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Negotiations over Grooming in Wild Vervet Monkeys (*Chlorocebus pygerythrus*)

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Abstract Mutual grooming plays a central role in the establishment and maintenance of social relationships in primates. Allogrooming has two main functions: hygiene and bonding with partners. The duration of grooming bouts is commonly used in studies of the functional aspects of grooming, but few reflect on the proximate mechanisms that determine grooming bout lengths. As it is highly unlikely that groomer and groomee prefer exactly the same bout length, we are likely to observe the result of some form of negotiation. We currently lack information about the signals that primates employ to inform others about their intentions and desires concerning grooming interactions. From October 2006 until April 2007 we studied three behaviors shown in grooming interactions that could potentially have a signaling function in the negotiation process over the initiation and length of grooming bouts among adult females of two vervet groups freely ranging in the Loskop Dam Nature Reserve, South Africa: approaching another individual as far as that resulted in a grooming session, changing of the body position by the groomed individual, and lip smacking. We found that "approach" did not reliably predict which individual would receive grooming first, although approaching individuals groomed significantly more than those approached. Thus, in

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the context of grooming interactions, moving toward a group member may signal the willingness to invest. Body part presentations appeared to be the main signal used to demand a prolongation of the grooming by the partner. Finally, lip smacking was used under potentially stressful circumstances, notably shortly before using the mouth to groom the partner or an attempt to touch a mother's infant. Our exploratory study hopefully inspires colleagues to start looking at the role of communication during cooperative interactions for a better appreciation of how animals manage cooperation and negotiate exchange rates.

Keywords Allogrooming · *Chlorocebus pygerythrus* · Negotiation · Signaling ·
Wild Vervet Monkeys

Introduction

Humans (*Homo sapiens*) often negotiate payoff distributions in cooperative interactions. In economics the term "negotiation" is typically used for the phase preceding the actual interaction of interest and is often tacitly assumed to result in binding agreements. The negotiation phase is, however, of interest by itself and can be modeled using bargaining game theory (Binmore 2010; Nash 1950; Rubinstein 1982). Nonhuman animals cannot be assumed to be able to conclude a binding contract, but they can potentially signal their intentions, desires, offers, etc. Thus, can such negotiation processes perhaps lead to implicit agreements at least? For members of a perpetual group, such as a group of primates, cooperation opportunities will frequently occur over periods that are very long relative to the length of single interactions. According to Binmore (2010) implicit agreements that are self-policing can be assumed if a game is repeated and the "folk theorem" applies.

The term "negotiation" is used in the context of several studies of animal behavior, even for organisms for which the use of cognitive mechanisms can safely be excluded (Akçay and Roughgarden 2007; Akçay and Simms 2011), but the term obviously has different meanings for different authors. Most empirical studies concern negotiations over parental care within reproductive pairs or between parents and offspring: birds (*Aves*: Hinde and Kilner 2007; Kosztolanyi *et al.* 2009; Lendvai *et al.* 2009; Lessells and McNamara 2012; Meade *et al.* 2011); beetles (*Coleoptera*: Smiseth *et al.* 2006). Other examples include vigilance and nest defense behavior (Bell *et al.* 2010; Sirot 2012; Trnka and Grim 2013) and experimentally induced negotiation among chimpanzees (*Pan troglodytes*) in a cooperation experiment (Melis *et al.* 2009). There have also been suggestions that hermit crabs (*Paguroidea*) negotiate over the exchange of shells when both indviduals can benefit from an improved fit (Hazlett 1978, 1996), but Doake and Elwood (2011) showed that it is not necessary to invoke negotiation processes to explain these exchanges. We here use the term negotiation for the exchange of signals in the context of cooperative interactions that by themselves are neither costly nor beneficial for the receiver, but potentially change the behavior of the receiver in favor of the sender.

Where the honesty of signals is of interest, cooperation theory can borrow from theoretical developments concerning mate choice, begging behavior, and agonistic conflict, a body of theory largely based on the handicap principle (Fraser 2013;

Grafen 1990a,b; Roberts 1998; Zahavi 1975, 1977a, 1977b, 1995). However, signals can also be used to solve coordination problems, which are often inherent to cooperation, and largely reduce the conflict of interest between sender and receiver. Signals used for coordination have been studied extensively in sibling negotiations over access to food brought by parents in birds (Bulmer *et al.* 2008; Dreiss *et al.* 2010; Johnstone and Roulin 2003; Roulin *et al.* 2000), but rarely in other contexts. The honesty of signals is not an issue in pure coordination problems without any potential conflict between the partners.

