

RESEARCH ARTICLE

Peering Is Not a Formal Indicator of Subordination in Bonobos (*Pan paniscus*)

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It has been suggested that peering behavior in bonobos is a formal signal acknowledging social dominance status. We investigated whether peering meets the published criteria for a formal signal of subordination in five captive groups of bonobos. The degree of linearity in the set of peering relationships was significantly high in all study groups, and a linear rank order was found. However, unidirectionality was low, and there was little correspondence between the peering order and the agonistic dominance rank. Therefore, peering does not satisfy the criteria of a formal subordination indicator. We also studied the relation between peering and agonistic dominance rank, age, and sex. Animals directed peering significantly more often at high-ranking animals in four of the groups. We suggest that peering is indirectly related to dominance rank by the resource-holding potential of individuals. In contexts where dominant individuals can monopolize resources, peerers may direct their attention at those high-ranking animals. When resources are distributed more evenly, high-ranking animals may peer down the hierarchy. We speculate on the reasons why a formal dominance or subordination signal appears to be absent in bonobos. *Am. J. Primatol.* 65:255–267, 2005. © 2005 Wiley-Liss, Inc.

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INTRODUCTION

The concept of formal dominance was introduced by de Waal (1986) after he found that certain species of primates show ritualized displays that are

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consistently exhibited by one member of a dyad and not by others. These signals, which include pant-grunting in chimpanzees [Bygott, 1979; de Waal, 1982; Nishida, 1983; Noë et al., 1980] and the silent teeth-baring display of longtailed [de Waal, 1977] and rhesus macaques [de Waal & Luttrell, 1985], are shown unidirectionally from subordinates to dominants, irrespective of social context. This contrasts with agonistic dominance hierarchies, which are based on behaviors such as aggression, yielding, or fleeing. These behaviors are all influenced by the social context, such as the presence of coalition partners. Therefore, de Waal [1986] proposed a double-layered hierarchy consisting of an agonistic hierarchy that is based on current interactions, and a formal dominance hierarchy based on ritualized signals that endorse long-term relationships [Preuschoft, 1999]. Formal dominance indicators are exchanged highly unidirectionally, correspond with the agonistic dominance hierarchy, and are consistent across contexts [de Waal & Luttrell, 1985]. It was later suggested [Preuschoft, 1999; Preuschoft & van Schaik, 2000] that “formal subordination indicators” would be a more appropriate term for the above-mentioned signals because these signals are actually emitted by subordinates toward dominants. “Formal indicators of dominance” are directed from dominants toward subordinates (e.g., formal biting in stump-tailed macaques [Demaria & Thierry, 1990]).

Apart from providing dominance measures that can be used to construct dominance hierarchies independently of social context, and apart from their implications for a double-layered dominance hierarchy, formal indicators of dominance and subordination can provide insights into the comparison of species’ dominance styles [de Waal, 1989b]. Preuschoft and van Schaik [2000] found that indicators of dominance or subordination are found in macaque species with strict dominance hierarchies, such as rhesus and long-tailed macaques. Species with relaxed dominance styles, such as lion-tailed macaques, do not show such formal indicators.

Although it is potentially very useful, the concept of formal dominance has received only marginal attention since its original description. Discussion has been mainly restricted to the issue of whether primates need certain cognitive capacities to recognize formal dominance [Maestriperi, 1996, 1999; Preuschoft, 1999]. Not much is known about the occurrence of formal indicators of dominance and subordination in primates other than macaques and chimpanzees, or about the relation between power asymmetries and the occurrence of such signals.

Bonobos constitute an interesting case in the study of formal indicators of dominance or subordination. While pant-grunting in the bonobo’s sister species, the common chimpanzee, is an example of a formal indicator of subordination, bonobos do not use pant-grunting as a greeting ritual [Furuichi, 1997; Furuichi & Ihobe, 1994]. Therefore, dominance hierarchies are typically studied at the agonistic level [e.g., Furuichi, 1997; Vervaecke et al., 2000] (Stevens et al., 2001). The lack of pant-grunting rituals in bonobos is also sometimes used to emphasize this species’ relaxed dominance style, which is supposedly less hierarchical than that of the common chimpanzee [de Waal, 1997]. Thus, at first sight the bonobo-chimpanzee differences in dominance relations, and the lack of a formal indicator of dominance in bonobos appear to follow the pattern observed in macaque species. However, we found that captive bonobos show asymmetrical and hierarchical relationships (Stevens et al., 2001). We would expect therefore that formal dominance relationships communicated via formal subordination signals are present in bonobos as well.

