

AN EXPERIMENTAL EVALUATION OF THE CONSISTENCY OF COMPETITIVE ABILITY AND AGONISTIC DOMINANCE IN DIFFERENT SOCIAL CONTEXTS IN CAPTIVE BONOBOS

by

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Summary

Bonobos have been described as a relatively egalitarian and female dominant species. The exact nature and quality of their dominance relationships and the existence of female dominance are current topics of dispute. We investigated the consistency across social contexts, the stability in time, and the degree of expression of the competitive feeding ability and agonistic dominance in a captive group of bonobos. First, we examined whether the competitive feeding ranks and agonistic ranks differed in different dyadic contexts, triadic contexts and the whole group context. For some pairs of animals the dominance relationships with respect to competitive feeding altered with different group compositions. The agonistic dominance relationships changed accordingly. The competitive feeding ranks and agonistic ranks in the experiments correlated strongly with each other. The alpha position was occupied by a female, but not all females outranked all males. We suggest that females can profit from each others presence to gain inter-sexual dominance. Second, although the agonistic rank order in the whole group remained the same over at least five years, some

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dyadic competitive feeding ranks changed over time, resulting in a stronger female intersexual dominance. Third, the degree of expression of the behaviors used to quantify dyadic competitive and agonistic dominance was not high, in line with the popular 'egalitarian' epithet. Notwithstanding its low consistency across contexts, the dominance hierarchy in the whole group has a strong predictive value for other social relationships such as grooming. Given this strong effect of rank on other behaviours and given the strong dependency of rank on social context, the choice of the right party members may be a crucial factor in the fission-fusion processes of free-ranging bonobos.

Keywords: bonobo (*Pan paniscus*), rank orders, feeding scores, agonistic ranks, peering.

Introduction

As in many primates, an important aspect of the social structure of bonobos in the wild and in captivity is the existence of dominance relationships among individuals. In general, the descriptive, predictive and explanatory value of the dominance concept has greatly improved by distinguishing between different types of dominance relationships. Such typification allowed to clarify the variation of social behaviour, most notably among several macaque species (*e.g.* de Waal, 1989). De Waal (1989) has made a distinction between agonistic dominance, competitive abilities and formal dominance. Agonistic dominance relationships are generally determined from dyadic exchange of aggressive or submissive behaviours (*e.g.* for bonobos: de Waal, 1989; Furuichi, 1992; Furuichi & Ihobe, 1994; Parish, 1994; Kano, 1996). In a previous study, we found that fleeing upon aggression is the most suitable behavioural measure of the agonistic dominance relationships. In addition, an identical dominance rank could be deducted from the direction of peering (Vervaecke *et al.*, in press). Peering behaviour results in tolerance by dominant individuals to subordinates and is considered to be indicative of the dominance relationships (Idani, 1995). On the basis of agonistic dominance relationships, bonobos have been ordered in an agonistic linear (or almost linear) hierarchy in which the females rank in general above the males (Parish, 1994; Furuichi, 1997; Vervaecke *et al.*, in press), an unusual phenomenon in the primate taxon (Kappeler, 1993). The competitive dominance, expressed in the differential abilities of two individuals to compete over a certain resource, has been measured in bonobos by access to natural food sources (in Lomako: White & Lanjouw, 1992; Hohmann & Fruth, 1993), access to provisioned food (in Wamba: Kuroda, 1984; Furuichi, 1989; Kano,

1992), access to a bundle of leaves (in captivity: de Waal, 1992), and access to an artificial termite mound (in captivity: Parish, 1994). Due to the possibility of social tolerance, competitive dominance ranks do not necessarily overlap with the agonistic dominance ranks, *e.g.* when an individual with a low agonistic rank is tolerated to share food with a higher ranking individual (de Waal, 1989; Parish, 1994). Often female bonobos support each other to obtain priority of access to food over males (Kano, 1992; Parish, 1994). Although bonobos can develop agonistic and competitive hierarchies, behaviors that express a formal dominance relationship, such as the bared-teeth display in macaques or the pant-grunting in chimpanzees (de Waal, 1982, 1989; de Waal & Luttrell, 1985) have hitherto not been recognised (de Waal, 1988; Furuichi & Ihobe, 1994).

