The influence of the steepness of dominance hierarchies on reciprocity and interchange in captive groups of bonobos (*Pan paniscus*)

Jeroen M.G. Stevens[1,2,4)], **Hilde Vervaecke**[1,2)], **Han de Vries**[3)] **& Linda Van Elsacker**[1,2)]

([1] University of Antwerp, Department of Biology, Universiteitsplein 1 B-2610 Wilrijk, Belgium; [2] Centre for Research and Conservation, Royal Zoological Society of Antwerp, Koningin Astridplein 26, B-2018 Antwerp, Belgium; [3] Utrecht University, Department of Behavioral Biology, Padualaan 14, P.O. Box 80.086, 3508 TB Utrecht, The Netherlands)

(Accepted: 16 June 2005)

Summary

Biological market models explain variability in reciprocity and interchange between groups. In groups with a shallow dominance gradient, grooming will be mostly exchanged for itself (i.e. exchange will occur). In groups with steep dominance hierarchies, interchange is expected: individuals will groom higher ranking individuals to get access to limited resources or commodities such as support in conflicts, and grooming will be traded for these commodities.

We examine patterns of reciprocity in grooming and support, and of interchange of grooming for support or for tolerance in six captive groups of bonobos. We test whether differences between groups in patterns of reciprocity and interchange can be attributed to differences in a measure of steepness of dominance hierarchies, which is based on dyadic agonistic interactions.

We found that grooming was reciprocal in some, but not all groups. Support was highly reciprocal, but this was a side effect of dominance in most groups. Interchange between grooming and support was observed in some groups. Corroborating earlier findings, this was a side effect of individuals preferring high ranking individuals as grooming and support partners, possibly because these high-ranking individuals provide more efficient support in conflicts. There was no evidence for interchange of grooming for tolerance.

Variability in grooming reciprocity was explained by differences in steepness of dominance hierarchies, as predicted by the biological market models. In groups with a shallow dominance hierarchy, grooming was more reciprocal. This was not true for reciprocity in

[4)] Corresponding author's e-mail address: jeronobo@skynet.be

support. There was some evidence that individuals groomed dominants more frequently in groups with a steep dominance hierarchy. The variation in interchange relations between grooming and support did not depend on the steepness of dominance hierarchies. We suggest that grooming in itself is a valuable commodity in bonobos, especially under captive conditions, which can be exchanged reciprocally. Bonobos may interchange grooming for another value equivalent, with food sharing as a very likely candidate. This interchange effects seem more dependent on potential to monopolise food than on steepness of dominance hierarchies per se.

Keywords: *Pan paniscus*, grooming, support, tolerance, reciprocity, interchange, dominance.

Introduction

Scientific interest in reciprocity (i.e. exchange of the same acts) and interchange (exchange of different kinds of acts) in apes stems from the fact that these primates are believed to have the mental capacities required for such complex trade mechanisms, while there is doubt about such capacities in monkeys (de Waal & Lutrell, 1988). A number of studies mostly of chimpanzees, and some of bonobos, have looked into the social marketplaces of apes, for evidence of reciprocity in grooming and support relations, and possible interchange of grooming for support (reviewed in Watts, 2002). However, evidence from these studies is not equivocal about the occurrence of reciprocity and interchange.

Reciprocity in grooming has been found among male chimpanzees in the wild (Watts, 2000, 2002), as well as for captive males and females (Hemelrijk & Ek, 1991) and for captive bonobos (Vervaecke et al., 2000b). Support was reciprocal among chimpanzee males in the wild (Mitani & Watts, 2001; Watts, 2002) and in captivity only when there was no clear alpha male (Hemelrijk & Ek, 1991). In captive bonobos, support was also reciprocal, but this was due to a tendency of high ranking individuals both giving and receiving more support (Vervaecke et al., 2000b).

Evidence of interchange in apes is even sparser. Although it can be expected that individuals groom others in return for tolerance, i.e. to receive less aggression, there was no evidence for this among wild chimpanzee males (Watts, 2002) or captive bonobos (Vervaecke et al., 2000b). Interchange of support for grooming was shown among wild chimpanzee males (Watts, 2002) and among captive chimpanzee females (Hemelrijk & Ek, 1991). Often apparent interchange is due to associations of either grooming or sup-

port to other factors, such as dominance or to reciprocity (Hemelrijk, 1990b; Hemelrijk & Ek, 1991).