The question of negotiation over grooming is complicated by the fact that grooming is not only exchanged against grooming. The emancipation from its hygienic function set the stage for grooming becoming a general currency that could be exchanged for a number of other favors as well. Seyfarth (1977) predicted that subordinate females exchange grooming for coalitionary support as well as for tolerance around food resources from high-ranking females. The emphasis was shifted from rank effects to more general trading rules with the introduction of the biological market paradigm (Noë and Hammerstein 1994, 1995; Noë *et al.* 1991). Biological market theory (BMT) explicitly views cooperation between unrelated individuals as a trade of goods and services, whose exchange rates fluctuate as a result of changes in supply and demand, a process that is essentially driven by partner choice. Individuals that can offer goods or services in high demand may use their privileged position to alter the exchange rate in their favor. The predictions of BMT conform with Seyfarth (1977) in that dominants should receive more grooming than they give because they have the highest resource holding potential with respect to other goods/commodities such as access to food or fighting ability [see Henzi *et al.* (2003) for a detailed comparison of Seyfarth's model with BMT]. In the more general terms of BMT: the quantity of grooming exchanged between two individuals will depend on their leverage (Lewis 2002) or "power" in economic jargon. The leverage of an individual will depend on its rank, but also on the supply and demand ratio of grooming as well as of commodities exchanged against grooming at the moment the interaction takes place. Many studies of grooming patterns in nonhuman primates have found such effects on grooming patterns (Barelli *et al.* 2011; Barrett *et al.* 1999; Chancellor and Isbell 2009; Fruteau et al. 2011a; Ginther and Snowdon 2009; Gumert 2007b; Lazaro-Perea *et al.* 2004; Löttker *et al.* 2007; Norscia *et al.* 2009; Payne *et al.* 2003; Port *et al.* 2009; Slater *et al.* 2007; Tiddi *et al.* 2010; Wei *et al.* 2012; Xia *et al.* 2012, 2013). A well-studied example is the exchange of grooming for permission to handle a mother's infant. This "baby market" was first described for baboons (*Papio ursinus*) by Henzi and Barrett (2002) and since reported for several other species: spider monkeys (*Ateles*: Slater *et al.* 2007), long-tailed macaques (*Macaca fascicularis*: Gumert 2007a), sooty mangabeys (*Cercocebus atys*) and vervets (*Chlorocebus pygerythrus*: Fruteau et al. 2011b), *cf.* Frank and Silk (2009) and Tiddi *et al.* (2010).

Grooming exchanges can be described as bargaining games (Binmore 2010; Nash 1950; Rubinstein 1982) between two players, but when they take place on "grooming markets" as described earlier, all group members have multiple outside options, which complicates the game considerably. A detailed game theoretical analysis of bargaining about grooming remains therefore outside our reach. Both beginning and ending grooming requires some coordination. This can be very basic when a given pair of animals has a fixed routine that remains stable over time. However, more than simple coordination can be expected when the initiative and the length of grooming are dependent on the market situation. Each individual has to find out the momentary value of its grooming relative to that of the partner by trial and error. We therefore expect negotiation to take place before and during each grooming session, as participants are testing the water and try changing investments and returns to their advantage. Based on numerous studies cited above, we assume the existence of a "grooming market" and therefore analyze our data and present our results in this context. We concentrated on behaviors that can potentially be used to signal: 1) the desire to start a grooming session (irrespective of the direction of grooming), 2) the desire to receive grooming, 3) the offer to start grooming, and 4) the desire to continue an ongoing grooming bout. In addition we looked for 5) possible signals that indicate that an individual has no aggressive intentions. Given that partners have to be at close range, repeated signals that reduce tension might be necessary in the absence of binding contracts.

We investigate the scope for negotiation in grooming exchanges in wild vervets (*Chlorocebus pygerythrus*). Allogrooming, or social grooming, is the most common form of affiliative behavior in nonhuman primates (Dunbar 1991; Leinfelder *et al.* 2001). The primary function of grooming was probably hygienic, notably the removal of ecto-parasites, and improving thermoregulation by improving the fur's loftiness (Johnson *et al.* 2004; Saunders and Hausfater 1988; Tanaka and Takefushi 1993). Proximate mechanisms evolved that make being groomed feel pleasant to ensure that individuals actively seek being groomed (Dunbar 2010; Keverne 1989). Probably because of this hedonistic aspect, grooming became "emancipated" from its purely hygienic function and obtained a social function as a means to establish and maintain good relationships between group members (Dunbar 2010; Dunbar and Sharman 1984; Sade 1972). We may assume that the length of an undisturbed grooming bout is often determined by a negotiation process, but we know very little about the behavior used in such negotiation processes. This gap in our knowledge is not restricted to grooming interactions but applies to cooperation in animals in which goods or services of variable value are exchanged in general. Most evolutionary cooperation models either assume that communication between partners is not an option or ignore its potential importance, an often unrealistic assumption (Noë 2006); *cf.* Bell *et al.* (2010), McNamara *et al.* (1999), Patricelli *et al.* (2011), and Sirot (2012) for notable exceptions.

We observed grooming interactions that we defined as "grooming bout" (uninterrupted grooming in one direction) and grooming session (multiple bouts interrupted by breaks of ≥5s). We analyzed three behavioral elements shown during grooming interactions by vervets that we identified in a preliminary study (van de Waal 2006) as candidates for signals used in negotiation: approaching a group member, soliciting the grooming of another body part by changing position while being groomed, and lip smacking while grooming. We asked the following questions: 1) Does an approach signal the intention to groom or the desire to be groomed? This was split into two sub-questions. 1a) Is the approaching individual more likely to start grooming? 1b) Does the approaching individual give more grooming than it receives over the whole grooming session that follows? 2) Does the presentation of body parts by the groomee (the individual being groomed) signal a demand for a prolonged bout of grooming received? A vervet normally reacts in one of three ways to the presentation of a body part: groom the part presented, present a body part of its own, or end the session. If most individuals react by grooming the presented part, we would expect to find a positive correlation between the number of body presentations and the duration of grooming received. In addition, the presentation of a body part should increase the probability that a partner that just stopped grooming will start grooming again. 3) Is lip smacking a signal that serves to reduce potential tension between the interacting partners? In that case, we predict high frequencies of lip smacking occurring mainly when the groomer's behavior is likely to cause stress in the groomee. This is potentially the case when the groomer uses the mouth to remove items from the fur, when the groomee holds an infant, and/or when the groomer ranks above (or "is dominant to") the groomee.

