction observed in our study. It could therefore be asked whether the concept of biological markets adds something new to the explanation of patterns of grooming in redfronted lemurs. According to Seyfarth’s (1977) model, an unequal distribution of grooming among group members results from the assumptions that the time available for grooming is limited and that, therefore, access to high-ranking grooming partners is restricted. Both assumptions do not seem to be met in redfronted lemurs, however, because these cathemeral animals spend considerable amounts of time resting,

with ample opportunities for grooming. Moreover, at least among females, it does not seem that low-rankers are excluded from access to high-rankers: low-ranking females were observed grooming with high-ranking females as often as high-ranking females groomed among themselves (unpublished data), yet the symmetry of grooming was very different between these categories. Similar results were obtained for chacma baboons (Henzi et al. 2003).

On the other hand, the mere finding that grooming is directed up the social hierarchy does not necessarily provide support for a biological market. To provide more conclusive evidence, it needs to be shown that commodities are exchanged and/or that the outcome of an exchange is affected by the availability of traders or commodities on the market. For instance, Henzi & Barrett (2002) and Gumert (2007b) showed that newborn infants may serve as 'commodities' in a grooming market and that their mothers obtained grooming from other females for permission to handle the infants. As a further example, as the supply of cleaners in a cleaner fish market increased, individual fish provided a better service to their clients (Soares et al. 2008). A very similar effect was found among the males in our study: subordinates increased their investment in grooming the dominant as the number of competitors increased, presumably because they became more vulnerable to eviction. Thus, market forces seem to affect the exchange of grooming in redfronted lemurs beyond the mere effect of dominance.

To our knowledge, our study is the first to investigate grooming in a primate in which the exchange of grooming is divided into several small parcels. A very similar form of grooming in impalas has been considered one of the 'classic' examples of reciprocal altruism (Hart & Hart 1992; but see Connor 1995a, b), and has been assigned to its predominant model, the Tit-for-Tat strategy (Axelrod & Hamilton 1981). Looking merely at the number of grooming episodes exchanged within a bout indeed gives the impression of high reciprocity and a Tit-for-Tat-like exchange. However, a closer examination of the grooming durations revealed that, in contrast to impalas, strict reciprocation can be offset by power differentials between individuals. Such power differentials are a common element of many primate societies, probably distinguish redfronted lemurs from impalas, and may thus be responsible for the lower degree of reciprocity in this species. Moreover, reciprocity is not hindered by the fact that redfronted lemurs cannot accurately assess the values of the benefits exchanged (Stevens & Hauser 2004), because reciprocation of grooming occurs in some dyads, and if it does not occur, both individuals firmly distribute grooming according to their standing in the marketplace.

CONCLUSIONS

In summary, even though grooming between redfronted lemurs takes place in an apparently highly reciprocal manner, and the prerequisites for reciprocal altruism are likely to be met (see Stevens & Hauser 2004), reciprocal altruism cannot explain all dimensions of this behaviour. Instead, as predicted by the biological market approach (Henzi & Barrett 1999), some degree of time matching occurred, but market effects accounted for the break-up of strict reciprocity. However, to dismiss reciprocal altruism completely as an explanation for the exchange of grooming in redfronted lemurs, one must show that grooming is not reciprocated on a larger timescale (functional reciprocation versus immediate reciprocation, Schino et al. 2003). As we focused on the exchange of grooming within bouts, our data are not sufficient to rule out this possibility completely.

Our study is the first to carry out a formal test of the biological market approach of social grooming in a group-living strepsirrhine primate. We could show that this behaviour serves a social function

in redfronted lemurs by providing evidence of market effects in this species. Because, unlike in anthropoid primates, grooming in lemurs is always reciprocal, but may differ in the degree of reciprocity, these animals represent an ideal model system to investigate further the biological market approach of grooming in primates. Experimental studies, in particular, would provide researchers with the opportunity to manipulate power differentials between individuals, for example by provisioning food resources that can or cannot be monopolized by dominants, which should translate into shifts in grooming reciprocity.