Grooming was correlated to support received in the study by Hemelrijk & Ek (1991), but the correlation was caused by a combination of reciprocity in grooming with an association between grooming received and support received. Similarly, Vervaecke et al. (2000b) found interchange between grooming given and support received among captive bonobos, but the correlation was influenced by dominance rank effects: because individuals preferred to groom higher-ranking ones, and high-ranking individuals provided support more often, a correlation between grooming given and support received arose. Furthermore, interchange sometimes depends upon social circumstances. For example, male chimpanzees exchanged grooming for support received, but only in periods when there was a clear alpha male (de Waal, 1978; Hemelrijk & Ek, 1991).

This brief review of literature on reciprocity and interchange in chimpanzees and bonobos shows that there is great variability across studies in the evidence for these phenomena. This has been partly attributed to social factors, such as stability of dominance hierarchies, which seem to influence interchange among captive chimpanzee males. However, biological market theory offers an alternative explanation for this variability. Biological markets are expected when individuals can choose between various partners, who can trade 'commodities' (Noë & Hammerstein, 1994, 1995). In primates, grooming can be considered such as a commodity, which can either be exchanged for itself, or interchanged for another commodity, such as support or tolerance (Barrett et al., 1999; Henzi & Barrett, 1999). The composition of the marketplace is then largely influenced by dominance relations between the traders (Barrett et al., 1999; Henzi & Barrett, 1999; Barrett & Henzi, 2001; Leinfelder et al., 2001). In groups characterised by a steep dominance hierarchy (van Schaik, 1989), dominants will more easily claim resources or offer services such as support in conflicts (Vehrencamp, 1983). Therefore lower ranking individuals will try to gain access to these resources or services by grooming dominants. In these groups, grooming will be traded for access to these resources (Barrett et al., 1999; Leinfelder et al., 2001). In egalitarian groups, characterised by a shallow dominance hierarchy (van Schaik, 1989) the distribution of resources will be less influenced by dominance rank (Vehrencamp, 1983) and, accordingly, grooming will be less biased by dominance. Rather, grooming will be exchanged

reciprocally. Among female chacma baboons (*Papio cynocephalus ursinus*), reciprocal grooming was indeed found in groups with shallow dominance gradients (Barrett et al., 1999). In groups with a relatively large dominance gradient interchange did occur: female baboons trade grooming for another currency, namely infant handling (Henzi & Barrett, 2002). Moreover, the authors showed that in the same group, a greater dominance gradient in response to changed environmental conditions, led to the expected shift from reciprocal to interchange trading (Barrett et al., 2002). Thus dominance gradients, or the steepness of a dominance hierarchy, prove essential in these biological markets. However, in these studies steepness of dominance hierarchies is measured indirectly from ecological competition for resources, i.e., resource holding potential (Henzi & Barrett, 1999; Barrett et al., 1999) or is defined on a dyadic level, as the rank distance between two individuals (Barrett et al., 1999; Henzi & Barrett, 2002). However, measuring such power differentials or steepness requires cardinal ranks (Flack & de Waal, 2004). Such a direct approach to calculate steepness from dominance matrices is now available: based upon the Normalised David's score (David, 1987; Gammell et al., 2003) which measures the success of individuals in dyadic conflicts, the slope or steepness of hierarchy can now be quantified as an index, ranging from 0 to 1. This allows for the predictions of biological market models to be directly tested (de Vries et al., in press).

Elsewhere, we established that our six study groups of bonobos differ in steepness of hierarchy (Stevens et al., in prep). Our current aim is twofold. First, we want to present new data on reciprocity and interchange in five groups of captive bonobos, and compare these data with earlier findings by Vervaecke et al. (2000b). Second, we want to relate possible differences in the importance of reciprocity and interchange in these groups, to differences in the nature of dominance relations. We test the following seven predictions

1. Grooming is reciprocal in bonobos. Reciprocity is independent of any associations between grooming given or grooming received and dominance. However, in the study by Vervaecke et al. (2000b) this was not the case. Therefore we test whether the reciprocity in grooming is independent of any associations between grooming given or received and dominance.