Materials and Methods

Study Species and Site

Vervets (*Chlorocebus* spp.) are found in most of sub-Saharan Africa. They live in stable social groups with linear hierarchies and female philopatry (Dunbar and Thelma 2001). The animals we studied belong to the southern African species *Chlorocebus pygerythrus*, sometimes also referred to as a sub-species: *C. aethiops pygerythrus*.

We conducted the study from October 2006 until April 2007 at the Applied Behavioural Ecology and Ecosystem Research Unit (ABEERU) research site of University of South Africa (UNISA) in the Loskop Dam Nature Reserve, Mpumalanga Province, South Africa. Two groups of free-ranging vervets, named Picnic group and Donga group, had been habituated to the presence of human observers before the start of the study. The Donga group consisted of 10 individuals: three adult males, six adult females, and one juvenile female. During the present study five females gave birth. The Picnic group consisted of 11 individuals: two adult males, three adult females, one juvenile male, and five juvenile females. During the present study all three females gave birth and one male joined the group. Thus, over a short period we observed grooming sessions in which one female carried a newborn and the other did not. We excluded these sessions from the analysis of "approaches," because grooming in order to gain access to infants can have a strong influence on grooming patterns (Fruteau et al. 2011b; Gumert 2007a; Henzi and Barrett 2002). We analyzed the behavioral elements "body presentation" and "lip smacking" in the context of all grooming sessions among adult females, but we noted whether the signaler continued with the grooming session or paid attention to her partner's infant.

We could identify all individuals by external morphological features. The first letter of each individual's code represents the group: D=Donga, P=Picnic and the number indicates the rank (highest rank is 1).

Data Collection

We followed the monkeys for 1–10 h/d during 110 d. Two observers recorded allogrooming interactions and agonistic conflicts on an *ad libitum* basis on hand-held computers (Palm Zire 31 running PenDragon 4.0). Our grooming sessions consisted of grooming bouts: a new grooming bout started whenever an individual changed roles (from groomer to groomee or vice versa) and it was recorded as continuous unless interrupted by another activity for >5 s even if there was no change in partners. We recorded for each allogrooming interaction: approaches (which individual approached the other), the number of body presentations (change of body position of the groomed individual), and the starting and ending time of each bout, as well as the total duration each partner spent grooming. We recorded grooming sessions on video (Panasonic NV-GS11) to analyze the frequency of lip smacking, because counts during direct observations were not feasible. During the data collection period, experiments involving food provisioning to one or all group members took place on 58 out of the 110 observation days (van de Waal *et al.* 2010). We did not distinguish between experimental and nonexperimental days in our analyses.

Data Analyses

Analysis of the Link Between Approach and Grooming Investment The primary objective of this analysis on groomers was to study the effect of them approaching or having been approached by their grooming partner. For this we calculated the relative time invested in grooming per grooming dyad as percentage of the total grooming time by the groomer and the groomee. Here, groomers could be either approaching or approached individuals. For one female we were not able to collect groom data of the condition in which she was approached and therefore this female was discarded from the analysis. Further, we corrected the test for expected rank order differences on grooming by adding information per grooming dyad whether groomers exchanged grooming with a more dominant or a less dominant individual.

This data set was tested using the Mass statistical package (Venables and Ripley 2002) in the R version 2.15. We used the groom data of the groomer vs. the groomee per unique dyad ($N = 59$) and analyzed these variables using a generalized linear mixed model (glmm) with a binomial error distribution using the function glmmPQL. Model parameters in this function are estimated using a maximum likelihood approach. To correct for pseudo-replication, identity of the groomer and the group were included in the model as random terms. The full model included the factors: 1) approaching individual (two levels: yes or no), 2) grooming a dominant (two levels: yes or no), and 3) the rank of the individual (1 to 6). Then nonsignificant higher level interaction terms were discarded until the model converged to significance. The final model included the two main factors approaching individual, and grooming a dominant. In this parametric model the assumption of normality was not violated (Shapiro–Wilk test, $P > 0.05$). This model is described in the results.

Body Presentation Analyses To calculate the link between the number of body presentations and the duration of grooming received per interaction for each individual in the role of groomee we conducted a linear mixed model (lme) using the lnme package of R. We transformed the data to meet the assumption of normal distribution. As the time data were overdispersed to large values, we used a “cubic root” transformation of the grooming time. After transformation, the residuals of the ANOVA were not significantly different from the normal distribution (Shapiro-Wilk normality test, $W = 0.9969$,

$P = 0.40$). To correct for pseudo-replication, the identity of the groomer and the group were included in the model as random terms.

