Time-matched grooming in female primates?
New analyses from two species

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The parcelling model of reciprocity predicts that grooming partners will alternate between giving and receiving grooming within grooming bouts, and that each partner will perform approximately as much grooming as it receives within each bout ('time matching'). Models of allogrooming based on biological markets theory predict that individuals of lower dominance rank will exchange grooming for tolerance from high-rankers, and therefore an inverse relation will be found between grooming partners' dominance rank distance and how closely they match each other's grooming contributions within each bout. We used weighted logistic regression and weighted least-squares regression to test these predictions using data from female white-faced capuchins, *Cebus capucinus*, and bonnet macaques, *Macaca radiata*. Only 5–7% of macaque grooming bouts, and 12–27% of capuchin grooming bouts, were reciprocated. However, (1) the duration of grooming by the first groomer significantly predicted whether the groomee would reciprocate at all, and (2) when bouts were reciprocated, the duration of grooming by the first groomer significantly predicted the duration of grooming by the second groomer. Grooming was most balanced among females of similar dominance ranks. Both the time-matching and rank-related effects were weak, although significant. These results indicate that although some form of time matching may be a general characteristic of grooming in female-bonded primate species, time matching accounts for relatively little of the variation in the distribution of grooming within bouts. We also draw attention to weighted regression as a technique that avoids pseudoreplication while using all available data.

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Allogrooming among adults, a phenomenon best known in primates, is also widespread in ungulates (e.g. Clutton-Brock et al. 1976; Hart & Hart 1992; Feh & de Mazieres 1993) and rodents (e.g. Stopka & Macdonald 1999; Stopka & Graciasová 2001). Allogrooming can impose costs on groomers in the form of decreased vigilance (Maestripieri 1993; Mooring & Hart 1995) and possibly decreased resting time (Dunbar & Sharman 1984; Dunbar 1992). Demonstrated or inferred benefits of being groomed include removal of ectoparasites (Saunders 1988; Tanaka & Takefushi 1993; Mooring et al. 1996; Zamma 2002), release of β-endorphins (Keverne et al. 1989), and heart rate reduction (Feh & de Mazieres 1993). Thus, allogrooming is likely to be a form of altruism (Hutchins & Barash

1976; Kurland 1977). Among primates, grooming interactions are disproportionately concentrated in kin dyads (Gouzoules & Gouzoules 1987; Schino 2001), a pattern explicable as an outcome of kin selection (Hamilton 1964). Several authors have proposed that grooming among nonkin is shaped by reciprocity (Trivers 1971). Grooming could be exchanged for coalitional support (Seyfarth & Cheney 1984), food (de Waal 1997), tolerance (Henzi & Barrett 1999), matings or information about reproductive status (Stopka & Macdonald 1999) or for grooming itself (Henzi & Barrett 1999; Silk et al. 1999; Stopka & Graciasová 2001).

Models of reciprocity generate predictions about the distribution of grooming within dyads and within grooming bouts. In Connor's (1995) parcelling model of reciprocity, an individual provides its partner with a small quantity of a desired resource or service and then waits for the partner to reciprocate before providing the next 'parcel' of the resource or service. In this model, cheating (i.e. not reciprocating a parcel, after which the cheater's

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partner would end the interaction) is not a profitable option, because the value to a cheater of an unreciprocated parcel is outweighed by the cost of foregoing the parcels that would be provided by the partner if the interaction continued. This model predicts that within allogrooming interactions, individuals will alternate between grooming and receiving grooming, and they will perform approximately as much grooming as they have just received. The parcelling model is supported by data on allogrooming in impala, *Aepyceros melampus* (Hart & Hart 1992; Mooring & Hart 1997) and rodents (Stopka & Graciasová 2001). In contrast, individuals following the raise-the-stakes (RTS) strategy (Roberts & Sherratt 1998) begin cooperative relationships by providing a small benefit to prospective partners, and increase their investment if this benefit is matched by the partner. Grooming partners following this strategy would also alternate roles between groomer and groomee, but would lengthen the duration of grooming episodes as a grooming interaction proceeded.