2. Support is reciprocal. In the study by Vervaecke et al. (2000b) this reciprocity was a by-product of a tendency to groom high-ranking individuals, combined with higher-ranking individuals providing more support in conflict. Therefore we test whether reciprocity is independent of any associations between support given or support received and dominance.
3. Grooming is negatively related to the amount of aggression received, and grooming received is negatively correlated to the amount of aggression given. These effects are independent of grooming reciprocity. Vervaecke et al. (2000b) found no interchange between grooming and tolerance.
4. Bonobos exchange grooming for support. Vervaecke et al. (2000b) found positive correlations between grooming given and support received, but not between grooming received and support given. We test whether correlations are independent of effects of reciprocity in grooming and support relations, and of the factor dominance (cf. Vervaecke et al., 2000b).
5. Grooming is more reciprocal in groups with a shallow dominance hierarchy.
6. Grooming is more rank-related in groups with a steep dominance hierarchy.
7. Interchange of grooming for tolerance or support is more important in groups with a steep dominance hierarchy.

Methods

Study groups

We present data on six captive groups of bonobos, representing 2153 study hours. For the analyses, only animals older than 7 years were considered, which resulted in a total of 30 different individuals (15 males and 15 females). The Planckendael study group (Belgium) was observed three times, and some individuals were present during more than one period. However, among these individuals significant changes in dominance hierarchy occurred (Stevens et al., in prep.). Moreover, in between each of the subsequent periods, a number of deaths occurred, juveniles became adults, and some animals were removed or introduced for management practices. For

more details regarding these group composition changes, see Stevens et al. (2003). Since group composition and age distribution of this group differed considerably between periods, we considered them as separate groups. Planckendael-1 refers to the group in 1992-1993 (3 males, 3 females), when 271 hours of data were collected by the second author and presented in Vervaecke et al. (2000a). All other data were gathered by the first author, using the same ethogram as Vervaecke et al. (2000a,b). Planckendael-2 refers to the 193 hour study period in November-December 1999 (3 males and 4 females), while Planckendael-3 refers to the group in November 2002 - February 2003, when 3 males and 3 females were studied for 505 hours. In Wuppertal Zoo (Germany) a group of 4 males and 2 females was studied for 203 hours in August-September 1999. The study group at Apenheul Primate Park (The Netherlands) contained 3 males and 5 females and was studied for 493 hours from February to April 2001. The group at Twycross Zoo (United Kingdom) contained 3 males and 3 females, and was studied for 490 hours from November-December 2001 and February 2002.

Further details on group relatedness and background of the individuals in different study groups can be found in Vervaecke et al. (2003) and Stevens et al. (2003).

Data collection

All data were collected by continuous observations and only interrupted by maintenance work or cleaning of the enclosure. Depending on the institution where bonobos were studied, observations started in the morning and ended at dusk, when bonobos started to make nests and social interactions generally ceased. In this way observations of 4 to 8 hours were made daily.

Grooming, aggression/submission interactions and support were scored by all occurrence sampling (Altmann, 1974). We analysed reciprocity in grooming bouts, rather than within-bout reciprocation. We analysed reciprocity between the frequency of grooming bouts, since this frequency was significantly correlated with the duration of grooming in all groups (rowwise matrix correlations: Planckendael-1: $\tau_{rw} = 0.92$, $p < 0.001$; Planckendael-2 $\tau_{rw} = 0.92$, $p < 0.001$; Planckendael-3: $\tau_{rw} = 0.82$, $p < 0.01$; Wuppertal $\tau_{rw} = 0.89$, $p < 0.001$; Apenheul: $\tau_{rw} = 0.89$, $p = 0.001$; Twycross: $\tau_{rw} = 0.72$, $p < 0.05$). In each grooming bout the participation of each partner was scored once. Subsequent switches between the active and passive role where not counted as new bouts (Vervaecke et al., 2000b).