Peering behavior was recently linked to dominance in bonobos. Peering is a highly ritualized behavior in which the actor stares at the receiver's face from a very close distance (up to a few centimeters) [Furuichi, 1989; Idani, 1995; Kano, 1992, 1996]. Johnson et al. [1999] suggested that peering functions as a "signal acknowledging female status." In agreement with results from field studies [Furuichi, 1989], Johnson et al. [1999] found that peering was mostly directed at older females. These females were thought to hold a high status because they were more often followed than other, supposedly lower-ranking animals. Vervaecke et al. [2000] examined peering during the feeding context as a possible sign of formal subordination in a captive bonobo group. They found that peering corresponded well with the agonistic hierarchy, and concluded that peering could be used as an additional formal dominance measure in bonobos to further clarify relationships.

In this study we look at the relation between peering and agonistic dominance in bonobos in more detail, and evaluate the suitability of peering as a formal subordination signal. We examine whether peering fulfills the published criteria of a formal signal of subordination [de Waal & Luttrell, 1985]. Thus we analyze 1) the linearity of the peering order, 2) the unidirectionality of peering within the dyads, 3) the correspondence of ranks based on peering and agonistic behavior, and 4) the consistency of a peering order across contexts. We also study the distribution of peering in the study groups to determine whether peering is indeed more directed at older, high-ranking females (Johnson et al., 1999), by examining the relation between peering and the variables, age, rank, and sex.

MATERIALS AND METHODS

Study Groups and Data Collection

A total of 15 different male and 14 different female bonobos in five different captive groups were studied for a total of 1,882 hr. Only adult and adolescent animals (≥ 7 years old) were considered in this study. In Wuppertal Zoo (Germany) a group of four males and two females was studied for 203 hr in August–September 1999. The study group at Apenheul Primate Park (The Netherlands) contained three males and five females, and was studied for 493 hr from February to April 2001. The group at Twycross Zoo (United Kingdom) contained three males and three females, and was studied for 490 hr in November–December 2001 and February 2002. The study group at Planckendael was observed during two periods: November–December 1999 (193 hr, three males and four females) and November 2002–February 2003 (505 hr, three males and three females). The group composition changed considerably between the two periods, and thus they were analyzed separately. More details regarding group composition at Wuppertal, Apenheul, and Twycross can be found in Vervaecke et al. [2003]. Details regarding the Planckendael group composition and housing can be found in Stevens et al. [2003].

All of the observations were made by the first author on a daily basis. They were conducted continuously throughout the day until dusk, when the bonobos started building their nest and social interactions generally ceased. When the animals were separated for cleaning or feeding, no observations were made. In this way, 6–8 hr of data were gathered per day.

Peering was defined as follows: "the actor stares at the receiver's face from very close distance, up to a few centimeters" [Idani, 1995; Kano, 1992, p. 200]. Since the number of subjects was small, visibility was high, and peering occurred relatively infrequently, we scored peering between adult group members using

all-occurrences sampling [Altmann, 1974]. In each case the actor (the peerer) and the receiver of peering (the peeree) were scored. When several actors peered at the same subject, this was broken down into dyadic interactions. In three of the study groups (Apenheul, Twycross, and Planckendael 2) the context of peering (defined as the activity of the peeree) was recorded as well. Contexts were defined as follows: 1) feeding: the peeree manipulates food with mouth or hands; 2) grooming: the peeree grooms a third individual; 3) self-grooming: the peeree grooms its own body; 4) coprophagy: the peeree manipulates feces with its hands or mouth; 5) manipulating object: the peeree manipulates an inedible object (e.g., cardboard box, plastic bottle, or piece of cloth); 6) other: the peeree performs a behavior that is not included in the above categories.

Data Analysis

Unidirectionality and linearity of peering behavior.

