VIVAMUS

Dominance and its Behavioral Measures in a Captive Group of Bonobos (*Pan paniscus*)

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We investigated the existence of a social dominance hierarchy in the captive group of six adult bonobos at the Planckendael Zoo. We quantified the pattern of dyadic exchange of a number of behaviors to examine to what extent each behavior fits a linear rank order model. Following de Waal (1989), we distinguish three types of dominance: agonistic dominance, competitive ability and formal dominance. Fleeing upon aggression is a good measure of agonistic dominance. The agonistic dominance hierarchy in the study group shows significant and strong linearity. The rank order was: 1. female (22 yr), 2. female (15 yr.), 3. male (23 yr.), 4. female (15 yr.), 5. male (9 yr.), 6. male (10 yr.). As in the wild, the females occupy high ranks. There is prominent but nonexclusive female agonistic dominance. Teeth-baring does not fulfil the criteria of a formal submission signal. Peering is a request for tolerance of proximity. Since its direction within dyads is consistent with that of fleeing interactions, it is a useful additional measure to determine agonistic ranks in bonobos. In competitive situations, the females acquire more food than other group members do. The rank obtained from access to food resources differs from the agonistic rank due to female intrasexual social tolerance, expressed in food sharing. We typify the dominance styles in the group as female intrasexual tolerance and male challenging of rank differences. The agonistic rank order correlates significantly with age and has a strong predictive value for other social behaviors.

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INTRODUCTION

The concept of dominance was developed to help to describe, explain and predict social relationships (Hinde, 1974). We investigated to what extent the concept of dominance can be used to describe bonobo social relationships. Van Hooff and Wensing (1987) and Noë *et al.* (1980) suggest several criteria that a behavioral variable should meet in order to justify the adoption of a dominance model: the behavior should allow for a linear ordering in the group; it should be expressed in most dyads as a predominantly unidirectional interaction; and, it should be expressed not just in a few but in most of the relationships in the group.

De Waal (1989) made a distinction between three types of dominance: agonistic dominance, formal dominance, and competitive ability. In an agonistic dominance relationship, the dominant animal has the power to limit the behavior of a subordinate to some extent by means of aggression or fighting abilities (Noë *et al.,* 1980). Agonistic dominance is expressed in the outcome of agonistic encounters, and indices of winning or losing conflicts are frequently used as operational measures. Since conflicts may also be resolved by deference of the loser without escalation (Drews, 1993), the spatial yielding of one individual to another may provide a good operational measure of submission or deference. When an aggression is ignored or not followed by submission of the target individual, the interaction may not express a mutually acknowledged dominance relationship. Submissive interactions are therefore usually considered as better indicators of a dominance relationship (Rowell, 1974; Kappeler, 1993).

Formal dominance is characterized by ritualized communication signals and greeting rituals of which the direction does not vary with social context. When the agonistic dominance relationship is accepted by the subordinate, aggressive conflicts are few (de Waal, 1989) and the subordinate acknowledges the higher dominance status of the other by showing formalized submissive signals. This implies that the formal and agonistic dominance relationships coincide. Unidirectional submissive signals such as the teeth baring in rhesus macaques (de Waal and Luttrell, 1985), the bowing and pant-grunting in chimpanzees (de Waal, 1982), or unidirectional dominance signals such as mock-biting in stump-tailed macaques (de Waal, 1996) are be reliable ritualized expressions of formal rank. To fulfil the criteria of an expression of formal dominance/submission, the behavior should be multicontextual and unidirectional. It should be expressed by different individuals and covary with other selected measures of agonistic rank.

The competitive ability reflects the capacity of an individual to obtain access to limited resources (usually food access is measured). The derived

rank order does not necessarily correspond to the agonistic dominance rank. The ability and motivation to compete may vary according to the resource that causes competition (Syme, 1974). Temporal variation in competitiveness implies that an individual not always shows the same tendency to use competitive ability. She can show a certain degree of respect for possessions of others or can allow others to share a resource. In this respect social tolerance is linked to a low competitive tendency (de Waal, 1989). De Waal (1989) described the occurrence of social tolerance as an aspect of the quality of the dominance and competitive relationships or the dominance style. In order to be a relevant concept, a dominance order should have a more general predictive value in the sense that the rank order should correlate with other social behaviors (Syme, 1974; Richards, 1974).