Acknowledgments

We thank the Malagasy Ministère de l'Environnement et des Eaux et Forêts, the Département Biologie Animale de l'Université d'Antananarivo and the Centre de Formation Professionnelle Forestière de Morondava for authorizing and supporting our research in Kirindy. We are also grateful to Jean-Pierre Ratolojanahary, Janna Etz, Fabian Nürnberger, Lantonirina Ratovonjanahary, Jessica Schäckermann, Annette Schneider and Friederike Scholz for their contributions to data collection. Finally, we thank Peter Henzi and an anonymous referee for their constructive comments on the paper. Funding was provided by the German Research Council (DFG: Ka 1082/9).

References

- Aureli, F., Preston, S. D. & de Waal, F. B. M. 1999. Heart rate responses to social interactions in free-moving rhesus macaques (*Macaca mulatta*): a pilot study. *Journal of Comparative Psychology*, **113**, 59–65.
- Axelrod, R. & Hamilton, R. D. 1981. The evolution of cooperation. *Science*, **211**, 1390–1396.
- Barrett, L. & Henzi, S. P. 2001. The utility of grooming in baboon troops. In: *Economics in Nature: Social Dilemmas, Mate Choice, and Biological Markets* (Ed. by R. Noë, P. Hammerstein & J. A. R. A. M. van Hooff), pp. 119–145. Cambridge: Cambridge University Press.
- Barrett, L., Henzi, S. P., Weingrill, T., Lycett, J. E. & Hill, R. A. 1999. Market forces predict grooming reciprocity in female baboons. *Proceedings of the Royal Society of London, Series B*, **266**, 665–670.
- Barrett, L., Gaynor, D. & Henzi, S. P. 2002. A dynamic interaction between aggression and grooming reciprocity among female chacma baboons. *Animal Behaviour*, **63**, 1047–1053.
- Barton, R. A. 1985. Grooming site preferences in primates and their functional implications. *International Journal of Primatology*, **6**, 519–532.
- Barton, R. A. 1987. Allogrooming as mutualism in diurnal lemurs. *Primates*, **28**, 539–542.
- Boskoff, K. J. 1978. The oestrus cycle of the brown lemur, *Lemur fulvus*. *Journal of Reproduction and Fertility*, **54**, 313–318.
- Box, G. E. P. & Cox, D. R. 1964. An analysis of transformations. *Journal of the Royal Statistical Society, Series B*, **26**, 211–246.
- Connor, R. C. 1995a. Impala allogrooming and the parcelling model of reciprocity. *Animal Behaviour*, **49**, 528–530.
- Connor, R. C. 1995b. Altruism among non-relatives: alternatives to the 'Prisoner's Dilemma'. *Trends in Ecology & Evolution*, **10**, 84–86.
- Duffy, K. G., Wrangham, R. W. & Silk, J. B. 2007. Male chimpanzees exchange political support for mating opportunities. *Current Biology*, **17**, R586–R587.
- Dunbar, R. I. M. 1992. Time: a hidden constraint on the behavioural ecology of baboons. *Behavioral Ecology and Sociobiology*, **33**, 35–49.
- Goosen, C. 1987. Social grooming in primates. In: *Comparative Primate Biology. Vol. 2B: Behavior, Cognition, and Motivation* (Ed. by G. Mitchell & J. Erwin), pp. 107–131. New York: A.R. Liss.
- Gumert, M. D. 2007a. Payment for sex in a macaque mating market. *Animal Behaviour*, **74**, 1655–1667.
- Gumert, M. D. 2007b. Grooming and infant handling interchange in *Macaca fascicularis*: the relationship between infant supply and grooming payment. *International Journal of Primatology*, **28**, 1059–1074.
- Hamilton, W. D. 1964. The genetical evolution of social behaviour I&II. *Journal of Theoretical Biology*, **7**, 1–52.
- Hart, B. J. & Hart, L. A. 1992. Reciprocal allogrooming in impala, *Aepyceros melampus*. *Animal Behaviour*, **44**, 1073–1083.
- Hemelrijk, C. K. 1994. Support for being groomed in long-tailed macaques, *Macaca fascicularis*. *Animal Behaviour*, **48**, 479–481.
- Hemelrijk, C. K. & Ek, A. 1991. Reciprocity and interchange of grooming and 'support' in captive chimpanzees. *Animal Behaviour*, **41**, 923–935.
- Henzi, S. P. & Barrett, L. 1999. The value of grooming to female primates. *Primates*, **40**, 47–59.
- Henzi, S. P. & Barrett, L. 2002. Infants as a commodity in a baboon market. *Animal Behaviour*, **63**, 915–921.