Bonobos have been described as egalitarians, characterised by a high degree of social flexibility (*e.g.* de Waal, 1995, 1997), implying that there is room for circumvention of rank-ruled interactions. If agonistic and competitive dominance relationships are easily influenced by social processes such as support, *etc.*, they will not be very consistent across context or stable over time. Consistency across context, stability over time and strong degree of expression are the most commonly described qualities of a clear-cut dominance hierarchy. First, with regard to *consistency across context*, primate dominance relationships are known to be prone to modification by other individuals or by group dynamics, which is indicated by the term 'dependent' as opposed to 'basic rank' (Kawai, 1965; de Waal & Harcourt, 1992). The tendency of dominance relationships to be independent from context and group composition, can be regarded as a measure of consistency. Second, a measure of *stability over time* refers to what extent ranks change or remain stable over time. Third, dominance relationships can differ in the *degree of expression*, in the absolute sense, *i.e.* that interactions used to measure a dominance relationship in a particular pair of individuals can be more or less frequently expressed or in the relative sense, *i.e.* that the difference in frequency of the behaviour used to measure the dominance relationship of two individuals can be more or less pronounced.

In this paper we aim to experimentally quantify the abovementioned qualities of the dominance relationships in a captive bonobo group. First, to examine *consistency across context*, we determined within a captive group of bonobos whether the agonistic and competitive dominance relationships

altered in different experimentally formed subgroups of two or three animals. We were interested to what degree the experimental competitive feeding rank orders obtained from the feeding scores overlap with the agonistic rank orders. Second, we evaluate the *stability over time* by comparing the experimental competitive feeding ranks as well as the agonistic ranks of the whole study group over a longer period of time. Third, we examine the *degree of expression* in the relative sense of the difference in competitive ability in the experimental feeding situations by assessing the degree in which the winning behaviour is consistently performed by either individual.

Materials and methods

Study animals

The six adult individuals of the Planckendael group were used as study animals (see Table 1).

Competitive tests

With regard to tests of competitive abilities, Syme (1974) stressed that the measure must be internally valid so that the competitive order is not merely a reflection of the individual ability to perform in the experimental situation. Further, the competitive order must be shown to have a degree of generality or external validity in the sense that it correlates highly with other internally valid dominance measures. We chose an experimental set-up that allowed for a clear expression of the competitive feeding ranks and the accompanying dominant or

TABLE 1. *The study individuals*¹⁾

	Sex	Year of birth	Origin	Age ²⁾	Weight ²⁾
Dzeeta	Female	1971	Wild	22	50 kg
Hermien	Female	1978	Wild	15	48 kg
Hortense	Female	1978	Wild	15	42 kg
Desmond	Male	1970	Wild	23	58 kg
Kidogo	Male	1983	Stuttgart	10	42 kg
Ludwig	Male	1984	Des × Dz ³⁾	9	52 kg

¹⁾ Source: Van Puijenbroeck & De Bois, 1994.

²⁾ Age and weight at time of study.

³⁾ Ludwig was hand-reared. The biological relatedness between Ludwig and Dzeeta seems not to be recognized by either of the two individuals: there is no expression of a particularly strong affiliation, nor is mating inhibited in this combination as seen in a natural mother-adult son bond.

submissive behaviours, uninfluenced by social tolerance, a factor that is known to alter the observed competitive rank order: the food pieces were not shareable giving little opportunity for the expression of social tolerance by food sharing. We set up a simple interactive competitive test, resulting in winner-loser interactions (*i.e.* obtaining a food item) in a dyadic as well as triadic setting. As competitive test we selected a simple 'task' for which differential performance abilities were unlikely: taking a food item equidistant (about 1.5 meter or less) from the tested individuals. Habituation to the competitive set-up was not required since all the animals daily used the test cages, were fed herein, and were often for brief periods kept in dyads or triads in these cages while the main hall was being cleaned or maintained. Syme (1974) suggested to test in dyadic situations as well as whole group situation. However, in a competitive whole group context, the lower ranking individuals tend to retreat and no longer interact. Since this retreat occurs to a lower degree in triads than in the whole-group setting, we opted for triadic tests. Further, in triads the effect of a certain third individual on the competitive relationships can be clarified.

Each possible dyad and triad of the Planckendael group participated in the feeding tests with five repetitions, at least on two different days. The dyads or triads were formed by the keepers in the mornings when the animals routinely transferred to smaller cages for cleaning procedures. Hortense and Hermien were in the company of their dependent infants during each session. The order in which the dyads and triads were selected was previously randomly determined. The experiments (5 repetitions of 15 and 5 repetitions of 20 triads) were spread between February 1993 and July 1993. Since the swelling phase is known to affect dyadic food access in common chimpanzees (Crawford, 1940), the tests were spread over different swelling phases (not more than 2 tests when maximally swollen).