We counted all forms of aggression in one matrix. Aggressions were scored following an standardised ethogram (see Vervaecke et al., 2000a; Sannen et al., 2004). When aggressive acts between the same individuals were repeated within 30 seconds, these were not scored as new aggression.

Pester: repeated intentions to approach individual(s), or to throw objects, with the intention to withdraw.

Threat: Sudden tense hand or body movements in the direction of a victim as well as slapping or hitting a victim, without moving.

Charge: Tensed running towards an individual, which may end in a contact aggression (kicking, hitting, biting).

Direct display: Tensed running towards another individual, or passing closely by another individual, usually while pushing an object. This could end in a collision or other form of contact aggression. Sometimes two individuals would display towards each other mutually (mutual display) or alongside each other (parallel display). These interactions where then counted as one aggression for each participant.

Support was defined as all instances where an individual A intervenes with an aggression within 30 seconds upon an agonistic interaction between two other individuals B and C to aid in attack or in defence (de Waal, 1978). We only studied triadic interventions: when more individuals joined in support, these were not considered here. All aggressions from individual C towards B were considered as opportunities for support, regardless of the reaction of the victim B. We then corrected for the opportunity for individual A to provide support to B in a conflict with C, by dividing the number of times A supported B by the number of conflicts B had with all group members except with A. This index was then multiplied by one hundred resulting in a percentage of support (Hemelrijk & Ek, 1991; Vervaecke et al., 2000b).

Dominance was measured by scoring 'fleeing upon aggression' as a behavioural measure for dominance interactions (Vervaecke et al., 2000a; Stevens et al., in prep.). A dominance hierarchy was constructed with the aid of MatMan (version 1.1.4.), which assigns individual ordinal ranks to all individuals, based on the number of wins and losses in dyadic conflicts (de Vries et al., 1993). The steepness of dominance hierarchies was determined by calculating normalised David's scores based on the normalised dyadic dominance index, and then calculating the slope of the straight line found by linear regression of these values on the ranks (de Vries et al., in press; Stevens et al., in prep.). This results in an index ranging from zero to one, in

which zero represents a shallow or egalitarian dominance hierarchy, in which rank differences are small (van Schaik, 1989). An index of one indicates that rank differences are large, resulting in a steep or despotic dominance hierarchy (van Schaik, 1989; de Vries et al., subm.).

Matrix analyses

We used rowwise matrix correlation tests to investigate whether individuals directed more grooming towards higher ranking individuals, or whether high-ranking individuals receive more grooming than lower ranking individuals (Hemelrijk, 1990a, b; de Vries et al., 1993). Reciprocity in grooming relations was studied by performing a rowwise matrix correlation between the grooming matrix and the transposed grooming matrix (Hemelrijk, 1990a, b). Because reciprocity may be an epiphenomenon of rank-related effects (Hemelrijk, 1990a) we used partial matrix correlations (Hemelrijk, 1990b; de Vries et al., 1993) to control for the effects of dominance on reciprocity.

To test whether grooming is interchanged for tolerance, we performed matrix correlations (1) between the matrix of grooming given and the matrix of aggression received; and (2) between the matrix of grooming received and aggression given (Watts, 2002). Finally we tested whether grooming was interchanged for support by analysing correlations between the following matrices: (1) grooming given and support received; (2) grooming received and support given; (3) grooming given and support given; (4) grooming received and support received. To exclude side-effects of dominance and reciprocity, each of these correlations was repeated, using partial rowwise matrix correlations (Hemelrijk, 1990b; de Vries, 1993) between two matrices, (e.g. grooming given and support) and controlling for a third (e.g. grooming received).

All rowwise matrix correlation tests were based on Kendall's type of correlation coefficient, because grooming is skewed and contains extreme values, which may strongly influence the outcome of matrix correlation tests based on Pearson correlation coefficients (de Vries et al., 1993; Vervaecke et al., 2000b).