- Henzi, S. P., Lycett, J. E. & Weingrill, T.** 1997. Cohort size and the allocation of social effort by female mountain baboons. *Animal Behaviour*, **54**, 1235–1243.
- Henzi, S. P., Barrett, L., Gaynor, D., Greeff, J., Weingrill, T. & Hill, R. A.** 2003. Effect of resource competition on the long-term allocation of grooming by female baboons: evaluating Seyfarth's model. *Animal Behaviour*, **66**, 931–938.
- van Hooff, J. A. R. A. M. & van Schaik, C. P.** 1994. Male bonds: affiliative relationships among nonhuman primate males. *Behaviour*, **130**, 309–337.
- Hutchins, M. & Barash, D. P.** 1976. Grooming in primates: implications for its utilitarian function. *Primates*, **17**, 145–150.
- Kappeler, P. M.** 1993a. Variation in social structure: the effects of sex and kinship on social interactions in three lemur species. *Ethology*, **93**, 125–145.
- Kappeler, P. M.** 1993b. Reconciliation and post-conflict behaviour in ringtailed lemurs, *Lemur catta* and redfronted lemurs, *Eulemur fulvus rufus*. *Animal Behaviour*, **45**, 901–915.
- Kappeler, P. M. & Port, M.** 2008. Mutual tolerance or reproductive competition? Patterns of reproductive skew among male redfronted lemurs (*Eulemur fulvus rufus*). *Behavioral Ecology and Sociobiology*, **62**, 1477–1488.
- Kapsalis, E. & Berman, C. M.** 1996. Models of affiliative relationships among free-ranging rhesus monkeys (*Macaca mulatta*) II. Testing predictions for three hypothesized organizing principles. *Behaviour*, **133**, 1235–1263.
- Kutsukake, N. & Clutton-Brock, T. H.** 2006. Social function of allogrooming in cooperatively breeding meerkats. *Animal Behaviour*, **72**, 1059–1068.
- Lazaro-Perea, C., de Fatima Arruda, M. & Snowdon, C. T.** 2004. Grooming as a reward? Social function of grooming between females in cooperatively breeding marmosets. *Animal Behaviour*, **67**, 627–636.
- Leinfelder, I., De Vries, H., Deleu, R. & Nelissen, M.** 2001. Rank and grooming reciprocity among females in a mixed-sex group of captive hamadryas baboons. *American Journal of Primatology*, **55**, 25–42.
- Löttker, P., Huck, M., Zinner, D. P. & Heymann, E. W.** 2007. Grooming relationships between breeding females and adult group members in cooperatively breeding moustached tamarins (*Saguinus mystax*). *American Journal of Primatology*, **69**, 1159–1172.
- Maestripieri, D.** 1993. Vigilance costs of allogrooming in macaque mothers. *American Naturalist*, **141**, 744–753.
- Manson, J. H., Navarrete, C. D., Silk, J. B. & Perry, S.** 2004. Time-matched grooming in female primates? New analyses from two species. *Animal Behaviour*, **67**, 493–500.
- Mooring, M. S. & Hart, B. L.** 1995. Costs of allogrooming in impala: distraction from vigilance. *Animal Behaviour*, **49**, 1414–1416.
- Noë, R.** 2001. Biological markets: partner choice as the driving force behind the evolution of mutualism. In: *Economics in Nature: Social Dilemmas, Mate Choice, and Biological Markets* (Ed. by R. Noë, P. Hammerstein & J. A. R. A. M. van Hooff), pp. 119–145. Cambridge: Cambridge University Press.
- Noë, R. & Hammerstein, P.** 1995. Biological markets. *Trends in Ecology & Evolution*, **10**, 336–340.
- Ostner, J. & Kappeler, P. M.** 1999. Central males instead of multiple pairs in redfronted lemurs, *Eulemur fulvus rufus* (Primates, Lemuridae)? *Animal Behaviour*, **58**, 1069–1078.
- Ostner, J. & Kappeler, P. M.** 2004. Male life history and the unusual sex ratios of redfronted lemur (*Eulemur fulvus rufus*) groups. *Animal Behaviour*, **67**, 249–259.