To test more specifically for a potential causal link between body presentation and prolongation of received grooming, we identified situations in which the groomer stopped (i.e., did not groom for >5 s) and quantified how frequently the groomer resumed grooming (for >5 s) after the groomee changed body position as opposed to situations in which the groomee did not change body position (see Table I for sample size).

Lip Smacking Analyses Lip smacking data were exclusively based on video recordings (see Table I for sample size). We analyzed the occurrence (presence/absence) and the frequency (smacks per second) under three circumstances: 1) when an individual groomed a partner with her hands, 2) when the groomer groomed with the mouth, 3) when the groomer attempted to interact with the groomee's newborn (<3 mo). Lip smacking by the groomee was never observed. Subsequent mouth use and infant handling attempts were considered as independent from each other if ≥5 s had elapsed between events. To estimate the probability of lip smacking when the groomer uses her hands (the standard form of grooming), we randomly picked the starting second of a 5-s

Table I Sample sizes per individual adult female in two groups (Donga: D1–D6; Picnic: P1–P3; numbers from highest ranking to lowest ranking female) for five behaviors linked to social interactions: approaching, body presentations, lip smacking occurrence, lip smacking frequency, and lip smacking frequency as a function of recipient's rank. (*Chlorocebus pygerythrus*; Loskop Dam Nature Reserve, South Africa; October 2006–April 2007).

	D1	D2	D3	D4	D5	D6	P1	P2	P3
Approaching									
N = interactions when approaching individual	57	85	62	46	90	74	14	14	4
N = interactions when approached individual	122	86	26	67	58	55	13	8	11
Body presentations									
N = total number of grooming bouts	279	241	88	149	173	58	44	29	19
N = TOTAL number of breaks between grooming bouts	273	227	87	130	170	53	41	29	18
Lip smacking occurrence (presence/absence)									
(a) When an individual groomed a partner with the hands	12	15	11	13	20	32	4	8	3
(b) When the groomer groomed with the mouth	8	20	5	3	18	17	1	11	2
(c) When the groomer attempted to interact with the groomee's newborn	6	7	1	1	6	5	1	4	2
Lip smacking frequency (smacks per second)									
(a) When an individual groomed a partner with the hands	2	2	-	1	-	1	-	1	1
(b) When the groomer groomed with the mouth	8	14	3	3	10	13	-	6	1
(c) When the groomer attempted to interact with the groomee's newborn	5	2	4	1	3	1	2	4	2
Lip smacking frequency and recipient rank [data only from the (b) context]									
N = number of lip smacking events analyzed for each recipient	4	15	3	11	14	4	5	1	1

observation interval for each grooming session and noted whether or not lip smacking occurred in that interval. If the groomer's mouth was not visible at the start of the picked interval, we let the video run until the next 5-s interval with the groomer's mouth visible to collect our data point. Sample sizes are given in Table I.

Whenever lip smacking occurred and the mouth of the subject was clearly visible, we calculated the frequency of mouth movements. A slow motion program (Windows Media Player) enabled us to count the number of lip smacks per second for 1) grooming with hands, 2) grooming with mouth, 3) infant-handling attempt (Table I for sample size).

A matched pair design allowed us to analyze whether the probability and/or the frequency of lip smacking differed between the three situations. For the context "grooming with mouth" we also calculated correlations between lip smacking frequency and the recipient's rank (see Table I for sample size).

Statistics

The female rank order was determined with Matman (Matrix manipulation and analyses package in The Observer, Noldus). In the following "rank" is used as shorthand for the place of an individual in the hierarchy of adult females, whereby rank 1 is assigned to the highest ranking female. Statistical analyses were carried out with SPSS (version 16.0 for Windows) unless specified otherwise in the text. All the tests performed with SPSS are nonparametric, two-tailed, and with α set at 0.05. When several calculations were conducted to answer the same question, we lowered the α-level using the sequential Bonferroni technique (Rice 1989).

Ethical Note

Our observations were approved by ABEERU boards of UNISA as well as Park Boards of the Mpumalanga Province, South Africa. Our data involve only observations in a natural context.

Results

How Does Approaching vs. Being Approached Affect Grooming Interactions?

Being the approaching or the approached individual did not significantly alter a female's probability to groom first (Wilcoxon signed ranks test: $N = 9$ dyads, $z = -0.770$, $P = 0.496$, Fig. 1).

Individuals that started grooming groomed most (groomers vs. groomees: glmm, $t(47) = 6.51$, $P < 0.001$), and the relative time invested in grooming was significantly higher when the groomer was the approaching individual than when she was the approached individual (glmm, $t(47) = 2.06$, $P = 0.045$). In addition, groomers groomed more when interacting when the groomee was dominant over the groomer than vice versa (effect of dominance: glmm, $t(49) = 2.71$, $P = 0.009$) (Fig. 2).