Each test combination had access to two cages of 3 by 5 meters and they were in auditive contact with the rest of the group in adjacent cages. In each test session 20 small food items were given (fresh and dried pieces of fruit, in total about 100 grams). The pieces were thrown between the animals at an estimated equal distance from each. In order to avoid a spatial monopoly and to avoid the development of stereotypy of response, the food was regularly thrown on a different place. Each 10 seconds a piece was thrown, unless the individuals were involved in a social interaction. In this case, the observer waited 30 seconds unless the interaction was terminated earlier. In case an item did not fall at equal distance of all individuals or in case it was taken by a dependent infant, a new item was thrown to a total of 20 unbiased throws or to assure a balance of the bias between the individuals.

Analysis of competitive abilities

The feeding score, the number of food items eaten by an individual, was used as an indication of the competitive ability. The possible maximal feeding score per dyad or triad and per animal was 100 (5 sessions \times 20 pieces of food). The competitive rank order was determined from the feeding scores. The individual with the highest feeding score within a dyad or triad ranked highest. In order to find out whether the ranks are independent of group composition, we first constructed the linear rank order of the individuals based on their feeding scores in the dyadic tests, and then compared this with the competitive dominance relationships in the different triadic tests. To evaluate the consistency of ranks across different social contexts, we checked whether the difference in feeding scores between two individuals in dyads was significantly different from the difference between these individuals in the presence of a third

individual by means of analyses of variance. Since this involved the performance of 15 tests, we used a Bonferroni-corrected alpha level of $0.05/15 = 0.003$. A significant result from an ANOVA was followed up by four comparisons in which the difference between the food scores in the dyadic tests was compared with this difference of the same pair of animals in each of the four triadic tests. Significance of these tests was also established at a Bonferroni-corrected alpha level. In two cases, where the requirements of homogeneity of variances and normality was not fulfilled, we performed the nonparametric Kruskal-Wallis test which was, in case of significance, followed up by the four comparisons of dyadic *versus* triadic outcomes according to the procedure described in Siegel & Castellan (1988). To test whether the average feeding scores of two animals in the five dyadic subtests differed from each other, the paired *t*-test was used. Hochberg's (1988) improved Bonferroni procedure was used to establish significance of these tests at a table-wide alpha level of 0.05.

Rank order analysis

Whole-group agonistic ranks were obtained from dyadic fleeing and peering interactions, both defined as submissive behaviours. The competitive rank order obtained from the feeding scores in the dyadic tests was compared with a rank order based on two other dominance related behaviours observed during the dyadic tests: fleeing upon aggression and peering, which are both considered as submissive behaviours. Since the possible space to flee was very restricted, yielding upon aggression and crouching upon aggression were also scored as signs of submission. Peering was defined as the prolonged gazing within 30 cm by an animal toward another (Idani, 1995). It is usually performed when another individual has monopolised an object, food or a grooming partner or when two individuals reunite after fission.

Hierarchical rank order analysis of agonistic ranks and competitive abilities was carried out with the aid of the software package MatMan (de Vries *et al.*, 1993). The behavioural variables (competitive feeding score, fleeing upon an aggression and peering) were evaluated as an expression of a dominance relationship by determining their linearity, uni-directionality and coverage (following van Hooff & Wensing, 1987; see also Vervaecke *et al.*, in press):

Linearity: Landau's index of linearity (*h*) was calculated and its significance tested (Appleby, 1983).

Uni-directionality: The directional consistency index (DC) gives the frequency with which the behavior occurred in its more frequent direction relative to the total number of times the behaviour occurred. The total number of times the behaviour occurred in the direction of the higher frequency (H) minus the number of times in the less frequent direction (L) is divided by the total frequency: $DC = (H - L)/(H + L)$. The number of one-way relationships, *i.e.* the number of dyads in which the behaviour is shown in one direction only, irrespective of the frequency of interaction within the dyads, and the number of two-way relationships were counted.

Coverage: The proportion of relationships in which a behaviour occurs was calculated. Blank relationships are relationships in which the behaviour occurs in neither direction.

Results

1. Consistency across contexts

We found that the competitive dominance of one individual over another is not always consistent between social contexts, but depends on the presence of other individuals. To evaluate whether the competitive dominance relationships differ in dyadic and triadic tests, we designated the animal with the highest feeding score as the dominant. Tables 3 and 6 present the total feeding scores obtained in the dyadic and in the triadic feeding tests. Table 2 presents a summary of the results. We found that overall the competitive dominance relationships in the triadic tests agree with the ones found in the dyadic tests, but with some notable exceptions. The most striking reversal in competitive dominance was seen between Desmond and Hermien. Whereas Hermien obtained clearly more food in the dyadic test, Desmond outcompeted Hermien in the triadic tests when one of the two lowest ranking males Kidogo or Ludwig was present, although they never supported him agonistically (Fig. 1). In these latter cases Desmond acted more self-assured and participated more intensely in the competition.