- Overdorff, D. J., Merenlender, A. M., Talata, P., Telo, A. & Forward, Z. E.** 1999. Life history of *Eulemur fulvus rufus* from 1988–1998 in southeastern Madagascar. *American Journal of Physical Anthropology*, **108**, 295–310.
- Payne, H. F. P., Lawes, M. J. & Henzi, S. P.** 2003. Competition and exchange of grooming among female samango monkeys (*Cercopithecus mitis erythrarchus*). *Behaviour*, **140**, 453–471.
- Pereira, M. E. & Kappeler, P. M.** 1997. Divergent systems of agonistic relationship in lemurid primates. *Behaviour*, **134**, 225–274.
- Rensing, S.** 1999. Immobilization and anesthesia of nonhuman primates. *Primate Report*, **55**, 33–38.
- Schino, G.** 2001. Grooming, competition and social rank among female primates: a meta-analysis. *Animal Behaviour*, **62**, 265–271.
- Schino, G.** 2007. Grooming and agonistic support: a meta-analysis of primate reciprocal altruism. *Behavioral Ecology*, **18**, 115–120.
- Schino, G., Scucchi, S., Maestripieri, D. & Turillazzi, P. G.** 1988. Allogrooming as a tension-reduction mechanism: a behavioral approach. *American Journal of Primatology*, **16**, 43–50.
- Schino, G., Ventura, R. & Troisi, A.** 2003. Grooming among female Japanese macaques: distinguishing between reciprocation and interchange. *Behavioral Ecology*, **14**, 887–891.
- Schino, G., Ventura, R. & Troisi, A.** 2005. Grooming and aggression in captive Japanese macaques. *Primates*, **46**, 207–209.
- Seyfarth, R. M.** 1977. A model of social grooming among adult female monkeys. *Journal of Theoretical Biology*, **65**, 671–698.
- Seyfarth, R. M. & Cheney, D. L.** 1984. Grooming, alliances and reciprocal altruism in vervet monkeys. *Nature*, **308**, 541–542.
- Silk, J. B.** 1982. Altruism among female *Macaca radiata*: explanations and analysis of patterns of grooming and coalition formation. *Behaviour*, **79**, 162–188.
- Soares, M. C., Bshary, R., Cardoso, S. C. & Côté, I. M.** 2008. Does competition for clients increase service quality in cleaning gobies? *Ethology*, **114**, 625–632.
- Sorg, J., Ganzhorn, J. & Kappeler, P. M.** 2003. Forestry and research in the Kirindy Forest/ Centre de Formation Professionnelle Forestière. In: *The Natural History of Madagascar* (Ed. by S. Goodman & J. Benstead), pp. 1512–1519. Chicago: University of Chicago Press.
- Sparks, J.** 1967. Allogrooming in primates: a review. In: *Primate Ethology* (Ed. by D. Morris), pp. 148–174. Chicago: Aldine.
- Stevens, J. R. & Hauser, M. D.** 2004. Why be nice? Psychological constraints on the evolution of cooperation. *Trends in Cognitive Sciences*, **8**, 60–65.
- Stopka, P. & Macdonald, D. W.** 1999. The market effect in the wood mouse, *Apodemus sylvaticus*: selling information on reproductive status. *Ethology*, **105**, 969–982.
- Trivers, R. L.** 1971. The evolution of reciprocal altruism. *Quarterly Review of Biology*, **46**, 35–57.
- Trivers, R. L.** 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man, 1871–1971* (Ed. by B. Campbell), pp. 136–179. London: Heinemann.
- Ventura, R., Majolo, B., Koyama, N. F., Hardie, S. & Schino, G.** 2006. Reciprocation and interchange in wild Japanese macaques: grooming, cofeeding, and agonistic support. *American Journal of Primatology*, **68**, 1138–1149.
- Vick, L. G. & Pereira, M. E.** 1989. Episodic targeting aggression and the histories of Lemur social groups. *Behavioral Ecology and Sociobiology*, **25**, 3–12.
- de Waal, F. B. M.** 1997. The chimpanzee's service economy: food for grooming. *Evolution and Human Behavior*, **18**, 375–386.
- Wimmer, B. & Kappeler, P. M.** 2002. The effects of sexual selection and life history on the genetic structure of redfronted lemur, *Eulemur fulvus rufus*, groups. *Animal Behaviour*, **64**, 557–568.