To check whether the absolute position in the female rank order might explain additive variation in grooming investment on top of the dominance relationship of the

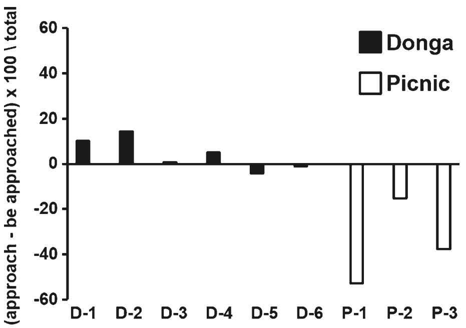

Fig. 1 An index of how the probability to be the first grooming recipient is affected by a female's role as the one that approaches or that is approached. A positive index means that approach is linked to being groomed first; a negative index means that approach is linked to grooming first. (*Chlorocebus pygerythrus*; Loskop Dam Nature Reserve, South Africa; October 2006–April 2007).

grooming dyad, we added this factor to the glmm model. However, "rank position" showed a highly significant relationship with "dominance relationship" in the glmm model (correlation factor: $R = -0.71$). When the rank position was used in the final model instead of the dominance relationship, this would result in a nonsignificant trend of the rank position on the investment in grooming (glmm, $t(6) = 2.11$, $P = 0.080$).

Do Body Presentations Prolong an Interaction?

Controlling for individual identity, the correlation between the number of body presentations and the mean duration of the grooming bout received was significantly positive (lme, $F(1,12) = 161.6$, $P < 0.001$, Fig. 3), without an effect of group identity ($F(1, 10) = 0.53$, $P = 0.48$).This significant effect of grooming length increasing with an

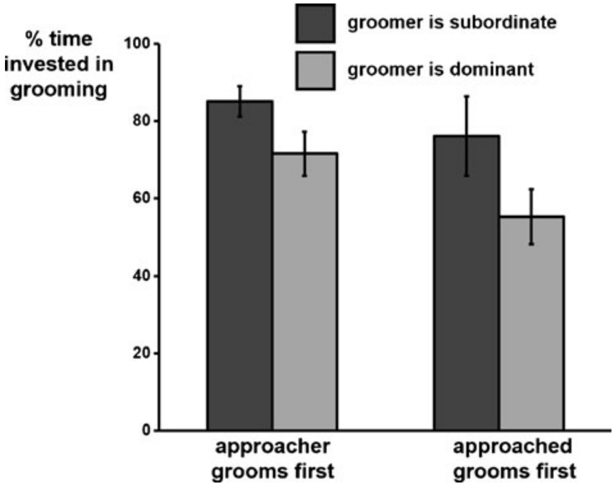

Fig. 2 The proportion of grooming of the groomer (first to groom) relative to grooming received by the groomee (%) vs. a female's role as the one that approaches or that is approached, and whether a dominant or subordinate is groomed. A more positive value means giving relatively more grooming. The figure shows means and standard errors. (*Chlorocebus pygerythrus*; Loskop Dam Nature Reserve, South Africa; October 2006–April 2007).

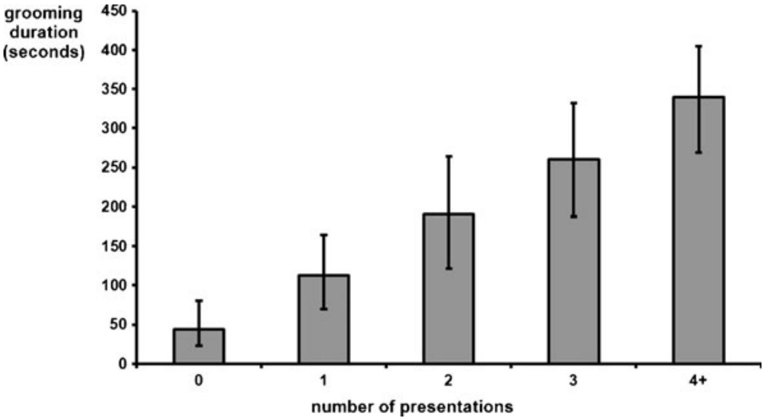

Fig. 3 Average grooming duration (seconds) per number of body presentations (0–1–2–3–4and more). Figure shows medians and interquartiles using mean values per individual. (*Chlorocebus pygerythrus*; Loskop Dam Nature Reserve, South Africa; October 2006–April 2007).

increase of body presentations could be due to the reaction of the groomer to the shifts in body position of the groomee, but also to the larger number of different positions taken by the groomee during interactions of longer duration. Therefore, we tested whether a change in body position of the groomee after a groomer stopped grooming increased the probability that the session continued. We found that the groomer restarted with significantly higher probability if the groomee responded to the termination with the presentation of a new body part than if the groomee did not change her body position (Wilcoxon signed rank test: $N = 9$ dyads, $z = -2.666$, $P = 0.004$, Fig. 4).

The Function of Lip Smacking

The likelihood that lip smacking occurred differed significantly between situations (Friedman test: $N = 9$, $\chi^2 = 16.188$, $P < 0.001$). *Post hoc* multiple comparisons

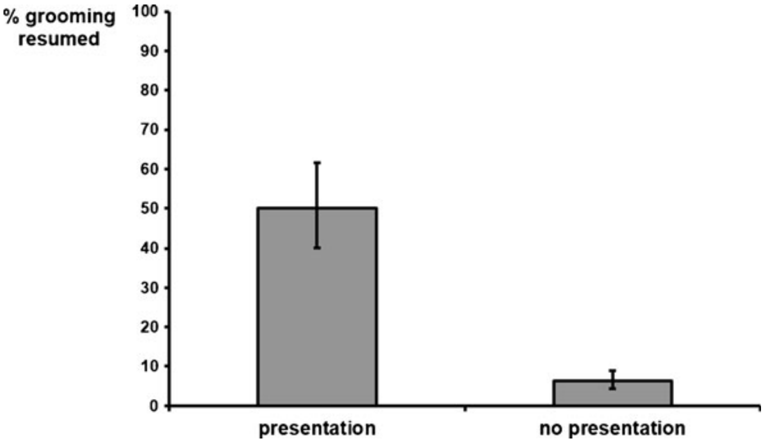

Fig. 4 Probability that a groomer resumed a grooming interaction and started a new bout when the groomee presented a new body part and when she did not present a new body part. Figure shows medians and interquartiles using mean probabilities per individual. (*Chlorocebus pygerythrus*; Loskop Dam Nature Reserve, South Africa; October 2006–April 2007).