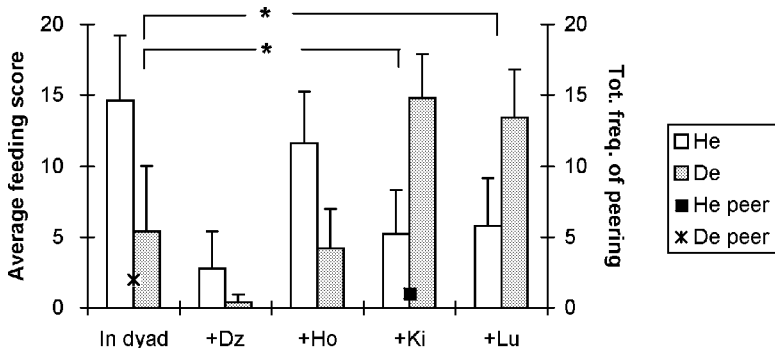


Fig. 1. Histograms of the average feeding scores of the pair Hermien-Desmond, first in the dyadic test (In dyad), then in four different triadic tests (with the name of the third individual on the X-axis). The feeding experiments were repeated five times (the bars show the standard deviation). The difference in feeding scores between Hermien and Desmond in the dyadic test differs significantly from the difference found between these two animals in the triadic test with Kidogo present and also in the triadic test with Ludwig present (ANOVA followed by four comparison tests with significance level corrected by Bonferroni technique). Note that the reversal in competitive dominance between Hermien and Desmond in the triadic test with Kidogo as compared to the dyadic test, is accompanied by a reversal in the direction of peering.

TABLE 2. *Summary of the results*

	dyadic tests	triadic tests	whole group
agonistic dominance	linear hierarchy Dz He De Ki Ho Lu (<i>cf.</i> Table 4)	dominance relationships from fleeing and/or peering same as in the dyadic tests. Exceptions: — He peers to De when Ki is present. — He peers to Ho when Dz is present.	linear hierarchy Dz He De Ho Lu Ki (1992-1997)
competitive dominance 1993 (this study)	linear hierarchy Dz He De Ki Ho Lu (<i>cf.</i> Table 3)	competitive dominance relationships same as in the dyadic tests. Exceptions: — De > He when Ki or Lu is present (sign.).	linear hierarchy Dz He Ho De Lu Ki
competitive dominance 1992 (previous study)	linear hierarchy Dz De He Ki Ho Lu	some competitive relationships depend on third animal present: <i>e.g.</i> He > De when Dz is present.	linear hierarchy Dz He Ho De Lu Ki

In Table 3 we present the total feeding scores obtained by the individuals in the dyadic tests. On the basis of these dyadic scores the individuals could be ordered into a completely linear rank order (Landau's linearity index $h = 1$; $p = 0.022$). The directional consistency index is not high (DC = 0.63), since in most combinations both individuals were able to obtain some food in the dyadic tests, with the exception of Ludwig who ate nothing in the dyadic test with Dzeeta. In the dyadic tests two females, Dzeeta and Hermien, were able to outcompete all the males in the sense that they obtained a higher feeding score (significant for all but Hermien-Desmond) (Table 3). Two males, Desmond (significant) and Kidogo (NS), obtained a higher feeding score than the female Hortense (Table 3).

Table 4 presents the frequencies of fleeing upon aggression and of peering performed in the dyadic tests, which were used by us as indications of agonistic dominance of the recipient. These two behaviors did not occur

TABLE 3. *Total feeding scores in the dyadic tests (number of times food is taken)*

	Other individual in dyad					
	Dzeeta	Hermien	Desmond	Kidogo	Hortense	Ludwig
Nr. of times individual takes the food						
Dzeeta	—	75	96*	95*	91*	100*
Hermien	25	—	73	89*	64	94*
Desmond	4*	27	—	98*	81*	90*
Kidogo	5*	11*	2*	—	52	63
Hortense	9*	36	19*	48	—	62
Ludwig	0*	6*	10*	37	38	—

Individuals in order of their dyadic competitive feeding rank.

The asterisk indicates a significant difference in feeding score between the two individuals (paired *t*-test; significance level controlled at table-wide α of 0.05).

equally frequently. Peering was expressed in almost all pairs, with a high unidirectionality and a Landau's linearity index of almost 1, implying that it was a good marker of dominance in the specific experimental context. Fleeing upon aggression had also a high unidirectionality but a low coverage (in 9 of the 15 dyadic tests it did not occur) and therefore also a low linearity index. All occurrences of aggression were followed by fleeing, yielding or crouching, except for three aggressions by Kidogo towards Ludwig that were followed by a counter aggression. Combining both peering and fleeing into one matrix resulted in a completely linear agonistic dominance hierarchy (Table 4).