Models of reciprocity based on the iterated two-person Prisoner's Dilemma game (Axelrod & Hamilton 1981) have emphasized the importance of repeated interactions within dyads as a route to the enforcement of cooperation. Defectors (or 'short-changers' in Roberts & Sherratt's 1998 variable investment simulations) are recognized and denied the benefits of future cooperation, causing them to receive lower long-term payoffs than cooperators. Evolutionarily stable variants of Axelrod & Hamilton's (1981) 'Tit for Tat' strategy (cooperate on the first interaction, then copy the other player's behaviour from the previous interaction) incorporate the possibility that partners receive unequal payoffs from cooperative dyadic interactions because they vary in the benefits they confer and the costs they incur in these interactions (Boyd 1992). Such variation, in conjunction with the ability to choose between prospective partners based on approximately accurate information, produces dynamics similar to those observed in market economies (Noë & Hammerstein 1995). Principles of supply and demand then determine the 'prices' of biological 'commodities', for example, as the supply of a commodity decreases while demand for it remains constant, suppliers of the commodity will be able to charge higher prices for it.

Demonstrating reciprocity requires demonstrating the contingent exchange of goods or services. Some experimental evidence indicates that primates engage in contingent exchanges of allogrooming for coalitional support (Seyfarth & Cheney 1984; Hemelrijk 1994) or food (de Waal 1997), but naturalistic observations of exchanges are more difficult to interpret. In general, few examples of reciprocal altruism have been demonstrated in nonhuman animals, and most of these involve short-term exchanges of low-cost commodities (McElreath et al. 2003). Biological markets theory has successfully predicted aspects of interspecific mutualisms, such as the exchange of protection for nectar between ants and lycaenid butterflies (Axén et al. 1996; Axén & Pierce 1998; Weith 1998, cited in Noë 2001), and the exchange of cleaning for food between cleaner fish and their clients (Bshary 2001).

Barrett et al. (1999) and Henzi & Barrett (1999) proposed that allogrooming among females of female-bonded (as defined by Wrangham 1980) primate species is parcelled into short episodes to prevent cheating, and that power asymmetries affect the distribution of grooming within dyads. When most grooming occurs between females of similar dominance rank, grooming is predicted to be 'time matched' within bouts, that is, the amount of time that the first groomer, A, grooms the second groomer, B, will be positively correlated with the amount of time that B groomed A within that bout. When female–female competition is mild, grooming will be traded primarily for grooming, so grooming will be closely balanced within bouts. When female–female competition is intense and dominance relationships powerfully affect access to resources, grooming will be 'traded' for tolerance, so grooming balance will be inversely related to rank distance and subordinates will groom dominants more than vice versa. Barrett et al. (1999) reported evidence supporting these predictions from four troops of wild chacma baboons, *Papio cynocephalus ursinus*. Time matching within bouts has also been documented among female blue monkeys, *Cercopithecus mitis*, in the Kakamega Forest of Kenya (Cords 2002). In a separate set of analyses, Barrett et al. (2000) looked for but did not find evidence that baboons' grooming patterns conform to the RTS strategy (Roberts & Sherratt 1998).

In this paper, we build on these findings in two ways. First, we examine whether they can be replicated in two other female-bonded species: white-faced capuchins, *Cebus capucinus*, and bonnet macaques, *Macaca radiata*. Second, we improve on Barrett et al.'s (1999) analytical techniques by using weighted logistic regression and weighted least-squares regression to address whether grooming is time-matched within bouts. Barrett et al. (1999) sought to solve the problem presented by the contribution by each dyad of multiple grooming bouts to the data set ('pseudoreplication', Hurlbert 1984; the 'pooling fallacy', Machlis et al. 1985) by randomly choosing one reciprocated grooming bout in each direction for each female–female dyad, and then using only the randomly chosen bouts in statistical analyses. This technique uses only a small portion of the available data, and it poses the risk of drawing an unrepresentative sample. In particular, excluding all unreciprocated bouts from analysis might make it more likely to find time matching. The method used here uses all available data and still avoids the pooling fallacy.