Hitherto the dominance relationships of bonobos (*Pan paniscus*) have been described piecemeal. With regard to current bonobo data on agonistic ranks we found no systematically recurring operational measure of dominance. Aggressions are used as well as submissions and displacements (Furuichi, 1992; Furuichi & Ihobe, 1994; Furuichi, 1997; Ihobe, 1992; Kano, 1992, 1996; Parish, 1994), whether these three behaviors are indeed markers of a similar rank structure has not been investigated. With regard to competitive abilities, data from free-ranging and captive bonobos indicate that females can regularly obtain feeding priority over males (Kano, 1992; Furuichi, 1989; Kuroda, 1984; Fruth, 1995; Hohmann and Fruth, 1993 & 1996; Parish, 1994 & 1996). Social tolerance, expressed in food sharing occurs among females and between the sexes (Parish, 1994, 1996; de Waal, 1992; Hohmann and Fruth, 1993, 1996; Kano, 1980; Kuroda, 1984; White, 1992). Concerning formal dominance, conspicuous ritualized submissive behavior, such as the pant-grunting in chimpanzees, appear to be absent in bonobos (Furuichi, 1992; Furuichi, Ihobe, 1994: 220; Kano, 1996). De Waal (1989) recognized a similar vocalization in bonobos but only in playful contexts. Individual attributes such as age (Furuichi, 1992; Furuichi, Ihobe, 1994; Furuichi, 1989, 1997; Kano, 1992; Parish, 1996) and sex (de Waal, 1997) can affect rank. With regard to the general predictive value of rank, few behaviors have been related to rank (male copulations: Kano, 1996).

Stanford (1998) disputed whether bonobo females exhibit a convincing form of agonistic dominance, except in feeding priority. Based on an unpublished manuscript by F. D. White in which individuals could not be recognized, he suggested that ''if social dominance is considered separately from priority of feeding access, the pattern of dominance in bonobos more strongly resembles that of chimpanzees''. According to Stanford (1998) findings of a strong female oriented affiliation have resulted in an emphasis on female power. However, field workers replied to Stanford, confirming

female dominance in *Pan paniscus* (Kano, 1998). The discussion illustrates a strong need for systematic data on the issue of dominance relationships in bonobos. Further, in case of female dominance, one may ask whether females actively dominate males or whether males merely defer to the females. To answer this question, a measure of dominance is required in which both the dominance and the subordinance of a relationship is expressed.

Previously, no one attempted systematically to evaluate the dominance relationships among bonobos in detail, by quantifying significance and strength of the linearity, directionality and coverage of the behaviors and their correspondence. We will describe these aspects of dominance in a captive group of bonobos. We also examine peering and teeth-baring as possible signs of formal dominance in the study group. Linear dominance hierarchies can be explained by individual attributes such as age and size. We present correlations of rank and the individual attributes age and weight—a factor that correlates with physical strength (e.g. Alcock; 1984: 361). The study group was the largest captive bonobo group and contained several males and females, a pattern that lies within the natural range of bonobo group compositions (Kano, 1992).

METHODS

Subjects

We used the six adults in the Planckendael group as subjects (Table I).

Observation Period

We scored all occurrences of the interactions between the adults, during 320 hours, randomly distributed between May 15, 1992 and March 26, 1993, with 34 hours of filmed feeding sessions (Altmann, 1974). Daily observation time ranged between 1 and 7 hours on 88 days.

Between May 15, 1992 and March 3, 1993 we selected ten random days when we measured the food intake during the evening feeding sessions in the entire group. To control for a possible effect of female swelling on feeding priority, we selected five days when the genitals of the cycling females were minimally swollen and five days when they were maximally swollen. In a period of 30 min, i.e. duration of the feeding session, we took six video scans of each individual.

Table I. The Subjects[a]

Name	Sex	Date of birth	Age[b]	Origin	Weight[b] (kg)
Dzeeta	Female	1970[c]	22	Wild	50
Hermien	Female	1978[c]	15	Wild	48
Hortense	Female	1978[c]	15	Wild	42
Desmond	Male	1971[c]	21	Wild	58
Kidogo	Male	1983	10	Stuttgart	42
Ludwig	Male	1984	9	Des × Dz[d]	52
Redy	Male	1990		Des × Ho	
Unga	Female	1993		? × He	

[a]Source: Leus and Van Puijenbroeck, 1996.
[b]Age and weight at time of study.
[c]Exact month or day of birth not known.
[d]Ludwig was hand reared. The biological relatedness between Ludwig and Dzeeta seems not to be recognized by either of them. There is no expression of a particularly strong affiliation, nor is mating inhibited in this combination as seen in a natural mother–son bond.

Ethogram

We scored the following dyadic behaviors in dyadic contexts; we excluded triadic interactions from analysis.

Aggressive interactions include the following behaviors:

Pestering aggression: a sequence starting as pestering but in which pilo-erection occurred.

Pestering: repeated intentions to approach or to throw things with the intention to withdraw and without pilo-erection or play-face, at times resulting in full approaches or aimed throwing of objects. This behavior is not counted as an aggressive interaction.

Aggression without moving: threat movements being sudden tense hand or body movement in the direction of another individual in nonplayful contexts, as well as hitting, biting, or slapping another individual.

Directed displays: tensed running in the direction of, parallel to or closely passing by another individual, usually while pushing an object. This could end in a collision or other contact aggression. Some interactions were analogous to the directed displays but the tension in the interaction was less obvious, and scored them as quasi aggression. Only in cases where the collisions of the quasi-aggressions were so hard that one individual lost its equilibrium, or when pilo-erection occurred, did we score the interaction as a directed display.