Comparison of Table 3 with Table 4 shows that a complete correspondence exists between the competitive and agonistic rank order in the dyadic context. Within all 15 dyads peering and fleeing upon aggression was performed only by those animals that obtained the least amount of food in the dyadic tests.

Also in the triadic tests a strong correspondence between the two dominance related behaviours and the amount of food obtained was found. The direction of fleeing upon aggression completely agreed with the competitive dominance relationships. With regard to peering there was only one interaction in which the direction of peering did not agree with the competitive dominance order between the two animals. Hermien peered once at Hortense in the triadic test with Desmond, even though in total Hermien obtained most food. This occurred in a tense situation when Hermien was embracing

TABLE 4. *Total frequencies of fleeing upon aggression and peering in the dyadic tests**)

	Receiver: other individual in dyad					
	Dzeeta	Hermien	Desmond	Kidogo	Hortense	Ludwig
Actor: individual freeing or peering						
Dzeeta	–	0	0	0	0	0
Hermien	2 (2,0)	–	0	0	0	0
Desmond	3 (1,2)	2 (2,0)	–	0	0	0
Kidogo	15 (15,0)	10 (5,5)	1 (1,0)	–	0	0
Hortense	2 (1,1)	4 (4,0)	9 (9,0)	3 (3,0)	–	0
Ludwig	37 (36,1)	1 (1,0)	1 (1,0)	1 (0,1)	4 (3,1)	–

*) Individuals in order of their dyadic competitive feeding rank.

Sum of peering and fleeing upon an aggression. In parentheses: first frequency of peering, then frequency of fleeing upon an aggression.

Hortense, apparently to calm her and herself down. Still, in accordance with her lower feeding score, Hortense peered in this triadic test more frequently at Hermien than *vice versa*.

In three cases the direction of peering as observed in the dyadic test was reversed in a triadic test (Table 5). The first case is the special one just described. In the other two cases this reversal was accompanied by a similar reversal in the competitive dominance relationships. These two cases involved Hermien and Hortense in the presence of Dzeeta, and Hermien and Desmond in the presence of Kidogo. The direction of peering covariated with the competitive dominance relationship.

The linear agonistic dominance hierarchy in the entire group differed from the agonistic and competitive dominance rank order in the dyadic tests. The agonistic whole-group rank order, *i.e.* when all the animals were present, was as follows: Dzeeta, Hermien, Desmond, Hortense, Ludwig, Kidogo (Vervaecke *et al.*, unpubl. data). A disparity between the whole-group agonistic ranks and the competitive/agonistic dominance ranks in the dyadic tests was found in the combination Kidogo-Ludwig. In the dyadic test Kidogo could obtain a higher feeding score than Ludwig (but NS) and Ludwig once fled for Kidogo. In the triadic tests also, Kidogo outcompeted Ludwig, unless Desmond was present. In that context, Kidogo participated less intensely in the competition than in the dyad with Ludwig, expressed in a lower number of intentions to grab the food. In the entire group (in which Desmond was always present) it was not possible for Kidogo to dominate

TABLE 5. *Total frequencies of peering and fleeing in the triadic tests*

Triad	Direction	Peer	Flee	Direction	Peer	Flee	Direction	Peer	Flee
DzHeDe	HeDz	9	1	DeDz		2	DeHe		1
DzHeKi	HeDz	6		KiDz	8		KiHe	5	
DzHeHo	HeDz	2		<u>HeHo</u>	<u>1</u>		HoDz	8	
DzHeLu	HeDz	5							
DzDeKi	DeDz		1	KiDe		1			
DzDeHo	HoDz	4		HoDe	2				
DzDeLu	LuDz		1						
DzKiHo	KiDz	3		HoDz	2				
DzKiLu	KiDz	5	1						
DzHoLu	HoDz	16							
HeDeKi	<u>HeDe</u>	<u>1</u>		KiHe	2				
HeDeHo	<u>HeHo</u>	<u>1</u>		HoHe	2				
HeDeLu	LuDe	1							
HeHoLu	HoHe	16							
HeKiHo	KiHe	1		HoHe	9				
HeKiLu	KiHe	8							
DeKiLu									
DeKiHo	HoDe	4							
DeHoLu	HoDe	7							
KiHoLu	HoKi		1	LuKi		1	LuHo		2

(*) Individuals in order of their dyadic competitive feeding ranks.