We used MatMan (version 1.1; Noldus Information Technology, Wageningen, The Netherlands), a software program designed to analyze sociometric matrices [de Vries et al., 1993] and calculate the degree of linearity h' in the matrix of dyadic peering relationships. The index h' , which is derived from Landau's index of linearity but is corrected for the number of unknown relationships, ranges between 0 (nonlinear) and 1 (completely linear) [de Vries, 1995; Landau, 1951]. We used a two-step randomization test to assess the statistical significance of h' [de Vries, 1995]. When h' turned out to be significant at the 0.05 level, we used the I&SI method to find the rank order that was most consistent with a linear hierarchy. The inconsistencies and strength of inconsistencies (I&SI) method reorganizes the peering matrix such that the number and total strength of the inconsistencies are minimized [de Vries, 1998].

As an additional descriptive measure for describing dominance relations, the directional consistency index $(DCI) = (H - L) / (H + L)$ is also calculated, which gives 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 direction (L) is divided by the total frequency [van Hooff & Wensing, 1987].

Correspondence with agonistic rank order.

We compared the rank order based on "peering" with the agonistic dominance hierarchy (Stevens et al., unpublished results), which was based on "fleeing upon aggression" as an operational measure [Vervaecke et al., 2000]. The resulting hierarchy was analyzed with MatMan in the same way as described above for the rank order based on peering. We then compared the number of consistent dyads for the two matrices. When the main direction of peering within a dyad corresponded with the main direction of "fleeing upon aggression" within that same dyad, this was called a consistent dyad. If main directions differed, the dyad was considered inconsistent. Whenever one of the behaviors did not occur within a dyad, this was considered an unknown dyad. We also performed Spearman rank correlations to compare the rank orders based on these two behavioral measures as an additional measure of correspondence between the two types of hierarchies.

Consistency of peering in different contexts.

We analyzed consistency across contexts in a similar way, by counting the number of consistent, inconsistent, and unknown dyads. We were unable to make rowwise matrix correlations between contexts because some contexts had a low frequency of peering.

Distribution of peering.

Data on peering were organized in sociometric matrices. First we studied the relative effect of the variables rank, age, and sex on peering behavior, with the dyad as an observational unit of analysis, using rowwise matrix correlations [de Vries, 1993; Hemelrijk, 1990]. These correlations accounted for individual variations in the tendency to perform or receive the behavior as expressed in the differences in row totals. We calculated Kendall's form of rowwise matrix correlations (τ_{rw}) and probability values, using MatMan [de Vries et al., 1993] and performing 20,000 random permutations [Jackson & Somers, 1989]. We performed analyses on the original peering matrix (with actors in rows, and receivers in columns) to determine which animals received peering. We used the transposed peering matrix (with receivers in rows, and actors in columns) to determine which animals performed peering. We then performed partial rowwise matrix correlations [de Vries, 1993; Hemelrijk, 1990] for both the peering matrix and the transposed peering matrix to tease apart the relative effect of each variable on peering behavior. By controlling for one of the three variables (matrix Z), we were able to clarify the relation between peering (matrix X) and the remaining variable (matrix Y).

All tests were two-tailed, with the critical significance level set at 0.05.

RESULTS**Properties of Peering Behavior: Linearity and Directional Consistency**

Peering occurred very frequently in all study groups (Table I). All peering relations were known in three of the study groups (Wuppertal, Twycross, and Planckendael 2). Peering was not observed in 4% of the dyads in Apenheul, or in 10% of the dyads in Planckendael 1. A significant (and in some groups perfect) linear rank order could be constructed based on peering behavior. The directional consistency index was low for some groups, and varied from 0.46 at Apenheul to 0.96 at Planckendael 1. In all but one group, peering was exchanged bidirectionally for more than 50% of the dyads. Only in Planckendael 1 was there a large proportion (71%) of one-way dyads.

TABLE I. Linearity and Unidirectionality of Rank Orders Based on Peering

| Group | Wuppertal | Apenheul | Twycross | Planckendael 1 | Planckendael 2 |
|----------------------------------|-----------|----------|----------|----------------|----------------|
| Number of subjects | 6 | 8 | 6 | 7 | 6 |
| Number of peering interactions | 647 | 1,638 | 1,045 | 269 | 565 |
| h' peer ^a | 1.00 | 0.90 | 1.00 | 0.95 | 1.00 |
| $p(h')$ | 0.02 | 0.001 | 0.02 | 0.01 | 0.02 |
| DCI ^b | 0.82 | 0.46 | 0.72 | 0.96 | 0.75 |
| % unknown relations ^c | 0 | 4 | 0 | 10 | 0 |
| % one-way relations ^d | 47 | 14 | 33 | 71 | 33 |
| % two-way relations ^e | 53 | 82 | 67 | 19 | 67 |
| % tied relations | 0 | 0 | 0 | 0 | 0 |

^a h' : linearity index, corrected for unknown or tied relationships [de Vries, 1995].