Short charges: tensed running at another individual over a few meters (up to five steps).

Full charges: tensed running at another individual over a longer distance.

All agonism could be accompanied by physical contact: hitting, kicking, biting, scratching. In case a behavior was repeated within 30 sec, we scored only one occurrence.

Aggression not followed by fleeing: the receiver of aggression does not flee or counteraggresses before fleeing.

Aggression followed by fleeing: the receiver of the aggression flees and does not stop fleeing before the aggression ceases.

Submissive interactions:

Yielding: an individual X retreats spatially within 30 seconds of another individual Y approaching within one meter or moving in its direction with its focus of attention X, without any other interaction occurring. X yields to or is displaced by Y.

Fleeing: an individual runs away after a quick aggressive approach or charge without indication of play, and the fleeing lasts at least until the aggression stops.

Peering is the fixed looking into the face of another individual with a calm facial expression for ≥ 2 sec (up to several minutes) from not more than an arm's length distance (adapted from Kano, 1992: 200). In every peering interaction we noted which of the two individuals had approached before peering. We only scored peering during the filmed feeding sessions.

Teeth-baring is silent retraction of the lips resulting in partial or complete exposure of the gums and teeth with the face directed to the partner (de Waal, 1988). We briefly described the contexts in which the behaviors occurred and only scored them during the filmed feeding sessions.

Rank Order Analysis

We carried out hierarchical rank order analysis with the aid of MatMan (De Vries *et al.,* 1993). We evaluated the behavioral variables as an expression of a dominance relationship following Van Hooff and Wensing (1987). Since in all behaviors analyzed there were tied or unknown relationships, we calculated the improved index of linearity (h') rather than Landau's index and tested it by means of a randomization test with the aid of MatMan (Appleby, 1983; De Vries, 1995). To qualify as a strongly linear hierarchy, the index of linearity should be ≥ 0.90 (Martin & Bateson, 1993).

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 behavior occurred (Van Hooff and Wensing, 1987). The total number of times the behavior occurred in the direction of the higher frequency (H) minus the number of times in the less frequent direc-

tion (L) is divided by the total frequency: DC = (H − L)/(H + L). This index varies between 0 (completely bidirectional) and 1 (completely unidirectional). It is equivalent but opposite to the directional inconsistency index (DI) (Noë *et al.,* 1980), which expresses the frequency of the behavior in its least frequent direction, as proportion of the total frequency: DI = L/(H + L). DI varies between 0 (completely unidirectional) and 0.5 (completely bidirectional). To facilitate comparison with other studies we present values of both indices.

As another descriptive measure we counted the number of one-way relationships, i.e. the number of dyads in which the behavior is shown in one direction only, irrespective of the frequency of interaction within the dyads.

To determine the coverage of a behavior, we calculated the proportion of dyads in which at least one act of the relevant behavior occurs. Blank relationships are dyads in which no acts of the relevant behavior occurs in either direction.

We examined the correspondence between the different behaviors with respect to the main direction of performance within the dyads, by counting the number of dyads in which the main direction of the behaviors of pairs were consistent, inconsistent or unknown (dyads in which one of the behaviors did not occur).

For the correlation between rank and individual factors age and weight, we calculated a Kendall τ. The relationship between sex and rank could not be tested statistically since there were only three males and three females.

Measurement of Food Intake

The subjects received four ten-liter buckets of whole, halved and quartered vegetables, fruits and a special cake. In order to obtain a distribution that was fairly monopolisable but still allowed all individuals to get a minimum of food, we distributed the food in two large piles, each about 3 m wide, separated from each other by about 6 m. We counted for each individual the number of scans in which food items of specific categories were obtained, defined as whole food lying within one meter of the subject and from which she or he was feeding. We used following categories: small: one food item; medium: 2–4 items; large: ≥5 items. The subject could also be looking for and gathering food while not yet holding one item manually or pedally, which we defined as foraging. Instances in which the subject had no food and was not foraging, we scored as no food. We filmed the

Table II. Frequency of fleeing from aggression[a]

Fleeing individual	Aggressor triggering the fleeing						
	Dzeeta	Hermien	Desmond	Hortense	Ludwig	Kidogo	Total
Dzeeta	—	0	0	0	0	1	1
Hermien	2	—	1	0	0	0	3
Desmond	30	18	—	0	0	4	52
Hortense	6	0	3	—	5	4	18
Ludwig	19	19	8	267	—	1	314
Kidogo	122	85	84	50	10	—	351
Total	179	122	96	317	15	10	739

[a]Observed during 320 hours. Rate/hour = 739/320 = 2.31.

food pile of each individual in a random order with registered time intervals of 5 min. Later we played back the videotapes and counted food piles.