Reciprocity and interchange in relation to steepness of hierarchies

We expected that grooming reciprocity is negatively related to the steepness of the dominance hierarchy. Therefore we calculated the correlation between

the τ_{rw} values of grooming reciprocity and the steepness of the dominance hierarchy across our six study groups. Similarly, we tested the correlation between the steepness of the group's hierarchy and the correlation between grooming received and rank, as well as between grooming given and rank. All tests were two-tailed with the critical p-value set at 0.05.

Results

Reciprocity in grooming

First, we calculated matrix correlations between the matrix of grooming frequency (grooming given) and the transposed matrix (grooming received) (Table 1, result 1). Grooming was reciprocal in Apenheul, Planckendael-2 and Planckendael-3. There was a trend in Planckendael-1. There was no correlation between grooming given and grooming received in Wuppertal or Twycross.

Next, we looked at the association between dominance rank and grooming given as well as grooming received. Grooming was more directed at high-ranking individuals in Planckendael-1, Planckendael-2 and in Twycross, but not in Planckendael-3, Apenheul or Wuppertal (Table 1, result 2). In none of the groups did individuals receive more grooming from high-ranking individuals than lower ranking individuals (Table 1, result 3). Because of the effects of dominance rank on grooming in some of the groups, it was necessary to perform partial rowwise correlations to control for any dominance effects on reciprocity (Table 1, result 4). After controlling for dominance, grooming was no longer reciprocal in Planckendael-1 (Vervaecke et al., 2000b). In the other groups however, we found that grooming was truly reciprocal and thus reciprocity was independent of dominance rank. In fact the correlations for Planckendael-2, Planckendael-3 became even slightly stronger.

Reciprocity in support

We found that there was a significant correlation between support given and support received in Planckendael-2 and Apenheul, while there was a trend in Planckendael-3 and Wuppertal. (Table 1, result 5). The findings for Planckendael-1 (Vervaecke et al., 2000b) were mostly confirmed in other

Table 1. Results of (partial) Kr tests of reciprocity in grooming and support and the relation dominance on grooming and support and dominance. Entries give τ_{rw} values (rows 1-3 and 5-7), and partial τ_{rw} values (rows 4 and 8), each based on 20000 permutations $^{\circ}p < 0.10$; $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.

	Planckendael-1	Planckendael-2	Planckendael-3	Wuppertal	Apenheul	Twycross
1. Grooming given and received	0.30°	0.34*	0.41*	−0.02	0.60***	0.20
2. Grooming given and rank	0.71*	0.58**	0.24	0.17	0.09	0.63*
3. Grooming received and rank	−0.26	0.09	−0.32	0.02	0.22	0.23
4. Grooming given/received Rank controlled	0.05	0.36*	0.53**	−0.02	0.60***	0.07
5. Support given and received	0.52*	0.53*	0.39°	0.45°	0.40*	0.44
6. Support given and rank	0.75**	0.54**	0.16	−0.10	0.46*	0.36
7. Support received and rank	0.61*	0.59**	0.56*	0.10	0.34	0.26
8. Support given/received Rank controlled	0.13	0.31	0.36°	0.47*	0.29	0.39

groups. However, because support was significantly more directed at high-ranking individuals in Planckendael-1, Plankendael-2 and Apenheul (Table 1, result 6), and because individuals were more likely to receive support from high-ranking individuals in Planckendael-1, Planckendael-2 and Planckendael-3 (Table 1, result 7) we performed partial matrix correlations to control for possible effects of dominance on reciprocity in support (Table 1, result 8). Correlation coefficients dropped in all the groups where dominance influenced support given or received. Only in Wuppertal was support in conflicts truly reciprocal, and independent of dominance rank.

Interchange of grooming and tolerance

We did not find any correlations between grooming given and aggression received, nor between grooming received and aggression given (Table 2, results 1-2). Controlling for the effects of reciprocal grooming relations did not change this (Table 2, results 3-4).

Interchange of grooming and support

The frequency of grooming given was correlated with support received only in Planckendael-1 and Planckendael-2 (Table 3, result 1). This indicates that in Planckendael-3, Wuppertal, Apenheul and Twycross individuals did not groom those animals they received support from more frequently. We did not find any correlations between grooming received and support given (Table 3, result 2), thus individuals did provide more support to those individuals they received more grooming from.