^bDCI: directional consistency index [van Hooff & Wensing, 1987].

^c% of unknown relation: percentage of total dyads in which peering was not observed.

^d% one-way relations: percentage of total dyads in which peering was observed only in one direction.

^e% two-way relations: percentage of total dyads in which peering was observed in both directions.

Correspondence With Agonistic Dominance Hierarchy

Consistency between the peering rank order and the agonistic dominance hierarchy differed considerably between the groups. The percentage of consistent dyads was very low in Apenheul (29%), moderate in Twycross (53%), and higher than 60% in Wuppertal (67%) and Planckendael 1 (62%) and 2 (80%). Ranks based on both behaviors were only significantly correlated in Planckendael 1 ($r_s=0.78$, $P=0.03$) and Planckendael 2 ($r_s=0.83$, $P=0.04$), but not the other groups (Wuppertal: $r_s=0.71$, $P=0.11$; Apenheul: $r_s=-0.29$, $P=0.29$; Twycross: $r_s=0.66$, $P=0.16$).

Contexts of Peering

We discerned five contexts in which peering occurred: feeding, allogrooming, self-grooming, coprophagy, and manipulating an object. In all groups, peering was mostly associated with feeding (Apenheul: 78%; Twycross 46%; Planckendael 2: 59%). Allogrooming also received considerable attention from the peerers (Apenheul 8%, Twycross 14%, Planckendael 2: 12%). Self-grooming evoked less interest (Apenheul 4%, Twycross 9%, Planckendael 2: 8%). Coprophagy was rare at Apenheul (<2%), but it occurred regularly at Twycross (18%) and Planckendael 2 (19%), and evoked interest from peerers in those groups.

Because of the relatively low frequency of peering in some contexts, it was difficult to make a statistical comparison across contexts, and the results must be interpreted cautiously (Table II). At Apenheul and Planckendael in particular there were many dyads with unknown main directions in several contexts. Hence, consistency across contexts was very low in those two groups. At Twycross, on the other hand, there was a very high correspondence in the direction of peering in different contexts. In that group the direction of peering was more consistent across different contexts.

Distribution of Peering and Rank, Age, and Sex

Relations between agonistic rank, age, and sex.

The matrices of rank, age, and sex were not consistently correlated in all of the study groups. Rank was only correlated with age at Twycross ($\tau_{rw}=0.83$, $P=0.03$) but not in the other groups (Wuppertal: $\tau_{rw}=0.28$, $P=0.58$; Apenheul: $\tau_{rw}=-0.08$, $P=0.90$; Planckendael 1: $\tau_{rw}=0.39$, $P=0.30$; Planckendael 2: $\tau_{rw}=0.55$, $P=0.19$). There was a trend for females to occupy higher-ranking positions compared to males at Apenheul ($\tau_{rw}=0.63$, $P=0.07$) and Planckendael 1 ($\tau_{rw}=0.76$, $P=0.06$). Age and sex were not correlated in any of the study groups (Wuppertal: $\tau_{rw}=-0.09$, $P=0.94$; Apenheul $\tau_{rw}=-0.32$, $P=0.46$; Twycross: $\tau_{rw}=0.36$, $P=0.50$; Planckendael 1: $\tau_{rw}=0.26$, $P=0.64$; Planckendael 2: $\tau_{rw}=0.27$, $P=0.61$).

Peering matrix.

The distribution of peering differed between the five groups studied (Table III). At Wuppertal there was no correlation between peering and the variables, rank, age or sex. At Twycross and Planckendael 1 and 2, animals directed significantly more peering at higher-ranking animals, and there was a similar trend in the Apenheul group. In the latter group, contrary to our expectations, the animals also received more peering from high-ranking animals (see below).