METHODS

Study Sites and Subjects

White-faced capuchins

We collected data on members of a single social group (Abby's group) in and just north of Lomas Barbudal Biological Reserve, Guanacaste, Costa Rica (centre of study group's home range: 10°30′N, 85°22′W). The area consists largely of highly seasonal tropical dry deciduous forest (Frankie et al. 1988) traversed by several permanent streams. We followed the social group from dawn to dusk

every day for up to 25 sequential days per month. Adults were easily identified by scars, hair colour patterns and facial contours. We collected data during May 1991−May 1993 (Perry 1996) and February−June 1997 (Manson et al. 1999). During the two study periods, the group contained five to eight adult females, three to four adult males and 11−15 immatures.

We collected data in the form of focal individual follows (Altmann 1974) during which all social behaviours and the identities of the interactants were narrated on to microcassettes. The onsets and terminations of grooming interactions were recorded to the nearest second. Behavioural definitions, and methods of calculating interobserver reliability, are described by Perry (1996). Dominance relationships were determined on the basis of the direction of avoids and cowers in dyadic interactions (Perry 1996). Maternal kinship among adults was unknown during the 1991−1993 observations and only one adult female−female dyad's kin relationship was known during the 1997 observations. Earlier observations of this population indicated that female−female grooming was disproportionately concentrated among dyads that were close in dominance rank (Perry 1996; Manson et al. 1999).

Capuchin research was approved by the Committee on Use and Care of Animals of the University of Michigan and the Chancellor's Animal Research Committee of the University of California, Los Angeles.

Bonnet macaques

Data were collected over a 4-year period in two, multimale, multifemale groups of bonnet macaques housed at the California Primate Research Center at the University of California, Davis. Both study groups were derived from a single group that was originally established for behavioural research in 1970−1971. Management policies were designed to replicate demographic features of free-ranging groups. No unfamiliar females were introduced into the group after it was initially established. Maturing males were periodically removed from the group to simulate emigration, and mature males were introduced occasionally to simulate immigration. Owing to natural recruitment, the group grew in size and eventually exceeded the capacity of the enclosure. One year before the present study began, the group was divided. In an attempt to mimic fission in free-ranging macaque groups, a number of the lowest-ranking females and all of their immature offspring were moved to another enclosure, while the remaining females and their offspring remained in the original enclosure. See Silk (1991) for additional details about the study groups.

The data included in this report were collected from 1984 to 1987. During this period, the larger group included 17−21 adult females and the smaller group contained seven to eight adult females. Both study groups were housed outdoors. The larger group's enclosure (35.5×70 m) was equipped with a number of raised wooden A-frame shelters and covered perches that provided protection from sun, wind and rain. The smaller group was housed in four octagonal enclosures (4.3 m diameter) connected by passageways (3.5×1.5 m). These enclosures were equipped with covered perches. Both groups were fed monkey chow twice a day and water was available ad libitum. Maternal kinship relationships are known for all individuals born in the group since 1970. Dominance relationships were determined on the basis of the direction of decided dyadic agonistic interactions and supplants (Silk et al. 1981).

Focal observations were conducted on all adult females in the study. Each focal sample lasted 15 min, and females in the study groups were observed on average 1.4 times per week (range 0−8). Observers entered information about the onset and termination of each grooming bout on a hand-held computer which recorded the time of each entry to the nearest second. Dominance ranks were assessed at 6-month intervals on the basis of clearly decided agonistic encounters and supplants. Earlier observations of this population indicated that female−female grooming was disproportionately concentrated among dyads that were close in dominance rank (Silk 1982).