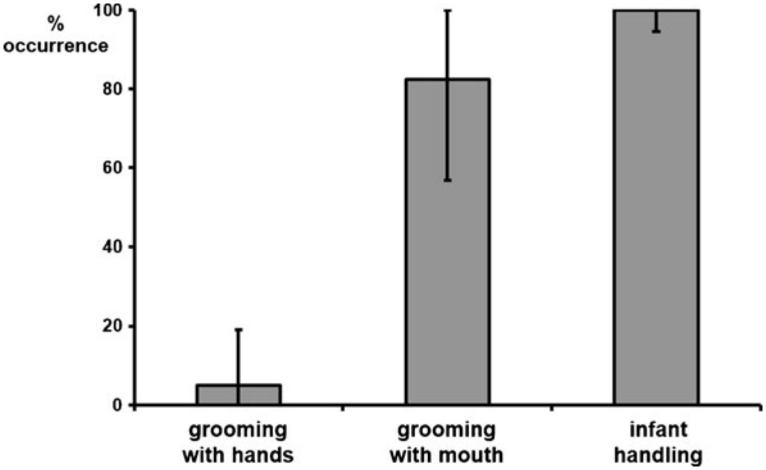

Fig. 5 Probabilities for the occurrence of lip smacking during grooming with hands, grooming with the mouth, and attempts to handle infants. Figure shows medians and interquartiles using mean values per individual. (*Chlorocebus pygerythrus*; Loskop Dam Nature Reserve, South Africa; October 2006–April 2007).

revealed that its occurrence was least likely during hand grooming and highest when one partner tried to interact with the other's newborn during the grooming session (*post hoc* comparisons with all $P < 0.05$, Fig. 5).

Lip-smacking individuals produced significantly more smacks per second when a grooming partner tried to interact with a newborn than in other situations (Wilcoxon signed ranks test: infant handling – grooming with mouth: $N = 8$, $z = -2.521$, $P = 0.008$, infant handling – grooming with hands: $N = 6$, $z = -2.201$, $P = 0.031$, Fig. 6). In addition, individuals produced significantly more smacks per second when they used their mouths than when they used their hands (Wilcoxon signed ranks test, $N = 6$, $z = -2.201$,

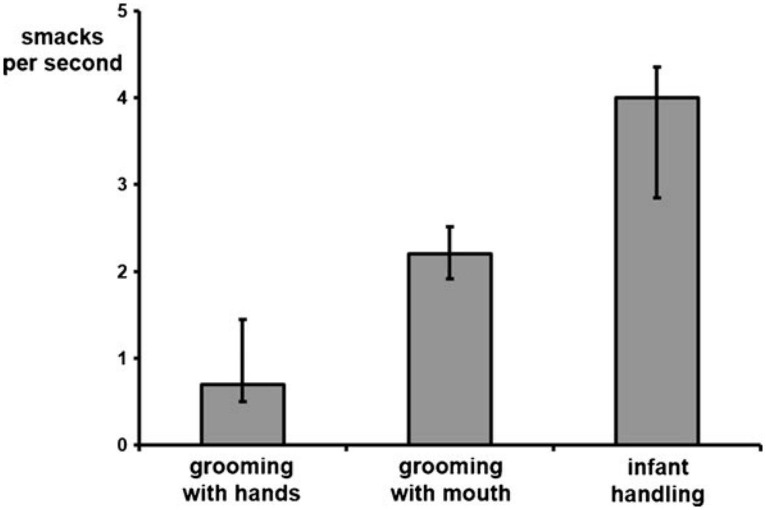

Fig. 6 Number of lip-smacks per second produced the groomer when grooming with hands, grooming with the mouth, or trying to handle an infant. Figure shows medians and interquartiles using mean values per individual. (*Chlorocebus pygerythrus*; Loskop Dam Nature Reserve, South Africa; October 2006–April 2007).

$P = 0.031$, Fig. 6). The frequency of lip smacking did not correlate in any obvious way with the rank of the groomee as the sign of the correlation coefficients differed between the two groups (Spearman rank correlations; Donga: $r_s = -0.257$, $N = 6$, $P = 0.623$; Picnic: $r_s = 0.500$, $N = 3$, $P = 0.667$, Fig. 7).