RESULTS

Evaluation of Behaviors with Regard to Dominance

Fleeing upon aggression (Table II) is a good dominance measure since it has a high and significant linearity index (h′ = .94; P = 0.036) and a high directional consistency (DC = .96) (Table VII). In only one dyad, the behavior did not occur.

The matrix of aggression not followed by fleeing (Table III) has a low and nonsignificant index of linearity (h′ = .51; P = 0.40), a low directional consistency (.54), and almost 67% of the dyads show bidirectional aggression (Table VII). The total proportion of aggression not followed by a submission was highest in the males and lowest in the females. For Desmond,

Table III. Frequency of aggression without fleeing[a]

Aggressor	Recipient of aggression (which does not flee)						
	Dzeeta	Hermien	Desmond	Hortense	Ludwig	Kidogo	Total
Dzeeta	—	7	1	13	0	5	26
Hermien	1	—	0	1	0	2	4
Desmond	9	34	—	3	1	13	60
Hortense	1	2	0	—	9	4	16
Ludwig	0	0	0	5	—	8	13
Kidogo	3	3	23	5	7	—	41
Total	14	46	24	27	17	32	160

[a]Observed during 320 hours. Rate/hour = 160/320 = 0.5.

Table IV. Frequency of yielding[a]

Yielding individual	Individual displacing other individual						
	Dzeeta	Hermien	Desmond	Hortense	Ludwig	Kidogo	Total
Dzeeta	—	4	1	2	9	19	35
Hermien	2	—	0	0	0	1	3
Desmond	2	0	—	2	2	1	7
Hortense	4	1	4	—	2	1	12
Ludwig	4	4	9	17	—	2	36
Kidogo	12	10	11	14	31	—	78
Total	24	19	25	35	44	24	171

[a]Observed during 320 hours. Rate/hour = 171/320 = 0.53.

39% of all his aggressions were ignored; 64% for Ludwig; 80% for Kidogo; compared to 13% for Dzeeta; 3% for Hermien and 5% for Hortense. High dyadic proportions of aggressions without fleeing occurred among Desmond and Hermien, as well as among the two lowest-ranking males and among the lowest- and highest-ranking male. This clearly shows the inadequacy of aggression not followed by fleeing as dominance marker.

The matrix of yielding (Table IV) shows good coverage but a low linearity and directional consistency index (Table VII). This is due to several dyads and especially the dyad Dzeeta-Kidogo: Dzeeta sometimes yielded for Kidogo's approaches whereas the reverse also occured.

Peering (Table V) occurred almost strictly unidirectionally resulting in the highest directional consistency index (.99) (Table VII). Due to low coverage (6 blank relationships), the linearity index was rather low (h' = .74, p = .18). The two younger males rarely performed peering.

Peering occurred seldom immediately upon an aggression (once by Hortense towards Dzeeta). Since the data are all obtained in a feeding context, all peering occurred when at least the actor or receiver foraged

Table V. Frequency of peering[a]

Peering individual	Recipient of peering						
	Dzeeta	Hermien	Desmond	Hortense	Ludwig	Kidogo	Total
Dzeeta	—	0	0	0	0	0	0
Hermien	31	—	0	0	0	0	31
Desmond	2	9	—	1	0	0	12
Hortense	46	40	6	—	0	0	92
Ludwig	2	0	2	0	—	0	4
Kidogo	2	0	0	0	0	—	2
Total	83	49	8	1	0	0	141

[a]Peering observed during 34 hours of feeding sessions. Rate/hour = 141/34 = 4.1.

for food or was close to a food resource. Although this was not systematically scored at that time, we observed peering in the non-feeding contexts during greeting, when another individual had kidnapped an infant or was holding an object, when another individual was grooming a third subject, when an individual was having sex with a third individual. In 100% of the cases it was the subject that peered towards another individual that had approached the individual. Hereupon, peering was often repeated while sitting next to the individual that was feeding, that was holding an object, or that was engaged in an interesting activity.

Teeth-baring (Table VI) was not unidirectional (DC = .75). There were some surprising bidirectional relationships. For instance, once the high-ranking Dzeeta bared her teeth after a counter aggression by Kidogo towards her and then she threw a tantrum. Higher-ranking Hermien bared her teeth on three occasions to Kidogo each time after he had repeatedly pestered her. The coverage was fairly good with only 3 blank relationships. The linearity index is significant (h' = .89, p = .043) (Table VII). Teeth-baring was usually done from a distance of 3 m, with the exception of Hermien, which bared her teeth at Dzeeta while embracing her. The most common context was immediately after aggression received (57%).