Bonnet research was approved by the Institutional Animal Care and Use Committee of the University of California, Davis.

Data Analysis

We reorganized our observations of female−female grooming into bouts using the same definition of bout as Barrett et al. (1999). Specifically, 'a grooming bout was defined as a continuous period of allogrooming involving the same two animals. A change of identity of one of the two animals or a shift in activity for more than 10 s signalled the end of a bout' (Henzi et al. 1997, page 1237).

Following Barrett et al. (1999), for each female in our data sets, we extracted all grooming bouts in which she was designated as the initial groomer (hereafter, the initiator), and sorted these bouts into clusters as a function of the identity of the other female (i.e. her grooming partner for that bout; hereafter, the recipient). This procedure gave us a maximum of $N(N-1)$ clusters per study group, where N is the number of adult females. We call these 'clusters' rather than 'dyads' because each dyad could yield two clusters: the bouts in which A groomed B first, and the bouts in which B groomed A first.

We used every grooming bout as a data point, but each grooming bout's contributions to the estimate of logistic and least-squares regression equations were weighted as an inverse function of the number of observed bouts in that cluster (i.e. weights were calculated as equal to $1/n$ where n is the number of bouts within each cluster). The degrees of freedom reflect the number of independent clusters present in the analysis, not the total number of data points in the analysis. Using this method, we were able to estimate a regression coefficient that considered all data, but ensured that every cluster contributed equally to its estimation, regardless of the number of observations within each cluster (Stata 2001, pp. 261−266).

We did not distinguish between grooming bouts that were terminated voluntarily and those that ended because of interference by another individual, because we

wanted our analyses to be directly comparable to those of Barrett et al. (1999), who did not make this distinction. Furthermore, it is our impression that the vast majority of grooming bouts in both species were terminated voluntarily.

To test the hypothesis that the amount of time the initiator groomed the recipient could predict the binary outcome that the recipient would reciprocate at all, we conducted a logistic regression with maximum-likelihood estimators (Gould 2000). Each observation was weighted as described above, and data from both species were pooled into one data set. Owing to a right-tailed skew in the distribution of the time the initiator groomed the recipient, we log transformed this variable before analysis. To explore species differences, we used a dichotomous variable to represent taxon in the model. Following the recommendation of Aiken & West (1991), the continuous variable (time initiator groomed the recipient) was zero centred (i.e. the mean was subtracted from each data point), the dichotomous variable (taxon) was dummy coded, and their two-way interaction was created using the product of the two terms before the analysis. When time is zero centred, the main effects of taxon reflect the difference between the two species on the dependent variable when time is held constant at its mean. This is because when interaction variables involving the product of a continuous and a dichotomous variable are added to a regression model, the main effect becomes a simple effect estimated when the continuous variable is zero. Therefore, the continuous variable must be zero centred at its mean such that the simple effect (in our case, species) is estimated when the continuous variable is held constant at its mean.

To test the hypothesis that grooming was time matched within the subset of bouts that were reciprocated, we conducted a weighted least-squares regression for grouped data in which the time that the recipient groomed the initiator was regressed on the time that the initiator groomed the recipient. We normalized grooming durations for this analysis (i.e. by subtracting the mean and dividing by the standard deviation). We used the independent variables and weighting schema described above.

To examine the effects of rank discrepancy on grooming time matching, we used the same weighted least-squares regression procedure described above, but regressed grooming discrepancy (duration of initiator grooms recipient minus duration of recipient grooms initiator) on rank distance (initiator's dominance rank minus recipient's dominance rank, with the alpha female's rank represented as '1'). We used the independent variables and weighting schema described above.

We carried out regression analyses using Stata 7.0 (Stata 2001).