Underlined: the direction of peering is reversed with respect to the peering direction in the dyadic tests.

Ludwig agonistically. A similar phenomenon occurred in the combination Hortense-Kidogo: Hortense agonistically dominated Kidogo in the whole-group situation, whereas this was reversed (but NS) in the dyadic feeding test in which Hortense peered three times at Kidogo.

2. *Changes over time of competitive ability*

In the dyadic experimental context, one interesting change has occurred since a prior study (see also Table 2). In previous experiments of the same sort carried out in March and April 1992, 13 months before the present study (Vervaecke *et al.*, 1992), Hermien could only outrank Desmond — in the sense of obtaining a higher feeding score — in triadic context in the presence of the dominant female Dzeeta. In time Hermien gained competitive feeding dominance over him in the dyadic context also. This improved competitive feeding ability disappeared however when either of

the other males was present in the feeding test. In the entire group Hermien can dominate Desmond agonistically but Desmond frequently challenges Hermien whereupon she does not submit. The reverse however does occur: she can dominate him by making him flee. It seems that in this particular dominance relationship Hermien needs the presence of other females to maintain her high inter-sexual rank. This is confirmed by a redirected aggression by Dzeeta and Hermien against Desmond (after Dzeeta had bitten Hermien) which was actually the only co-operative aggression which we observed during the feeding experiments of the present study.

In the entire group context there have been no agonistic dominance reversals from 1992 up to the beginning of 1997.

3. Degree of expression of competitive ability

As can be seen in Table 3, the differences in competitive ability were most prominent between the dominant female and the other individuals and next between the most dominant male and the other individuals. The inter-sexual feeding rank order was clear for the dominant female and all the males. The second ranking female ranked significantly higher than the two lowest ranking males only, whereas there was a somewhat less difference in competitive ability between her and the highest ranking male. The lowest ranking female was significantly dominated by the highest ranking male but the rank difference between her and the other male Kidogo, who obtained a slightly higher feeding score, was not clear. Among the females two of the three combinations had non-significant differences in feeding scores (2/3), among the males one of the three (1/3), between the sexes three of the nine combinations (3/9). All but two of the six combinations with non-significant differences in feeding scores were animals of adjacent ranks in the linear hierarchy (Table 3).

The strength of the competitive feeding dominance of one individual over another (as measured by the difference of the respective feeding scores) was dependent on the presence or absence of other individuals. In Table 6 we have indicated where a significant difference was found between the difference in the competitive abilities of the two animals in the dyadic test and this difference in the triadic tests. In 7 cases the competitive dominance is significantly weaker in a triadic test than in the corresponding dyadic test and in 1 case the competitive dominance of one animal over the other was

TABLE 6. *Total feeding scores in triadic tests (Tr) and dyadic tests (Dy)*

	Dz	He	De		He	De	Ki
Tr	84	14	2	Tr	26	74	0
				Dy	73	27	
	Dz	He	Ki	Dy	89–		11–
Tr	61	37	2				
					He	De	Ho
	Dz	He	Ho	Tr	58	22	20
Tr	84	5	11	Dy		81–	19–
	Dz	He	Lu		He	De	Lu
Tr	97	3	0	Tr	29	67	4
Dy		94–	6–	Dy	73	27	
				Dy	94–		6–
	Dz	De	Ki		He	Ho	Lu
Tr	86	12	2		86	12	2
Dy		98–	2–	Tr			
	Dz	De	Ho		He	Ki	Ho
Tr	83	16	1	Tr	94	1	5
Dy		81–	19–	Dy	64+		36+
	Dz	De	Lu		He	Ki	Lu
Tr	76	24	0	Tr	95	5	0
Dy		90–	10–				
	Dz	Ki	Ho	Tr	De	Ki	Lu
Tr	51	24	25		91	4	5
	Dz	Ki	Lu	Tr	De	Ki	Ho
Tr	91	9	0		84	0	16
	Dz	Ho	Lu	Tr	De	Ho	Lu
Tr	95	5	0		93	5	2
				Tr	Ki	Ho	Lu
					79	21	0

The dyadic scores are only shown for those pairs for which the difference in feeding scores obtained in the dyadic tests differs significantly from the difference in the triadic tests. Each triad is ordered according to the dyadic competitive feeding rank Dz > He > De > Ki > Ho > Lu (*cf.* Table 3).