Peering was directed more at older individuals at Twycross, and there was a similar trend at Planckendael 2. There was no effect of the sex factor on peering

TABLE II. Consistency of Peering Across Contexts*

| | Apenheul | | | Twycross | | | Planckendael 2 | | |
|-------------------|----------------|--------------|-----------|----------------|--------------|-----------|----------------|--------------|-----------|
| | % inconsistent | % consistent | % unknown | % inconsistent | % consistent | % unknown | % inconsistent | % consistent | % unknown |
| Manipulate object | | | | | | | | | |
| Feeding | 4 | 50 | 46 | 7 | 73 | 20 | 13 | 0 | 87 |
| Grooming | 11 | 32 | 57 | 7 | 73 | 20 | 7 | 7 | 86 |
| Selfgrooming | 7 | 32 | 61 | 0 | 73 | 27 | 7 | 7 | 86 |
| Coprophagia | 14 | 7 | 79 | 7 | 73 | 20 | 7 | 7 | 86 |
| Feeding | 28 | 36 | 36 | 20 | 67 | 13 | 20 | 40 | 40 |
| Grooming | 18 | 46 | 36 | 7 | 67 | 26 | 27 | 40 | 33 |
| Selfgrooming | 18 | 7 | 75 | 0 | 87 | 13 | 20 | 67 | 13 |
| Coprophagia | | | | | | | | | |
| Grooming | 14 | 32 | 54 | 7 | 67 | 26 | 7 | 33 | 60 |
| Selfgrooming | 7 | 11 | 82 | 20 | 67 | 13 | 7 | 53 | 40 |
| Coprophagia | | | | | | | | | |
| Selfgrooming | 11 | 7 | 82 | 7 | 73 | 20 | 13 | 54 | 33 |

*Behavioral categories: see Materials and Methods. % inconsistent: percentage of total dyads in which the direction of peering in context A was opposite to the direction of peering in context B. % consistent: percentage of total dyads in which the main direction of peering in context A corresponds with the direction of peering in context B. % unknown: percentage of total dyads in which peering was not observed in context A and/or context B.

in any of the groups; thus, peering was not significantly more directed at females than at males.

Although rank, age, and sex were not consistently correlated in the study groups, partial matrix correlations revealed interesting effects (Table IV).

When controlled for the variable "age," the correlation between peering and rank was no longer significant for Twycross and Planckendael 2. Similarly, the correlation between age and peering dropped when rank was controlled for. The variable "sex" had less influence on the correlation between peering and age. At Planckendael 1 the correlation between peering and rank dropped when sex was controlled for. Similarly, the trend at Apenheul vanished when sex was controlled for. In these two groups, the fact that peering was mainly directed at high-ranking animals was due to a correlation between rank and sex.

Transposed peering matrix.

The effects of rank, age, and sex on the transposed peering matrix were less robust in most groups (Table V). Contrary to our expectations, the transposed peering matrix was correlated with the variables rank and sex at Apenheul. Hence, in that group the animals received more peering from high-ranking animals than from low-ranking animals, and received more peering from females than from males. At Planckendael 2 there was a negative correlation between the

TABLE III. Kendall's Tau Correlations Between the Peering Matrix, Representing to Which Individuals Peering Is Directed (Matrix X) and the Variables Rank, Age, and Sex (Matrix Y)

| Matrix X | Matrix Y | Wupperta (n=6) | Apenheul (n=8) | Twycross (n=6) | Planckendael 1 (n=7) | Planckendael 2 (n=6) |
|----------|----------|-------------------|-------------------|-------------------|-------------------------|-------------------------|
| Peering | Rank | 0.37 | 0.32 ^a | 0.62 ^b | 0.68 ^b | 0.46 ^b |
| Peering | Age | 0.17 | 0.01 | 0.68 ^b | 0.48 | 0.36 ^b |
| Peering | Sex | 0.51 | 0.34 | 0.36 | 0.53 | 0.18 |

^a0.05 < *P* < 0.10.

^b*P* < 0.05.

n, number of subjects per group.

TABLE IV. Kendall's Tau Partial Correlations Between the Peering Matrix (Matrix X) and the Variables Rank, Age, and Sex (Matrix Y), Controlled for the Variable in Matrix Z

| Matrix X | Matrix Y | Matrix Z | Wuppertal (n=6) | Apenheul (n=8) | Twycross (n=6) | Planckendael 1 (n=7) | Planckendael 2 (n=6) |
|----------|----------|----------|--------------------|-------------------|-------------------|-------------------------|-------------------------|
| Peering | Rank | Age | 0.34 | 0.32 ^a | 0.14 | 0.61 ^b | 0.33 |
| | Rank | Sex | 0.23 | 0.14 | 0.55 ^a | 0.50 ^a | 0.43 ^b |
| | Age | Rank | 0.07 | 0.03 | 0.37 | 0.32 | 0.15 |
| | Age | Sex | 0.25 | 0.13 | 0.63 | 0.41 | 0.33 |
| Sex | Rank | 0.43 | 0.19 | 0.17 | 0.03 | -0.02 | |
| | Sex | Age | 0.54 ^b | 0.36 ^a | 0.17 | 0.48 | 0.09 |

n, number of study animals per group.