Finally, to examine whether our subjects used the RTS strategy (Roberts & Sherratt 1998), we followed Barrett et al. (2000) in dividing grooming bouts into episodes, which are defined as continuous periods within bouts during which the same individual is acting as groomer. For example, suppose that individual A groomed individual B for 22 s, followed by a 3-s pause, after which B groomed A for 17 s, immediately after which A groomed B for 5 s,

then A and B moved apart. We would code these events as a single grooming bout during which A groomed B for 27 s and B groomed A for 17 s, and we would record that the bout consisted of three episodes. For all grooming bouts consisting of three or more episodes, we used sign tests to determine whether episode length increased as bouts proceeded, and we used Friedman ANOVA tests to determine whether episode lengths varied systematically as a function of their temporal position within bouts. For the sign tests, the null hypothesis was that each successive episode had a 0.50 probability of being longer than the preceding episode. For example, in a bout consisting of three episodes, the probability of consistent increase throughout the bout was $(0.50)(0.50) = 0.25$. We carried out this analysis on the white-faced capuchin data only, because only 25 bonnet macaque grooming bouts involved three or more episodes. These bouts represent only 0.05% of the total number of bonnet macaque grooming bouts, a sample too small for meaningful analysis.

Characteristics of the Data Set

White-faced capuchins

At Lomas Barbudal, observations during 1991−1997 yielded 723.6-h focal follows of nine females ($\overline{X} \pm SE = 80.4 \pm 20.0$ h/female, range = 4−140 h/female). The 1991−1993 study period yielded 603.6 h of focal follows, during which we observed 1050 grooming bouts, of which 287 (27.3%) were reciprocated ($\overline{X} \pm SE = 36.2 \pm 5.3$ bouts per cluster, range = 3−119) and the 1997 study period yielded 120 h of focal follows, during which we observed 459 grooming bouts, of which 56 (12.2%) were reciprocated (14.2 ± 4.4 bouts per cluster, range = 1−94). Relative dominance rank did not change in any of the dyads present in both the 1991−1993 study period and the 1997 study period (Manson et al. 1999), so we were able to pool data from the two periods. The entire white-faced capuchin data set consisted of 48 clusters, as defined above, including 38 clusters in which at least one reciprocated grooming bout occurred.

Bonnet macaques

In the large group, 5584 focal samples on 27 adult females (1396 h) were collected. The number of samples per female varied because some females matured during the study period and some females died. Each focal female was observed for a mean $\pm$ SE of 51 ± 5.0 h, range 5.75−76.5 h/female. Females in the large group participated in 3007 grooming bouts, of which 209 (7%) were reciprocated. In the small group, 2375 focal samples on 12 adult females (594 h) were collected. Each of the females in the small group was observed for a mean $\pm$ SE of 51.2 ± 8.6 h, range 7.0−88.0 h/female. Females in the small group participated in 1469 grooming bouts, of which 74 (5%) were reciprocated. The entire bonnet macaque data set consisted of 486 clusters, including 150 clusters in which at least one reciprocated grooming bout occurred.
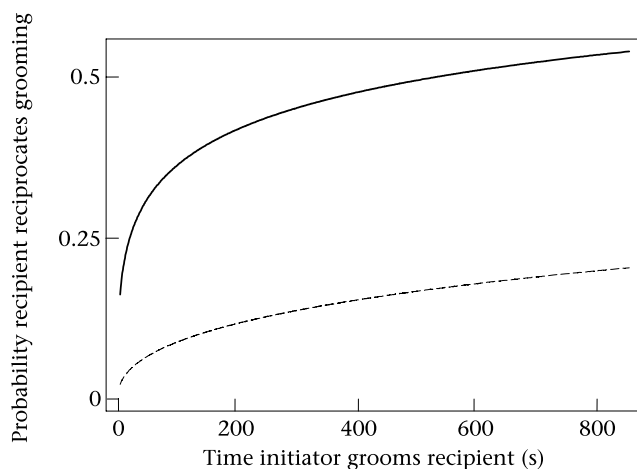
RESULTS