– (+): in triadic test is the food score difference significantly smaller (greater) than in dyadic test. *Italics*: significant reversal in food score difference in triadic test as compared with the dyadic test.

significantly stronger in a triadic context than in the corresponding dyadic context (Table 6). In some pairs of bonobos the presence of a high ranking individual suppressed previously clear differences in feeding scores since the two other individuals lowered their participation in the competition. In other combinations, only one individual retreated from the contest scene. Between Hermien and Hortense the difference in feeding score became more expressed in the triad with Kidogo, since both Hortense and Kidogo tended to retreat from contest. Finally, it was observed that the competitive dominance relationship of Hermien over Desmond in the dyadic test reversed when either Kidogo or Ludwig was present in the triadic test, related to an increase in assertivity by Desmond (Fig. 1).

Discussion

Our main goal was the evaluation of the effect of a certain third individual on the competitive and agonistic dominance relationships, in an experimental set-up that allowed for a clear expression of the competitive feeding ranks and the accompanying dominant or submissive behaviours, uninfluenced by social tolerance. As such, these experiments satisfied our expectations. Peering and fleeing, the behaviours used as indicators of subordination frequently occurred. Peering occurred more often in the experimental context than in the whole group situation in the larger hall, which is probably due to the forced closer proximity. Similarly, the restricted escape possibilities in the experimental set-up, may have resulted in the submissive fleeing or yielding reaction upon each aggression in the feeding experiments. By submitting readily the animals possibly avoided an escalation of aggression. The fact that the competitive feeding ranks and the agonistic ranks in the dyadic and triadic feeding tests strongly overlapped (Table 2), indicates the validity of the measures that were used. In the whole-group situation the competitive feeding ranks differ from the agonistic ranks due to the social tolerance expressed among the females in food-sharing (Vervaecke *et al.*, in press).

Our main result is that the competitive and agonistic dominance relationships in the experiments are *not consistent across social context* in the sense that they alter in different group compositions (see Table 2). The fact that the ranks obtained from pairwise testing of all possible dyads in the group

differed from the ranks in other social contexts, has been reported for several other primate species (reviews: Popp & DeVore, 1979; Bernstein, 1981; Harcourt & de Waal, 1992). The rank of philopatric infants often depends on the maternal rank (*e.g.* Dunbar, 1988). Support interactions can cause dramatic rank changes as in male common chimpanzees, indicated by terms such as chimpanzee politics (de Waal, 1982) or alliance fickleness (Nishida, 1983). In some species however, the phenomenon of dependent ranks has not been documented such as in female pigtailed macaques (Messeri & Giacomini, 1986) and among lower ranking male baboons coalitions have little effect on the rank order (Walters & Seyfarth, 1986). Changes in rank orders in different social contexts or 'dependent ranks' have been reported for free-ranging bonobos too. In the wild, fission fusion is the normal social dynamic of this species (review: Van Elsacker *et al.*, 1995). In Wamba the social position of a male — the philopatric sex — is dependent on the group composition. Sons that remain in the presence of their mothers can co-feed with the female core of the group and thus profit from their mother's rank. It is hypothesised that a male can rise in rank as his mother grows older, but drops in rank in case his mother dies when he is still a young adult (Furuichi, 1989, 1992; Kano, 1992; Furuichi & Ihobe, 1994). An adult male was seen to assume a lower rank when he joined another subgroup independently than when he joined the subgroup with four other males (Kano, 1992, p. 182). Within a party (a group of animals travelling together and remaining in vocal contact) males can increase their rank relative to other males by changing to a different subparty (a group of individuals using a separate feeding site) (Kano, 1996). Young immigrant females focus their interactions upon one specific senior, high ranking female and remain in her presence (Idani, 1991), resulting in priority of access (Furuichi, 1997, p. 869).

With regard to *inter-sexual dominance relationships*, we found that even in the dyadic context the generally stronger males do not use their fighting abilities. If strength was the key factor determining the hierarchy we would expect a strong correlation between dyadic rank and the weight of the individuals. This correlation is however low (weight-rank from dyadic feeding score or dyadic agonistic rank: $r_s = 0.12$, NS). In the recent debate on the nature of female dominance, it was questioned whether all females can evoke submissive male behaviours (Stanford, 1998). We found convincing evidence for female dominance in the sense that the female with the highest dyadic competitive ability can dominate all the males, regardless of group

composition. For the other females, inter-sexual dominance may vary with group composition. A male can be outcompeted by a female in dyadic context (*e.g.* Hermien-Desmond) but he can take courage in the presence of a lower ranking individual to outcompete the female. Thus group composition seems an important factor in obtaining or maintaining female inter-sexual dominance. Furuichi (1997, p. 869) indeed "found a general tendency for males to show more a submissive attitude towards females when the latter were part of a large aggregation". Female coalitions against males may be crucial for maintaining a high inter-sexual rank (Parish, 1996; Furuichi, 1997), which may possibly be the case in our study group too (Vervaecke *et al.*, unpubl. data).