Fleeing upon an aggression and peering best fulfil the criteria of dominance markers, whereas aggression, yielding and teeth-baring are inadequate due to the low directional consistency. The adequacy of fleeing and peering is further confirmed by the correspondence of these two behaviors with respect to the main direction of performance within the dyads, presented in Table VIII. We find a high correspondence between fleeing and peering, without inconsistent dyads. With regard to the rank orders, we find that the dyads that could be ranked reliably from the peering interactions rank in a manner that overlaps their agonistic fleeing rank order. The agonistic rank derived from fleeing shows that the alpha or highest position

Table VI. Frequency of teeth-baring[a]

Individual baring teeth at other individual	Recipient of teeth-bearing						
	Dzeeta	Hermien	Desmond	Hortense	Ludwig	Kidogo	Total
Dzeeta	—	1	0	0	0	1	2
Hermien	9	—	1	0	0	3	13
Desmond	1	2	—	0	0	0	3
Hortense	3	1	0	—	1	0	5
Ludwig	7	1	0	1	—	0	9
Kidogo	11	5	6	2	0	—	24
Total	31	10	7	3	1	4	56

[a]Teeth-baring observed during 34 hours of feeding sessions. Rate/hour = 56/34 = 1.65.

Table VII. Linearity, unidirectionality, and coverage of the different behaviors

	Fleeing on aggression	Aggression not followed by fleeing	Yielding	Peering	Teeth-baring
h'[a]	0.94 ($p = 0.036$)	0.51 ($p = 0.40$)	0.49 ($p = 0.46$)	0.74 ($p = 0.18$)	0.89 ($p = 0.043$)
DC[b]	0.96	0.54	0.63	0.99	0.75
DI[c]	0.02	0.23	0.185	0.005	0.125
Blanks[d]	1 6.7%	2 13.3%	1 6.7%	6 40%	3 20.0%
One-way[e]	8 53.3%	3 20%	2 13.3%	8 53.3%	7 46.7%
Two-way[f]	6 40%	10 66.7%	13 80.0%	1 6.7%	5 33.3%

[a] h', improved linear hierarchy index (De Vries, 1995).
[b] DC, directional consistency index (Van Hooff & Wensing, 1987).
[c] DI, Directional inconsistency index (Noë et al., 1980). DI = 0.5–0.5 DC.
[d] Number and percentage of blank relationships or noncoverage.
[e] Number and percentage of one-way relationships.
[f] Number and percentage of two-way relationships.

Table VIII. Correspondence between the behavioral measures (total of 15 dyads)

	Consistent dyads (n)	Inconsistent dyads (n)	Dyads for which one of the two behaviors did not occur or in which the main direction was unknown (n)
Fleeing–peering	8	0	7
Fleeing–teeth-baring	10	0	5[a]
Peering–teeth-baring	9	0	6
Yielding–fleeing	10	3	2
Yielding–peering	3	5	7
Yielding–teeth-baring	2	7	6[a]
Aggression no fleeing[b]–fleeing	5	7	3
Aggression no fleeing–peering	3	5	7
Aggression no fleeing–teeth-baring	6	3	6[a]
Aggression no fleeing–yielding	6	7	2

[a]One dyad for teeth-baring was a tie.
[b]Aggression no fleeing = aggression not followed by fleeing.

in the group is occupied by Dzeeta. The second ranking subject is Hermien. Then comes Desmond, which can outrank Hortense. The difference in dominance between Dzeeta and Hermien as well as between Hermien and Hortense is not expressed in many agonistic interactions. Hermien fleed twice from Dzeeta, and we saw no flight between Hermien and Hortense. The two lowest positions are occupied by the younger males Ludwig and Kidogo.

Peering provides very similar information about the rank order to that of fleeing. Since peering and fleeing correspond strongly with respect to the main direction of performance within the dyads, peering allows us to further clarify the relationships between Dzeeta and Hermien as well as between Hermien and Hortense: Dzeeta ranks higher than Hermien and Hermien ranks higher than Hortense.

Competitive Feeding Ranks

The competitive feeding rank from high to low (based on the number of large feeding piles) is: Dzeeta, Hermien, Hortense, Desmond, Ludwig, Kidogo. On the extreme sides of the competitive hierarchy Kidogo most often had no food, whereas Dzeeta most often had very large piles of food

(Table IX). When large piles are considered, the three females clearly outranked the three males. Additionally, the males most often had no food. The male Desmond nevertheless ranks close to the lowest-ranking female with regard to medium and large piles. He occasionally obtained very large piles ($\geq$10 items), which the two other males never managed. In all scores Desmond outranks the two other males Kidogo and Ludwig, which are close in rank to each other at the bottom of the competitive feeding hierarchy. Among the females, Hermien outranks Hortense in the large and medium categories. The capacity to obtain large piles of food correlates strongly with the agonistic rank (based upon fleeing and peering) (Rs = .94, p = .035) but not completely.

Correlation Between Rank and Individual Factors

The agonistic rank order correlates significantly with age only ($\tau = 0.69$, $P_r = .04$) but not with weight ($\tau = 0.28$, $P_r = 0.31$). With regard to sex and rank, two of the three females dominate all males, and the third female dominates two males. So, there is partial, but no complete female dominance in the study group.