Discussion

All three behavioral patterns we investigated, approaching, presenting body parts and lip smacking, seem to serve as signals in negotiation processes, but with different and complementary functions. An *approach* might indicate either an individual's desire to receive grooming or the willingness to groom. Overall, our results are more in line with the latter hypothesis, as most grooming in the subsequent grooming session was done by the approaching individual. This was also true when controlling for the well-established fact that dominants receive more grooming than subordinates do (Balasubramaniam *et al.* 2011; Barrett *et al.* 1999; Carne *et al.* 2011; Fruteau et al. 2011a; Nakamichi 2003; Payne *et al.* 2003; Port *et al.* 2009; Schino 2007; Seyfarth 1977; Singh *et al.* 2006), *cf.* Macdonald *et al.* (2013). The effect was not very strong, however, and approaching was not a reliable indicator of who groomed first. Our results suggest that *body presentations* are the key signal used when the individuals ask for more grooming and direct the groomer to those body parts that have not yet received its attention. The groomee can thus signal that it is not yet willing to reverse roles on which the groomer can then either accept and groom the newly presented part of the groomee's body or present its own body for a bout of reversed grooming. In the latter case the groomee can either accept and groom in turn, or end the session. Van

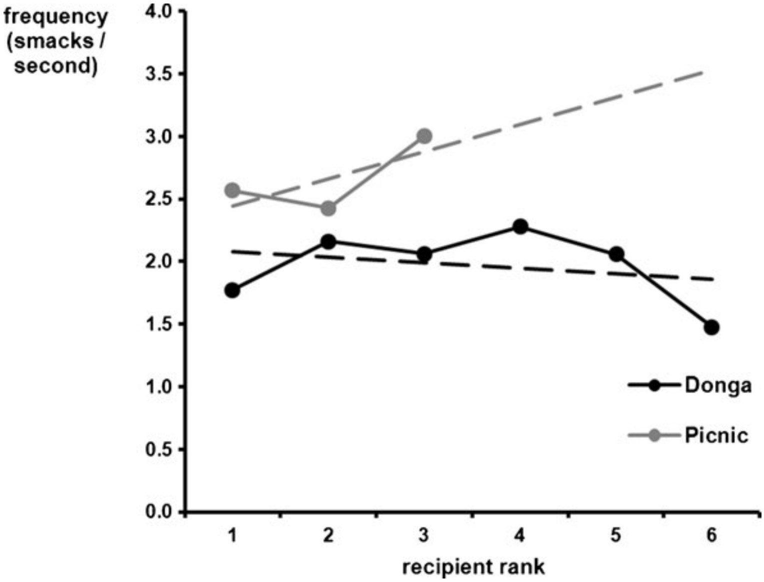

Fig. 7 Mean lip-smacks per second performed by groomers during grooming-with-mouth events in relation to the recipient's rank. (*Chlorocebus pygerythrus*; Loskop Dam Nature Reserve, South Africa; October 2006–April 2007).

Hooff (1967) suggested that the function and form of *lip smacking* in many nonhuman primate species and across different contexts is either appeasement when directed to a subordinate individual or a request for tolerance when directed to a dominant individual. Our findings are in line with these assumptions as we observed both a higher probability of signal occurrence and a more intense signal in potentially stressful situations. Grooming individuals notably used lip smacking during grooming bouts in which they used their mouth for grooming and when they groomed mothers holding small infants. Grooming with the mouth tends to bring the groomer closer to a mother's infant and hence there might be a causal link between our two situations. Lip smacking may not signal an offer to groom or demanding for grooming as such, but rather prevent an anxious groomee from breaking off the session. In addition, it may calm the infant down. The groomer better sends an appeasing signal that soothes both the mother's and her infant the latter influence each other's anxiety state, which is rather likely to be the case. Finally, the significant results reported here for all three parameters were obtained in spite of small sample sizes and conservative statistical tests. We could also not control for genetic relationships, although it is likely that closely related females hardly need to negotiate over grooming.

Which Game Do Grooming Primates Play?

Primates living in stable groups have repeated interactions with the same partners. Thus, various mechanisms may promote stable cooperative behavior like kin selection (Hamilton 1964a,b) and/or partner control mechanisms like partner choice in a biological market (Bshary and Noë 2003), attitudinal reciprocity (de Waal 2000), or interdependency (Raihani and Bshary 2011; Roberts 2005). Over the course of repeated interactions, any immediate inequalities should level out due to continuous changes in needs. Nevertheless, grooming exchanges within each dyad are unlikely to settle into fixed values that remain stable over time, because the relative values of a unit of grooming each member has to offer vary over time for two reasons. 1) The intrinsic value of each partner depends on alternative commodities it may have to offer. In the case of adult females the strongest fluctuations are probably due to changes in the reproductive cycle: the presence of newborns (Fruteau et al. 2011b; Gumert 2007a; Henzi and Barrett 2002; Slater *et al.* 2007) and willingness of males to offer grooming in exchange for sex (Barelli *et al.* 2011; Gumert 2007b; Norscia *et al.* 2009). Further fluctuations may be due to changes in dominance status and the resulting changes in value of agonistic support and tolerance near resources. 2) The extrinsic value of the grooming each individual has to offer depends on fluctuations on the grooming market. The outside options change over the long term, notably due to changes in the composition of the groups, changes in the dominance hierarchy and changes in the reproductive cycle of each of the females, but also over the short term as a result of fluctuations of the number of potential partners available for grooming in the immediate vicinity. Grooming sessions by the same dyad may thus vary from day to day and even from hour to hour in overall length and the degree of asymmetry (Schino *et al.* 2009). Thus, negotiations during an interaction may be essential in stabilizing cooperative long-term relationships by avoiding that individuals feel cheated. We will therefore focus our discussion on how negotiation may affect the outcome of single interactions.