^a0.05 < *P* < 0.10.

^b*P* < 0.05.

TABLE V. Kendall's Tau Correlations Between the Transposed Peering Matrix, Representing From Which Individuals Peering Is Received (Matrix X) and the Variables Rank, Age, and Sex (Matrix Y)

| Matrix X | Matrix Y | Wuppertal (n=6) | Apenheul (n=8) | Twycross (n=6) | Planckendael 1 (n=7) | Planckendael 2 (n=6) |
|-----------------------|----------|--------------------|-------------------|-------------------|-------------------------|-------------------------|
| Transposed peering | Rank | -0.45 ^a | 0.53 ^b | -0.22 | -0.26 | -0.35 |
| | Age | -0.41 | -0.15 | -0.44 | -0.46 | -0.64 ^b |
| | Sex | -0.07 | 0.69 ^b | 0.26 | -0.11 | -0.24 |

^a0.05 < P < 0.10.

^bP < 0.05.

n, number of subjects per group.

TABLE VI. Kendall's Tau Partial Correlations Between the Transposed Peering (Matrix X) and Variables Age, Rank, and Sex (Matrix Y) Controlled for the Variable in Matrix Z

| Matrix X | Matrix Y | Matrix Z | Wuppertal (n=6) | Apenheul (n=8) | Twycross (n=6) | Planckendael 1 (n=7) | Planckendael 2 (n=6) |
|-----------------------|----------|----------|--------------------|-------------------|--------------------|-------------------------|-------------------------|
| Transposed peering | Rank | Age | -0.38 | 0.53 ^a | 0.29 | -0.10 | 0.00 |
| | Rank | Sex | -0.46 ^b | 0.17 | -0.39 | -0.27 | -0.29 |
| | Age | Rank | -0.33 | -0.13 | -0.60 ^b | -0.40 | -0.58 ^b |
| | Age | Sex | -0.42 | 0.10 | -0.60 ^b | -0.45 | -0.62 ^a |
| | Sex | Rank | 0.11 | 0.54 ^a | -0.41 | -0.14 | -0.10 |
| | Sex | Age | -0.12 | 0.28 ^b | 0.50 | 0.01 | -0.09 |

^aP < 0.05.

^b<0.05 < P < 0.10.

n, number of subjects per group.

transposed peering matrix and the variable age, indicating that the animals received less peering from older animals than from younger animals.

Partial matrix correlations (Table VI) revealed that the effect of rank on the transposed peering matrix at Apenheul dropped when sex was controlled for. However, when age was partialled out, the correlation between the transposed peering matrix and sex remained significant, even though the correlation coefficient dropped. This indicates that high-ranking animals perform more peering than low-ranking ones independently of the age of the animals. Similarly, the relation between the transposed peering matrix and the variable sex dropped when we controlled for the age variable, but remained significant when we controlled for the rank variable. The effect of the age variable on the transposed peering matrix at Planckendael 2 lasted, even when we controlled for the rank and sex variables.

DISCUSSION

We found that although the linearity of the peering rank order was significant and high ($h' > 0.90$ in all groups), the criterion of unidirectionality in peering behavior was not met in four of the five groups. Moreover, the direction

of peering seemed to be context-dependent. Clearly, in most groups, peering does not fulfill de Waal and Luttrell's [1985] criteria of a formal indicator of subordination. Preuschoft [1999] provided additional criteria, but these apply only to behaviors that are exchanged unidirectionally, and therefore were not further investigated.

In contrast to earlier findings, we found no evidence that peering was directed more often at older animals, or more at females compared to males. Peering was directed at dominant individuals in most study groups. However, after we controlled for sex or age, rank only correlated significantly with peering in one group, and almost significantly in another group. Thus, we suggest that peering should not be used in determining dominance relations in bonobos. While linear hierarchies can be found in captivity [Vervaecke et al., 2000] (Stevens et al., unpublished results), this requires considerable sampling effort and may be more difficult in the wild, especially in species with fission-fusion societies. Indeed, studies on wild bonobos have indicated that dominance relations between low-ranking individuals are often unclear [Furuichi, 1989, 1997; Kano, 1992]. As a consequence, individuals are often assigned a group rank, rather than ordinal ranks [Furuichi, 1997; Kano, 1992].