Time Matching

Grooming by initiator and probability of reciprocation

Logistic regression results revealed a main effect for the time the initiator groomed the recipient on the probability that the recipient reciprocated the grooming (model $\chi^2_3 = 81.92$, $P < 0.0001$). The regression revealed increases in the probability of reciprocation as a function of the time the initiator groomed for both species (white-faced capuchins: $b \pm SE = 0.37 \pm 0.15$, odds ratio = 1.40; bonnet macaques: $b \pm SE = 0.45 \pm 0.08$, odds ratio = 1.57) with no significant differences between the slopes. Results remained significant when each species was analysed separately. A main effect for species was found as well (model $\chi^2_3 = 52.95$, $P < 0.0001$). On average, bonnet macaques were less likely to reciprocate than white-faced capuchins ($b \pm SE = -1.89 \pm 0.26$, odds ratio = 0.15; Fig. 1).

Time matching within reciprocated grooming bouts

When we used only reciprocated grooming bouts in the analyses, the results of a weighted least-squares regression analysis revealed a significant main effect for time matching ($F_{2,187} = 6.68$, $P < 0.001$). Slopes assessing time matching were positive for white-faced capuchins ($b \pm SE = 0.34 \pm 0.10$, $\beta = 0.31$) and for bonnet macaques (0.12 ± 0.08, $\beta = 0.11$) with no significant differences between the two slopes. However, only the capuchin slope remained significantly greater than zero when data from the two species were analysed separately (white-faced capuchins: $F_{1,37} = 11.05$, $P = 0.001$; bonnet macaques: $F_{1,149} = 2.31$, $P = 0.13$). The regression also revealed a main effect for species ($F_{1,187} = 13.79$, $P < 0.0001$) indicating that the average duration for grooming bouts was longer for bonnet macaques than for white-faced capuchins ($b \pm SE = 1.85 \pm 0.50$, $\beta = 0.82$; Fig. 2).

Grooming and Dominance Rank Distance

Grooming discrepancy within bouts was greater in dyads consisting of distantly ranked females than in dyads consisting of closely ranked females. Weighted least-squares regression revealed a significant main effect for rank distance ($F_{2,187} = 7.72$, $P < 0.001$; Fig. 3) and no main effect for species. Results remained significant when each species was analysed separately. The slope predicting grooming discrepancy by rank distance yielded a regression coefficient $\pm SE$ of 5.80 ± 1.63 ($\beta = 0.27$) for capuchins, and 2.25 ± 1.42 for macaques ($\beta = 0.10$), with no significant difference between the slopes for each species. This shows that for every one unit difference in rank distance between the initiator and the recipient, a 5.80-s groom-time discrepancy is expected for white-faced capuchins, and a 2.25-s groom-time discrepancy for bonnet macaques.
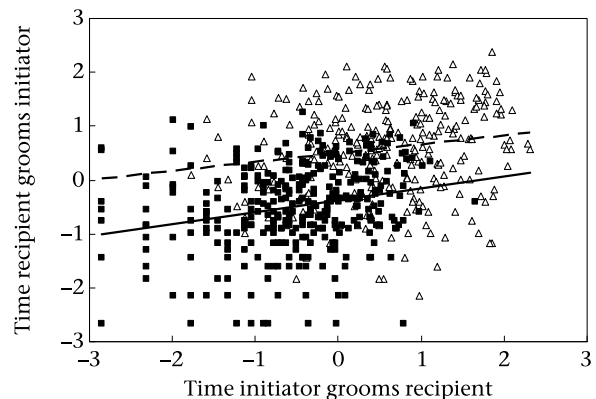
Raise-the-Stakes

White-faced capuchins

We recorded 159 grooming bouts from 31 clusters (see Methods for definition) that consisted of three or more episodes. Table 1 shows for bouts consisting of each number of episodes from three to 10 (the maximum number observed), how many bouts showed a consistent increase in episode length throughout the bout. There was no indication that episode length consistently increased as bouts progressed (Table 1). In 17 of the 28 clusters that engaged in at least one bout of three or more episodes, we observed no bouts in which episode duration consistently increased.