The frequency of grooming given was positively correlated with the frequency of support provided in Planckendael-1, Planckendael-2. In Twycross this effect only reached a trend (Table 3, result 3). In Apenheul and Twycross was the frequency with which grooming was received, correlated with the frequency of support received (Table 3, result 4).

Because grooming was reciprocal in some groups, and support in some of the groups (see Table 1), partial matrix correlations were performed to unmask any effects of reciprocity on the interchange between grooming and support (Table 3, results 5-8). Like in Planckendael-1 (Vervaecke et al., 2000b) the interchange of grooming and support received in Planckendael-2 was independent of reciprocity in grooming (Table 3, result 5). Except for Apenheul, the partial correlation did not change correlation coefficients in

Table 2. Results of (partial) Kr test of interchange between grooming and tolerance. Entries give τ_{rw} values (rows 1-2), and partial τ_{rw} values (rows 3-4), each based on 20000 permutations $^{\circ}p < 0.10$.

	Planckendael-1	Planckendael-2	Planckendael-3	Wuppertal	Apenheul	Twycross
1. Grooming given/Aggression received/	0.23	0.14	0.16	−0.18	0.05	−0.13
2. Grooming received/Aggression given	−0.30	0.19	0.22	0.10	0.01	−0.17
3. Grooming given/Aggression received/ Controlled for grooming received	0.13	0.09	0.10	−0.18	0.05	−0.18
4. Grooming received/Aggression given/ Controlled for grooming given	−0.06	0.23°	0.18	0.10	0.00	−0.04

Table 3. Results of (partial) Kr test of interchange between grooming and support. Entries give τ_{rw} values (rows 1-4), and partial τ_{rw} values (rows 5-10), each based on 20000 permutations $^{\circ}p < 0.10$; $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.

	Planckendael-1	Planckendael-2	Planckendael-3	Wuppertal	Apenheul	Twycross
1. Grooming given/Support received	0.66**	0.55**	0.22	0.12	0.05	0.17
2. Grooming Received/Support given	−0.11	0.21	−0.21	−0.20	0.17	0.17
3. Grooming given/Support given	0.52*	0.47*	−0.14	0.02	−0.02	0.47°
4. Grooming received/support received	0.15	0.13	−0.17	−0.16	0.26*	0.52*
5. Grooming given/Support Received/ Grooming received controlled	0.66***	0.54*	0.32	0.12	−0.13	0.19
6. Grooming Received/Support given/ Grooming given controlled	−0.16	0.07	−0.17	−0.20	0.22	0.09
7. Grooming given/Support received/ Support given controlled	0.52*	0.40°	0.30	0.13	0.07	0.07
8. Grooming received/Support given/ Support received controlled	−0.22	0.17	−0.16	−0.14	0.07	−0.08
9. Grooming given/Support received/ Rank controlled	0.40	0.31	0.08	0.11	0.02	0.13
10. Grooming received/Support given/ Rank controlled	0.13	0.20	−0.17	−0.20	0.07	0.09
11. Grooming given/Support given/ Rank controlled	0.03	0.22	−0.20	0.04	−0.06	0.34
12. Grooming received/support received Rank controlled	0.40*	0.10	−0.01	−0.17	0.29	0.49*

the other groups much either. Controlling for reciprocity in support diminished correlation coefficients slightly, but the interchange still remained significant in Planckendael-1 and Planckendael-2 (Table 3, result 7).

Because both grooming given and received, and support given and received were influenced by dominance rank (see Table 1), we performed partial matrix correlations, with dominance as the controlling variable (Table 3, rows 9-12). The results from partial matrix correlations with dominance as controlling factor partly corroborate the results of Planckendael-1 (Vervaecke et al., 2000b): in Planckendael-2, where grooming was correlated with support received, this effect disappeared when controlling for the factor dominance (Table 3, result 9). Thus apparent interchange of grooming and support is merely a side-effect of a tendency of bonobos to groom dominant individuals more frequently, and of dominant individuals to provide more support. There was some influence of the factor dominance on the correlation between grooming received and support given, for example in Planckendael-1, but partial correlations did not yield significant results (Table 3, result 10).