DISCUSSION

Evaluation of Behaviors as Dominance Markers

In order to quantify the dominance relationships in our study group we first evaluated which behavioral measures were most suitable. Fleeing

Table IX. Competitive feeding scores during feeding sessions, expressed in the number of scans (total scans per individual = 60) in which the individuals possessed a food stock (large, medium, or small) or when no feed was obtained[a]

Feeding category[b]	Dzeeta	Hermien	Hortense	Desmond	Ludwig	Kidogo	Rs
Large ($\geq$5)	36	26	21	12	2	1	0.94[c]
Medium (2–4)	16	31	23	24	16	13	0.55
Small (1)	0	1	3	3	19	14	−0.93
No food	1	0	3	13	15	21	−0.89
Forage	7	2	10	8	8	11	−0.84

[a]Observation period: 30 minutes/day on 10 days.
[b]In the feeding categories, we find for each individual the number of scans in which food items of specific categories were obtained, defined as whole food items lying <1m from the subject and from which she or he was feeding.
[c]The p value of the Spearman rank correlation coefficient between the agonistic rank orders and the large feeding category: P = 0.035. Agonistic rank order from high (6) to low (1) = Dzeeta, Hermien, Desmond, Hortense, Ludwig, Kidogo.

upon aggression best fulfils the criteria of agonistic dominance marker. In this behavior, a submissive act follows upon an aggression so that the dominance of the aggressor is clearly acknowledged. Aggression which elicits no sign of submission does not fit a linear rank order. This is in line with Furuichi's observations (1997) that aggressions contradicted the linearity in rank order among the males. Yielding is difficult to interpret since the motivations of an individual retreating from another approaching one does not always appear to be related to dominance, such as for instance in the case of a female retreating due to sexual avoidance which we observed upon approaches by the sexually interested lowest-ranking male to the alpha female. According to Furuichi (1997) ''retreat by females seemed to represent a refusal to associate with approaching females rather than a submissive attitude.''

Further, our results show that teeth-baring does not fulfil the criteria of formal submission signals. It is not unidirectional and it occurred only in a limited number of contexts within and out of the feeding setting. Like de Waal (1988) we found that teeth-baring is shown mostly after receipt of aggression but the direction of the behavior did not strictly follow the agonistic dominance hierarchy. We think the behavior expresses uncertainty or fear, related to a context in which a severe escalation of aggression towards multiple actors is imminent or to an unexpectedly harsh interaction, upsetting high- as well as low-ranking individuals. Therefore, the behavior is not analogous to silent teeth-baring in rhesus macaques (de Waal and Luttrell, 1985), and since it is not consistently unidirectional it cannot serve as a sign of formal dominance.

Conversely, peering has high unidirectionality. Only once peering occurred bidirectionally: when Hortense had monopolized a twig dipped in honey the higher-ranking Desmond peered at her while she licked the treat, and he respected her ownership. Not all dyads perform peering. It appears to require fairly close proximity, which seems difficult to bridge for the two lowest-ranking males. Although we merely scored the behavior during feeding, the observations within this setting and other unpublished data show that peering occured in several contexts, which agrees with Kano's (1992: 141, 191, 200) observations. Accordingly, it may fulfil functions other than mere begging as suggested by de Waal (1988: beg-staring). We interpret peering as signaling a request for peaceful tolerance of proximity, and on occasion it appears to signal submission. The same polyvalence was reported by Jordan (1977), Furuichi (1989) and Idani (1991), who interpreted peering as a formal greeting or appeasement behavior in group reunions, as a begging behavior that seems to induce the peaceful tolerance of proximity and as begging behavior for any kind of friendly interaction (Kano, 1992: 200). Overall, since the behavior shows a strong correspondence with fleeing

and reveals a similar rank order, it can be a very useful datum to determine dominance relationships, especially between females. We need to further examine systematically whether the behavior occurs unidirectionally regardless of the presence or absence of supporters and is in this respect context-free, and to what extent it is ritualized, which is required for a behavior to qualify as a formal signal (de Waal and Luttrell, 1985).

Dominance Hierarchy

The main result is that the dominance relationships were not distributed randomly in our group: we found significant and strong linearity of the dominance hierarchy. Kano (1996) found that the males at Wamba could be ranked linearly and he derived rank orders among bonobo males from aggressive (bite, hit, slap, charge, branch dragging charge, chase, pseudo-charge, threaten) or submissive (flee, avoid, scream, crouch) interactions. Furuichi (1992) and Furuichi and Ihobe (1994) used aggressive (running approach, threat, physical attack, chase) and submissive (retreat, jump aside, flee) behaviors to measure dominance. They divided the males into classes—high-, middle- or low-ranking—based on the frequency of aggressions. There was a linear rank order among the males that was rigid among high-ranking males but less clear among low- and middle-ranking males. In the captive group of Stuttgart, Parish (1994) also found a linear rank order, and she used agonistic interactions and displacements when the bonobos were not at the artificial termite fishing site.