If peering is not a formal indicator of subordination, questions arise as to what its function is, and why it is related to dominance in at least some contexts. Various researchers have offered hypotheses. It was first described by Kano [1980] as a begging gesture. However, peering is rarely followed by an actual food transfer [Furuichi, 1989; Kuroda, 1984] (unpublished data), and other explanations have been put forward. In cases in which social interaction does occur after peering, the behavior is considered to be "a solicitation for initiating affiliative interactions" [Idani, 1995]. But peering is not followed by any social interaction in most cases, and the peerer or peeree usually leave after the behavior is performed [Furuichi, 1989; Idani, 1995, p 377], so its function is less clear in such cases. Furuichi [1989] proposed that one important function of peering may be self-presentation by young females to senior females. Similarly, Kano [1992] noted that peering may be a kind of precopulatory behavior, but admitted that it rarely occurs in sexual contexts. Vervaecke et al. [2000, p 60] offered a more general concept of peering as a "request for social tolerance." Thus far, the activity of the recipient of peering just before an animal starts to peer has received no systematic attention. We found that bonobos peer most often at individuals that have an interesting material resource (e.g., food or objects) or behavioral commodity (e.g., grooming). Rather than signaling subordination, peering seems to indicate interest in these resources or commodities, perhaps without the intention of obtaining them. For example, Johnson et al. [1999] reported a change in peering direction between two female bonobos after one of them gave birth, which may simply indicate that the dominant female of the two was showing interest in the infant involved.

The relation between peering and interest in resources or commodities may also explain the relation between peering and dominance, and the inconsistencies we found in this study. Usually, but not always, dominant individuals have a higher resource-holding potential. In such cases, subordinates may approach dominants and peer at them. However, one can imagine that when food is dispersed, young and quick subordinates will be better at obtaining it than large and slow dominants. These dominants could then later try to take away these resources from the subordinates, but then other factors, such as "respect for possession" [Kummer et al., 1974] may come into play. The fact

that peering order is more closely associated with agonistic dominance in some groups (Planckendael 1 and 2), and far less in others, may be explained by the different feeding protocols used for these groups. At Planckendael 1 and 2, the bonobos were fed twice a day, in the morning and evening. In those groups, competition for access to food was intense (an earlier study showed that dominant females were able to monopolize food, or at least the preferred food items [Vervaecke et al., 2000]). At Apenheul, the bonobos were fed up to five times per day, and food was often handed out by the keepers to the animals individually. In this way, low-ranking individuals at Apenheul had more chances to obtain food. Possibly, this resulted in more peering by high-ranking toward low-ranking animals.

The question of whether bonobos possess formal indicators of dominance or subordination remains open. Perhaps they do possess such indicators, but they have remained unnoticed. However, after 1800 hr of observation we did not see any conspicuous dominance displays that occurred often in all adult individuals. Other researchers have also noted this lack of ritualized signals of status communication [e.g., Furuichi & Ihobe, 1994]. Another possibility is that the correlation between the occurrence of such indicators in despotic species (as macaques have been described [Preuschoft & van Schaik, 2000]) may not be found in other species. Unfortunately, not enough data from non-macaque species are available to test that hypothesis. Finally, it is possible that the asymmetric relations we found in bonobos (Stevens et al., unpublished results) are a side-effect of life in stable and relatively small groups in captivity. It may be that bonobos have not yet responded to these artificial circumstances by developing formal indicators of dominance or subordination. Conversely, in small groups in captivity, frequency of peering behavior may be higher than in the wild.

More data are needed before we can conclude whether other behaviors fulfill the criteria of formal indicators in bonobos. The possible function of peering to formally communicate tolerance, and its relation to resource-holding potential deserves further investigation. By experimentally manipulating competitive abilities in different contexts (for example, by providing low-ranking individuals with resources, and studying the direction of peering within dyads), more insights can be obtained. It may also be worthwhile to investigate the relation between peering and dominance and competitive abilities in other, closely related species. For example, peering also occurs in chimpanzees [Mori, 1984], but thus far it has received far less attention in that species than in bonobos.

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