In addition to group composition and the occurrence of coalitions, age has been suggested as an important factor in the acquisition of female dominance. *Over a longer period of time*, the agonistic whole-group rank order appears stable since we observed no rank reversals in a period of five years following the study period. However, in the dyadic competitive feeding ranks we documented an interesting change in ranks in which a female could outcompete a male in dyadic context, which she did not succeed in 13 months prior to the study. This suggests that as females age, their ability to dominate a male improves, possibly by the gradual development of stronger female intra-sexual bonds. Increasing age and strength of social bonds greatly affect bonobo dominance relationships. Longer term rank data on free-ranging bonobos come predominantly from the Wamba site where the groups tend to be relatively large and more stable in comparison to other sites (White, 1992). There, prolonged female bonds, increased parity and age have been suggested by the researchers at Wamba as intervening variables in acquisition or maintenance of high rank (Furuichi, 1989; Kano, 1992). Male rank depends on the mother's rank and presence (Furuichi, 1989, 1992; Furuichi & Ihobe, 1994) although some old adult males seem to keep their acquired rank independent of their mothers presence (Kano, 1992). As an alternative or additional strategy to female bonding, the sexual proceptivity of the female may be an important asset in inter-sexual dominance acquisition (de Waal, 1997). One female bonobo (about 12 years) that was kept in a dyad with a male for several years was tested in the presence of a male (about 12 years) in an identical experiment as in our present study. The feeding score was very much in favour of the male (he took 95 food items *versus* 5 for the female) who assertively took food from

the females mouth in case she managed to take a food item, while she regularly presented for sex and continued to participate in the competition (Vervaecke *et al.*, 1992). Young, sexy females may employ their sexuality in the inter-sexual dominance struggle, whereas older females in addition can rely on their well developed affiliative bonds.

The (relative) *degree of expression of the difference* in dyadic competitive ability was not convincingly high in the sense that of the 15 dyadic combinations, 6 showed a non-significant difference in feeding score. In the same line, a low (absolute) degree of expression of the dominance relationships in the frequency of the agonistic behaviours was seen in the whole-group situation (Vervaecke *et al.*, in press) as well as in free-ranging bonobos (Furuichi, 1997), and may have contributed to their general description as egalitarians (de Waal, 1995). Overall, the differences in competitive abilities were not highly expressed and easily affected by the presence of a third individual. In situations where dominance relationships are not very outspoken and may differ between different contexts, we do not expect to find a formal dominance hierarchy. We did find that subtly expressed competitive dominance relationships still can have a *high potential explanatory value* since they correlated strongly with other dominance measures. In the whole-group situation, the observed agonistic and competitive ranks correlate significantly with each other and with other social behaviours such as grooming and support behaviour (Vervaecke *et al.*, 1996).

The results of our study suggest that with shifting group compositions, which is the typical grouping pattern for *Pan* (Goodall, 1986; Kano, 1992) and *Ateles* (Robinson & Janson, 1987), there should be ample room for rank shifts. In a free-ranging bonobo community, rank related differences in the tendencies to leave a party can be expected. According to Kano (1996), a bonobo male can manipulate his rank or status by choosing the party or subparty he joins, that is, the partners with whom he associates. Given the fact that food conditions rarely force bonobos to travel in small parties (Chapman *et al.*, 1994), females are generally expected to stay in the presence of at least another female companion in their party to improve their competitive feeding abilities within the parties. White (1988) found that both females and males tended to leave a party in the company of others, but if an individual left alone it was likely to be a male (see also Kano, 1992, p. 71). Before immigration, young nulliparous females have a weak bonding attachment and opportunistically join any party and community

going through a 'wandering stage' (Kano, 1992, p. 76, 78). Young newly immigrated females invest highly in the development of a strong bond with an older dominant female (Idani, 1991) and in case of party fission, they are expected to stay in the same party in order not to loose their dominant potential ally. Similarly, young males, that were reported to profit from the presence of their mother, are expected to remain in the same party as their mother to improve their dependent rank. For low ranking males without a mother in the group there may be a strong need to change the composition of a party or to avoid the presence of certain individuals. Only for the two lowest ranking males of our study the feeding score often dropped to zero in the triads, indicative of their relatively weak competitive ability in group. Since a bonobo's competitive feeding ability depends strongly on the identity of the others in the party (s)he belongs to, bonobo party dynamics might be better understood by investigating in how far his/her agonistic dominance relationships in the current party influence the decision to migrate, alone or in the company of others, to a different party.

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