Another main finding is the prominent but nonexclusive female dominance in the study group in the sense that the two highest positions are occupied by females and the two lowest by males. We reviewed published and unpublished evidence on intersexual dominance relationships in captive bonobo colonies worldwide and found consistently the alpha position is occupied by a female, while males tend to occupy middle or low ranks (Table X). Further, it appears that female dominance cannot be attributed to mere male deference but is expressed in female dominance as well as male subordinance behaviors. The males aggressively challenged higher-ranking females, which merely ignored these efforts. In the free-ranging Wamba group ''close dominance status between the sexes'' was reported by Furuichi (1992, 1997) and Kano (1992). Kano (1992: 188) stated that ''the female has about the same rank as the male,'' though in his reply to Stanford's article (1998) he noted that females are ''dominant in the feeding context.'' Furuichi (1992, 1997) concluded that there is a close dominance status between the sexes since the frequencies of interactions in which males were dominant were nearly equal to those in which females were

Table X. Female dominance in captive bonobo groups

Group	Alpha position (years)	Rank order of other individuals (years)	Year	Source
Koln	Female (17)[a]	Female (6)–male (17)–male (9)–female (3)	1993	Personal observation
Stuttgart 1	Female (25)	Female (23)–female (4)–female (14)–male (25)–female (6)	1991–1992	Parish, 1994
Stuttgart 2	Female (27)	Female (25)–female (8)–male (28)–female (6)	1993–1994	Franz, 1998
Stuttgart 3	Female (28)	Female (26)–female (8)–male (14)–male (29)–female (7)	1994	Franz, 1998
Leipzig	Female (17)	male (17)–male (21)	1999	De Ridder, personal communication
Apenheul §	Female (13)	Female (8)–female (12)–male (16)–female (10)–male (18)–female (6)–male (8)–male (13)	1998	De Ridder, Stevens, personal communication
Twycross	Female (21)	Female (9)–male (18)–male (8)	1998	De Ridder, personal communication
Wuppertal	Female (29)	Female (15)–male (15)–male (32)	1995	Franz, 1998
Planckendael	Female (22)	Female (15)–female (23)–female (15)–male (9)–male (10)	1992–1993	This study

[a]Ages derived from Leus and Van Puijenbroeck, 1996.
[b]Preliminary rank order based on fleeing on aggression.

dominant. In our study group not all adult females dominate all adult males: one male could outrank a female agonistically and often aggressively challenged one of the females that dominated him. These results were confirmed in a dyadic experimental context in which he was dominated by one and dominated the other female (Vervaecke *et al.,* 1999). Generally however, aggression by the males is more frequently ignored by the other individuals than female aggression is. An important difference between studies on captive versus free-ranging bonobos is the absence of mature mother-son bonds in most captive groups. In free-ranging bonobos (Furuichi, 1997) the ranks of sons are said to be dependent on their mothers' ranks. A mature son of a high-ranking female may acquire high status as his mother grows older, but he will drop in rank in case his mother dies when he is still a young adult. An old adult male may keep his acquired rank independently of his mother's presence (Furuichi, 1992; Furuichi and Ihobe, 1994; Furuichi, 1989; Kano, 1992). The kin factor may render the intersexual dominance relationships in free-ranging groups more difficult to disentangle.

We found that the agonistic dominance relationships are not equally clearly expressed in all dyads. Aggression followed by fleeing was most frequently expressed in intersexual interactions by the males and less in female intrasexual interactions. In free-ranging bonobos, agonistic ranks are not so frequently expressed in conflicts among females versus among males (Furuichi, 1992, 1997; Furuichi and Ihobe, 1994), similar to our group. For the Wamba females, agonistic interactions were too infrequent to determine a linear rank order, which does not necessarily imply that dominance relationships are absent. We found relatively few agonistic interactions among the females. However, in these combinations there was a clear unidirectional peering relationship, and the ranks obtained from teethbaring were also similar to the agonistic fleeing ranks. In an experimental competitive context, the dyadic competitive rank between the females was similar to their agonistic rank in the group (Vervaecke *et al.,* 1999). Thus the rank order between the females is the same when derived from the (scarce) agonistic interactions, peering, competitive feeding abilities in the entire group as well as experimental dyadic feeding priorities. Since all these behaviors indicate a similar direction of the relationship and because the observation period has been sufficiently long and the quantitative criteria of dominance behaviors are fulfilled, i.e. unidirectionality, we conclude that a rank order among the females is present and behaviorally significant, in spite of the infrequent expression of the dominance relationships. In comparison, among female chimpanzees, dominance relationships are vague and not clear-cut and expressed in few interactions (Goodall, 1986; Nishida, 1979; captivity: de Waal, 1982) so that often only broad rank classes

(high, middle, low) instead of ordinal ranks are assigned to them. Yet, in the wild their rank class is significantly related to their lifetime reproductive output (Pusey *et al.,* 1997).