DISCUSSION

Both bonnet macaques and white-faced capuchins showed time matching in female–female grooming. The longer the initiator groomed her partner, the more likely her partner was to groom her in return. Furthermore, in

Figure 1. Logistic regressions showing probability of grooming reciprocation by the recipient as a function of the duration of grooming (s) by the initiator for white-faced capuchins (—; $N = 1509$ bouts) and bonnet macaques (- - -; $N = 4476$ bouts). Note that grooming duration is untransformed, to make interpretation easier, although the statistical analysis (see text) was carried out on log-transformed zero-centred data.

Figure 2. Among reciprocated grooming bouts, recipient's grooming time as a function of initiator's grooming time for white-faced capuchins (■, —; $N = 342$ bouts) and bonnet macaques (△, - - -; $N = 282$ bouts). Grooming durations (s) are log transformed and normalized.
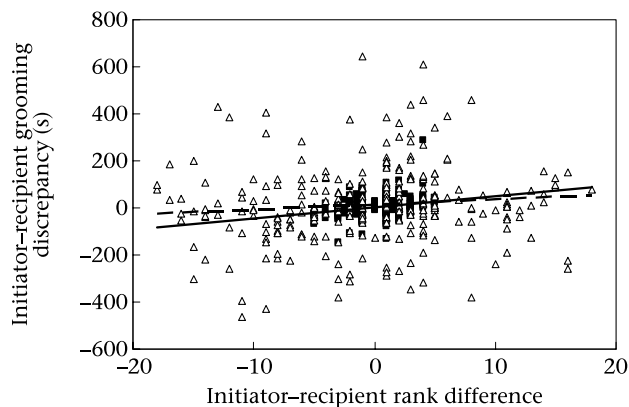
Figure 3. Among reciprocated grooming bouts, difference between initiator's grooming time and recipient's grooming time as a function of the dominance rank difference between the two monkeys for white-faced capuchins (■, —; $N=342$ bouts) and bonnet macaques (△, - - -; $N=282$ bouts).

reciprocated grooming bouts, the contributions of each partner tended to be positively correlated. However, even in reciprocated bouts, the amount of time that one female groomed another was a poor predictor of the amount of time that she would be groomed in return. When white-faced capuchins were considered alone, and when data from the two species were pooled, we obtained a statistically significant association between the two partners' grooming durations, but when bonnet macaques were considered alone, we did not, although the two species' slopes did not differ significantly. When white-faced capuchins reciprocated grooming within bouts they did not consistently raise the stakes, and bonnets rarely reciprocated within bouts at all.

The statistical methods that we used to assess reciprocity are an improvement over those used by Barrett et al. (1999) because they allowed us to use all of our data, and still avoid pseudoreplication. In addition, we were able to include both reciprocated and unreciprocated grooming bouts in the same analyses. We were also able to assess the species (or population) differences within the same model. We believe that the methods used here are advantageous

Table 1. Results of sign tests and ANOVA to test for raising the stakes within grooming bouts in white-faced capuchins

No. of episodes per bout (no. of bouts)	Increase across bout			Friedman ANOVA		
	Yes	No	Sign test P	χ^2	df	P
3 (83)	20	63	0.52	1.599	2	0.44
4 (37)	2	35	0.86	1.802	3	0.61
5 (17)	0	17	—	4.836	4	0.30
6 (10)	0	10	—	4.957	5	0.42
7 (7)	0	7	—	—	—	—
8 (3)	0	3	—	—	—	—
9 (2)	0	2	—	—	—	—
10 (1)	0	1	—	—	—	—

because they reduce the risk of drawing conclusions from an unrepresentative subsample of the available data.