The question of interest here is whether and how individuals decide on the length of grooming bouts they provide using information received shortly before and during grooming sessions. There are some constraints on the possible length of a grooming bout, as daytime grooming usually takes place during breaks in foraging activities, but these breaks are in general considerably longer than the average grooming session. In the absence of any strong external cue a stable compromise about the amount of grooming exchanged would be hard to reach, without information exchange and ongoing negotiation. Do our results indeed show such an information exchange and does the whole process warrant the label "negotiation"?

An individual that approaches a group member to start a grooming session is normally speaking likely to be more motivated to interact than the stationary individual. Our results confirm that the approached individual indeed interprets this as a signal that its partner is willing to accept a higher grooming given/grooming received ratio than it would do otherwise. The grooming ratio shifts to the advantage of the approached individual even if the approaching animal is not the first to groom. A second piece of information available to both partners is that the dominant of a dyad on average grooms less than the subordinate does under comparable circumstances. This asymmetry is explained by the fact that dominants can offer alternative commodities, such as tolerance in food patches and support in conflicts, that subordinates cannot offer (Barrett *et al.* 2002; Barrett and Henzi 2006; Chancellor and Isbell 2009; Henzi *et al.* 2003; Newton-Fisher and Lee 2011; Port *et al.* 2009; Tiddi *et al.* 2011, 2012). We do not have the impression that vervets can coerce subordinate into grooming them as has been reported for Barbary macaques (Carne *et al.* 2011), and grooming bouts were not continued by subordinates under any overt aggression or threat by dominants.

At the onset of a grooming session both partners therefore have some information about the time the partner might be willing to groom, but this information is incomplete and needs to be updated during the transaction by probing the partner's motivation either to change roles or to continue grooming. The only way to know whether a partner is satisfied with the amount of grooming received is to stop grooming and see how the other reacts. It is difficult to observe the difference between the ending of a grooming bout by lack of motivation to continue or by a desire to obtain information about the partner's motivation, however. What we could observe is that a vervet unsatisfied by the length of a grooming bout received presented another part of its body for grooming. We did not observe alternative signals that could serve the same function, such as vocalizations and facial expressions, neither threatening nor friendly. Aggressive acts directly following grooming sessions were not observed either, making the existence of "punishment" of short-changing groomers unlikely. Sessions can also be aborted by groomees that are too anxious, however, and lip smacking seems to have the function of reducing such anxiety.

Vervet grooming interactions are probably best viewed as a dyadic nonzero sum game with incomplete information at the outset, and with outside options for both players, following the classification proposed by Binmore (2010). Such a game is perhaps best modeled as a Bayesian game in which the players arrive at a Bayesian equilibrium (Binmore 2010), which differs from interaction to interaction depending on the momentary motivational state of the players. Another often explored option would be a tit-for-tat (TFT)-like strategy in which each bout is matched by a reciprocal bout of the same length, but such a solution would perhaps be an option for species that can groom each other simultaneously only and thus match each other's investment instantaneously. But even chimpanzees, which show such simultaneous grooming, do not use this solution consistently and often groom unidirectionally too (Fedurek and Dunbar 2009). In species that take turns within grooming sessions rather than grooming simultaneously, the first grooming bout of each session has the character of a "sealed bid." A TFT-like strategy would not solve the problem of who starts and which bout length to start with, unless, the individuals have a fine-tuned feeling for the length of bouts and a good memory for bouts given and received during the previous session. Our observations rather suggest that the length of a grooming bout was contingent on information exchanges during that bout. A series of grooming sessions of a pair of vervets thus resembles an iterated coordination game with information exchange much more than the iterated Prisoner's Dilemma without information exchange that has traditionally been used as a model for this type of cooperation (Raihani and Bshary 2011; Sachs *et al.* 2004).

When a grooming session poses problems of coordination rather than control, the problem of the honesty of signals becomes less acute, but does not disappear altogether. A certain amount of conflict over the length of grooming bouts remains and thus the potential of gaining a larger share by exaggerating the level of desire signaled. This becomes obvious in an anecdotal manner when individuals first offer a new body part and then start to groom their partner when the latter ignored their request.

In conclusion, we propose that within a repeated game structure vervets arrive in each grooming session on average at a compromise over the length of time each of them invests without *a priori* binding agreements and obviously without verbal negotiation. This should not be surprising, because any grooming session must have some finite length and some ratio of grooming given and received. That both individuals largely agree over these parameter values is suggested by the fact that aggression during and after grooming is rare and that grooming within the same dyad is often repeated. Such mutual consent would be hard to reach without ongoing negotiation providing each individual with enough information to adjust its own demands to the willingness of the partner to provide grooming. We see two main avenues for future research. First, our exploratory study should be followed by studies that explicitly test the generated hypotheses, notably in vervets. Second, it would be important to conduct similar studies with other species. Such studies could both broaden the catalogue of signals potentially used in negotiation and verify the generality of our observed patterns. We believe that a broad comparative approach is most likely to unravel the scope for negotiation within primate grooming markets.

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