The association between grooming given and support given dropped to non-significant levels in all groups, suggesting that this was a side-effect of the individuals' tendency to both groom and support high ranking individuals more often (Table 3, result 11).

Vervaecke et al. (2000b) also found that, when rank was controlled for, the correlation between grooming received and support received became stronger, indicating that certain individuals are preferred independent of their rank, perhaps because they can provide some other service in return. We found a similar effect in Twycross, where this correlation remained significant even when controlled for dominance, but not in the other groups (Table 3, result 12).

Influence of steepness on reciprocity and support

Grooming reciprocity was not significantly stronger in groups with a shallow dominance hierarchy (Pearson $r = -0.58$, NS). However there was a significant effect when the partial rowwise correlations, controlled for the factor 'dominance' were considered (Pearson $r = -0.86$, $p = 0.03$, see Figure 1). Reciprocity in support was not stronger in groups with a shallow dominance hierarchy (Pearson correlation $r = -0.38$, NS). The correlation

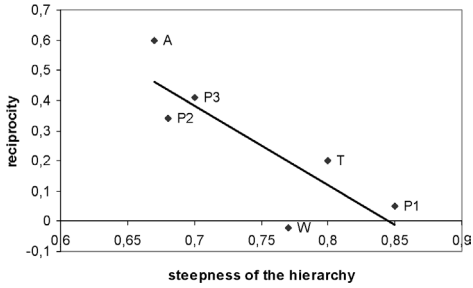

Figure 1. Correlation between the steepness of the dominance hierarchy (based upon normalised David's scores) and the reciprocity in grooming bouts (as indicated by the τ_{rw} values, with the factor rank partialled out). P1 = Planckendael 1; P2 = Planckendael 2; P3 = Planckendael 3; A = Apenheul; T = Twycross; W = Wuppertal; Pearson correlation: -0.86, $p = 0.03$.

became stronger when reciprocity, controlled for dominance, was considered but the effect did not reach significance (Pearson correlation $r = -0.51$, NS). The strength of the correlation between grooming received and dominance rank was moderately, but not significant related to the steepness of the dominance hierarchy (Pearson $r = 0.56$, NS). Grooming was related to rank in Planckendael-1 and Twycross, the two steepest dominance hierarchies, but also in Planckendael-2, where steepness of hierarchy was only moderate.

As indicated above, grooming was not traded for tolerance. The strength of these correlations did not depend on steepness of the hierarchy (grooming given-aggression received Pearson $r = -0.28$, NS; grooming received — aggression given: Pearson $r = -0.67$, NS).

None of the correlations between grooming and support were significantly related to the steepness of dominance hierarchies. The steepness of the hierarchy was not correlated with the strength of correlations between grooming received and support given (Pearson correlation $r = -0.21$, NS), nor with the strength of correlations between grooming given and support received (Pearson correlation $r = 0.46$, NS), between grooming given and support given (Pearson correlation $r = 0.49$, NS) or between grooming received and support received (Pearson correlation $r = 0.13$, NS).

Discussion

This study on a larger set of captive bonobo groups partly confirmed the earlier results from Vervaecke et al. (2000b). The most important similarity was

that support seemed reciprocal, but this was due to a side effect of dominance. We also found that grooming relations were reciprocal in most of the groups. On the other hand, we found that the influence of dominance rank on this reciprocity differed in some of the groups. Regarding interchange, we found little evidence that grooming was interchanged for tolerance, which confirmed again the findings by Vervaecke et al. (2000b). While we found some evidence for the interchange of grooming for support, this seemed to be a by-product of dominance-effects on grooming given and support received, as suggested by Vervaecke et al. (2000b): because individuals prefer to groom high-ranking others, and because high-ranking individuals provide more support, a correlation between grooming given and support may appear. Like Vervaecke et al. (2000b), we found no evidence that individuals received more grooming from those individuals they supported more often.