Our results are consistent with the general patterns observed among baboons (Barrett et al. 1999, 2000), suggesting that some form of time matching may be a widespread characteristic of female–female grooming in female-bonded primate species. However, it is important to realize that the proportion of reciprocated grooming bouts varies considerably across these populations. Among bonnet macaques, only 5–7% of all grooming bouts were reciprocated within bouts, while 12–27% of all bouts were reciprocated among capuchins. In the four groups of baboons that Barrett et al. (1999) studied, 31–51% of all grooming bouts involved within-bout reciprocation. Henzi et al. (1997) suggested that 'within-bout reciprocation is essential for the maintenance of grooming dyads over time'. Our data suggest that this is not always true. Grooming was evenly balanced within dyads in the majority of capuchin dyads (Manson et al. 1999), but there was no within-bout reciprocity in the majority of grooming bouts. This means that the females in these groups continued to groom each other over many months even though the great majority of grooming bouts were unidirectional.

Reciprocation within or across bouts may not be necessary if females trade grooming for other commodities. Evidence that grooming disparities increased with rank distance in our study groups suggests that females may trade grooming for support, tolerance near resources, or access to infants. Earlier work on the bonnet macaque groups suggested that females were less likely to be harassed while they were grooming higher-ranking females, but the majority of females did not exchange grooming for support from nonrelatives (Silk 1982). Previous work on the capuchins suggests that females that groom often also tend to support one another often (Perry 1996), but it is not clear whether this pattern is independent of maternal kinship.

Reciprocation within bouts may not be necessary if females reciprocate grooming over longer time spans. Previous analyses of grooming in the two bonnet study groups indicate that, in contrast to the white-faced capuchins, grooming was significantly unbalanced in the great majority of female dyads (Duffy 1999), demonstrating that discrepancies in the amount of grooming given and received within bouts are not corrected over longer time periods.

Reciprocity within bouts may also not be necessary if grooming partners are close kin or grooming serves non-utilitarian functions. Kin selection could favour frequent and unreciprocated grooming among close kin, as long as the conditions of Hamilton's rule were met. Grooming might also provide information to participants or other group members about the quality of the grooming pair's social relationship (Dunbar & Sharman 1984; Dunbar 1993).

Although grooming disparities were correlated with rank distance in both of our study populations, rank distance accounted for relatively little of the variation in grooming disparities in either species. The weakness of this relation may be partly because dominance rank

provides a relatively poor measure of a social partner's 'market value'. The value of a high-ranking female's tolerance may depend, for example, on the abundance and distribution of local resources, and this may vary over time and space. Thus, Barrett et al. (2002) showed that the magnitude of grooming disparities within bouts decreased in one baboon group as the intensity of within-group resource competition was relaxed. Females' attractiveness may also be influenced by their reproductive status. Adult females may become more attractive grooming partners to males when they are sexually receptive and more attractive to other females when they have young infants (Barrett & Henzi 2001). Finally, the value of grooming as a commodity itself may fluctuate. A given unit of grooming may be more valuable at the beginning of a grooming bout than at the end, or more valuable at times of high tick density than low tick density. These sorts of factors would weaken the statistical relation between rank distance and grooming disparities.

Taken together, the data from baboons, bonnet macaques and capuchins suggest that a variety of forces may influence the dynamics of grooming in nonhuman primate species. In some dyads and in some contexts, nepotistic benefits may shape the distribution of grooming. In other dyads and other contexts, partners may exchange grooming for itself, parcelling grooming into short episodes. At other times, the same animals may exchange grooming for other benefits, including access to infants, support in coalitions and tolerance. In some situations, grooming may function as a signal of relationship quality. To understand the dynamics of grooming in primate groups, we may need to consider the roles of all these forces. This will require both comprehensive data and appropriate analytical methods.

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