Competitive Abilities

As in most other reports on free-living and captive bonobos, female feeding priority was the rule in our study group (Wamba: Kano, 1992; Wamba: Furuichi, 1989, 1997; Stuttgart: Parish, 1994, Lomako: Hohmann and Fruth; 1993). At Wamba, female feeding priority is reported by Kano, (1992) and Furuichi, (1989, 1997). Whereas young or newly immigrated females may be chased from food resources by the males, adult females could usually displace adult males (Furuichi, 1989). However, according to Kuroda (1984) the Wamba males can obtain highly-prized food resources. In Lomako, Hohmann and Fruth (1993) observed five times that females controlled access to captured duikers. Parish (1994) described the competitive relationships between an adult male and three adult females as female dominance based on feeding priorities at a site where the captive subjects could fish for sweets.

We found that one female that agonistically ranked lower than the male, could frequently get bigger food piles than his. This was due to her strong affiliation with the highest-ranking females, which consistently allowed her to share the same food piles. Thus, the competitive abilities are partly uncoupled from the agonistic ranks due to the social tolerance of the higher-ranking females. Parish (1994 & 1996) noted a clear expression of social tolerance in cofeeding behavior, which was most frequent in high-ranking individuals, all of which were females (Parish, 1994, 1996). Cofeeding occurs among bonobos in San Diego (de Waal, 1992). At Lomako (Zaire) Hohmann and Fruth (1993, 1996) observed meat-sharing by females, which generally share food more frequently than males do. Kano (1980), Kuroda (1984) and White (1992) observed frequent food sharing between males and females and among females.

Agonistic Rank and Individual Factors

In our study group, age and rank correlate significantly. For females, increasing age and adulthood of sons correlates to a higher and more stable social rank (Furuichi, 1989, 1997). Parish (1996) and Jordan (1977) also found age-graded ranks for captive female bonobos. In chimpanzee females, rank also correlates with age (de Waal, 1982; Goodall, 1986) and residence

status (Nishida, 1989). Although bonobo males are physically stronger than females because of their higher body weights (Jungers and Susman, 1984; Parish, 1996) they do not necessarily dominate the females. Strength is clearly not an important factor in determining the hierarchy. Parish (1996) suggested that female dominance may be acquired by intrasexual coalitions (Vervaecke *et al.,* in prep a). In order to determine dyadic rank orders, we only quantified dyadic agonistic interactions. When a single female aggresses a male he might not flee or may initially quickly display towards her before fleeing, which seldom occurs in coalitions.

Dominance Styles

Our subjects exhibit different dominance styles, which are manifest as differential expressions of their social tolerance. Other behavioral aspects we did not quantify systematically, e.g. occurrence of respect for possessions, pestering, the direction of contra support, quasi-aggression, support these differences in dominance styles. Among the females, there was frequent food sharing, relatively little aggression, and a frequent occurrence of peering: the request for the tolerance of proximity. Quasiaggression or display, in which the tension was not clearly expressed, occurred mostly among the females, among which the dominance style ranged from strict (Dzeeta) to mellow (Hermien) in the dominant females and from obedient (towards Dzeeta) to trusting (towards Hermien) in the subordinate females. When Dzeeta aggressed Hortense, the latter occasionally (n = 3) showed very strong signs of distress, expressed in temper tantrums. Between the sexes, the dominance style of the dominant females was despotic. The subordinate males react at times terrified and at other times challenging. It seems they react less terrified during attacks by single females compared to attacks by several females (Vervaecke *et al.,* in prep a). Especially, Desmond frequently challenged Hermien aggressively. Kidogo showed a similar challenging quality in his relationship towards Hortense and Dzeeta, yet this was less clearly expressed. Sometimes when Desmond aggressed the dominant female Dzeeta, it elicited temper tantrums by Dzeeta (n = 2) and subsequent female coalitions against him. Pestering, which can be considered a mild form of challenging, occurred predominantly from male to female. There is generally little expression of social tolerance by the females towards the males. Between the dominant male and subordinate female, Hortense was trusting, whereas Desmond showed a mellow dominance style, expressed in his respect for her possessions. The lowest-ranking male frequently challenged the dominant male, which subsequently confirmed his status by aggressing him. Pestering was performed by Kidogo

to Ludwig, especially toward Desmond. There is no expression of social tolerance in food sharing among the males, and they seldom request proximity by peering.

Predictive Value of Rank

With regard to the general predictive value of rank, agonistic rank in the study group has a strong and significant predictive value with regard to the distribution of grooming and support behavior (Vervaecke *et al.,* 1996 & in prep b). Kano (1996) found that high-ranking males copulated more frequently, though Furuichi (1997) suggested that they possibly do so because they are allowed in the central part of a mixed party. In another free-ranging bonobo group Fruth and Hohmann (1997) found that 60% of the infants were sired by the two highest-ranking males. Yet, overall very few rank-related processes have been described for bonobos.

In conclusion, our study shows clear potential for a linear social dominance hierarchy in bonobos, with prominent but nonexclusive female dominance.

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