The question now remains — why don't bonobos in captivity interchange grooming for support. Leinfelder et al. (2001) offered various scenarios in which grooming would be only reciprocal. The first is when dominance relations are relaxed and rank order is not steep. Our previous analyses have shown that the dominance hierarchies in all the bonobo groups we sampled were clearly linear and steep (Stevens et al., in prep.), so this possibility does not apply. Second, the 'value equivalent' of support may not be large enough – that is, the benefits of supporting an individual do not measure against the value of grooming an individual (Leinfelder et al., 2001). Vervaecke et al. (2000c) found that support in Planckendael functioned mainly to maintain high ranks. Bonobos usually support winners in conflicts, that is individuals who were already dominant over the victims (Vervaecke et al., 2000c; unpubl. data), so the costs as well as the benefits of support may be not so high in groups with stable dominance hierarchies. A third possibility is that the benefits of grooming itself are strong enough so that grooming is traded for itself (Henzi & Barrett, 1999). Our finding that grooming was reciprocal in most of the groups seems to support this hypothesis. Franz (1999) already showed that grooming in captive bonobos is concentrated on body parts that are inaccessible to the groomee, which supports the hygienic function of grooming behaviour (e.g. Tanaka & Takefushi, 1993). The production of β-endorphins (Keverne et al., 1989) and the stress reducing effects for the groomee (Boccia et al., 1989) may also play an important part, especially in captive conditions. Indeed, we found that in the Planckendael group, bonobos groom each other more frequently during the winter, when they are

confined to the indoor enclosure, compared to the summer, when they have access to a large outdoor enclosure (Van Dyck et al., 2003). This increase in grooming may be a strategy to cope with increased aggression under the crowded conditions in winter (Sannen et al., 2004). Grooming in itself thus may be a valuable, stress-reducing commodity.

While grooming in itself carries substantial benefits and thus can be traded for itself, the relations between grooming and dominance in some of the groups, suggest that there is some advantage in grooming high-ranking bonobos. This opens the possibility that grooming is interchanged for some other 'value equivalent' than support or tolerance (Barrett et al., 1999). Given our result that rank-related grooming was not correlated to steepness of the hierarchy, this advantage seems not necessarily stronger in groups with a steeper hierarchy.

Grooming for access to food seems a very likely candidate for interchange in bonobos. In chimpanzees, de Waal (1997) showed that chimpanzees shared more food with those individuals that groomed them, two hours prior to feeding.

Like chimpanzees, bonobos also share food, such as meat or large fruits (Kuroda, 1984; Fruth & Hohmann, 2002), but they are less tolerant in interactions over food then chimpanzees (de Waal, 1992). Fruth & Hohmann (2002) did not find that dyads which shared more food groomed each other more often than dyads that did not share food. Still, in a species which is relatively intolerant in food contexts, grooming prior to feeding may increase the probability of later food sharing. Grooming high ranking group members is advantageous, when these can monopolise food items. Such an effect was shown by Vervaecke et al. (1999) in the Planckendael colony. Although monopolisation of resources is expected in despotic groups (Vehrencamp, 1983), i.e. groups with a steep dominance hierarchy (van Schaik, 1989), this need not be the case with monopolisation of food, which may depend on other factors, such as spread of feedings, or complexity of the enclosure. Future studies may focus on the relation between food sharing and grooming in bonobos. Moreover, our approach to the biological markets of grooming differed slightly from the approach in other studies, in that we analysed reciprocity in bouts, rather than within bout reciprocity or time matching (Barrett et al., 1999; Manson et al., 2004). Finally, we combined data of male and female bonobos, which may also have influenced our data, since intersexual

markets of grooming probably also include the interchange of grooming for sexual contacts. These relationships will be investigated in future research.

Acknowledgements

We are grateful to the directory and keepers of Planckendael Wild Animal Park (Belgium), Apenheul Primate Park (The Netherlands), Wuppertal Zoo (Germany) and Twycross Zoo (United Kingdom) for their help and interest in this study. This research was funded by a PhD grant of the Institution for the Promotion of Innovation through Science and Technology in Flanders (IWT-Vlaanderen: grant number 3340). We thank the Flemish Government for structural support of the CRC of the RZSA.

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