# The Bonobo's Adaptive Potential: Social Relations under Captive Conditions

Jeroen M.G. Stevens[1,2], Hilde Vervaecke[3], and Linda Van Elsacker[1]

## Introduction

By the end of the 1990s, the reputation of bonobos as a peaceful, egalitarian ape with strong female dominance through female bonding was firmly established (de Waal 1995; de Waal and Lanting 1997; Parish and de Waal 2000; de Waal 2001). Stanford (1998) questioned this reputation, and stated that our knowledge on bonobos lagged behind our knowledge of chimpanzees, because the latter has been studied for a longer span and at more study sites. Knowledge about bonobos stems mainly from captive studies which may not be representative (Stanford 1998). Stanford (1998), Franz (1999) and Hohmann et al. (1999) pointed out that the reported strong female bonds of captive bonobos (Parish 1994, 1996, Parish and de Waal 2000) may be a side effect of life in captivity, similar to chimpanzee females in captivity, wherein similar female bonds occur (de Waal 1982, Baker and Smuts 1994). It certainly cannot be denied that captivity affects behavior, especially in species with fission-fusion systems, such as chimpanzees and bonobos (de Waal 1994). In the wild they form temporary subgroups, "parties," whose composition changes constantly (Van Elsacker et al. 1995). However, in captivity, chimpanzees and bonobos are usually kept in stable groups (but see Fortunato and Berman, this volume), which will certainly influence their social relations. Since the two species, kept under similar conditions, display different behavioral strategies, captive studies can also provide conclusive data on interspecific differences (de Waal 1994).

Moreover, observations made of groups in captivity can yield interesting results because of greater visibility of the study subjects, which can reliably be followed

---

[1] *University of Antwerp, Department of Biology, Universiteitsplein 1, B 2610 Wilrijk, Belgium*

[2] *Centre for Research and Conservation, Royal Zoological Society of Antwerp, Koningin Astridplein 26, B 2018 Antwerp, Belgium*

[3] *Centre for Ethology and Animal Welfare, KaHoSint-Lieven, Belgium*

T. Furuichi and J. Thompson (eds.), *The Bonobos: Behavior, Ecology, and Conservation*

on consecutive days (de Waal 1994). This is especially the case when groups are kept under naturalistic conditions. Under such circumstances, captivity offers an interesting perspective to studying the adaptive potential of a species, which is defined as "the entire range of conditions to which a species can adjust without compromising its health, biological functions (such as reproduction) or major parts of its behavioral repertoire (such as species-typical communication)" (de Waal 1994, p246). A comparison between the behavior of chimpanzees at Arnhem zoo with that of chimpanzees in Tanzania, showed that bonds between males were similar, but "females seem an almost different species in captivity compared to what we know about them living in the wild" (de Waal 1994, p248). While chimpanzees have been kept under naturalistic conditions, including multimale, multifemale groups, since the 1970s, bonobos were for a longtime relatively rare in zoological collections, resulting in very small groups or breeding pairs. Male bonobos were transferred to other zoos when reaching adolescence to avoid inbreeding, while females often remained in the natal group. Only in the 1990s, after field research showed that wild bonobo females migrate and males are philopatric, and that wild communities sometimes contained as many adult males as females (Kano 1992, Hashimoto et al. 2008), did zoos begin to mimic their natural social conditions (Mills et al. 1997). The effect of captivity on relationships between bonobos has not yet been thoroughly studied.

The circumstances under which individuals can display their behavioral repertoire are of particular interest in the light of intraspecific differences. Research with chimpanzees showed a remarkable flexibility, both in captivity (Baker and Smuts 1994, de Waal 1994) and in the wild, where different chimpanzee cultures were documented (Wrangham et al. 1994, Whiten et al. 1999). Chimpanzees can occupy a range of habitats, from dry savannah woodlands, to tropical rain forests, which explains part of the variability (Boesch 2002). While bonobos were long believed to be exclusive inhabitants of dense tropical rain forest, recent research showed that they occupy gallery forests in the southern part of their range (Thompson 2002). Moreover, wild bonobos also showed flexibility, and there are cultural differences between study sites (Hohmann and Fruth 2003a). Hence, the typical distinction between savannah-dwelling chimpanzees and the bonobos from the rain forest became blurred. In addition to comparing bonobo behavior from different field sites, research on captive bonobos and comparisons with data from the wild can shed light on their flexibility. In chimpanzees, a comparison between female relationships at Arnhem Zoo with a colony at Detroit Zoo showed remarkable differences, with competition between females being more expressed in the recently formed colony at Detroit (Baker and Smuts 1994). In bonobos, very little is known about differences between naturalistic groups in captivity, as most studies have focused on single groups with multiple males and females (Vervaecke et al. 1999, 2000a, b, c, Palagi et al. 2004, Paoli et al. 2006) or on multiple groups with one, or at most two, adult males per group (Franz 1999, Parish 1994, 1996).

As a second point of criticism, Stanford (1998) argued that much of the knowledge on social behavior stemmed from only a few captive colonies (Yerkes and San Diego Zoo), which may have biased our knowledge on bonobos. The idea of peaceful, female dominated and egalitarian bonobos may characterize some, but not all zoo groups.

We aim to review our further investigations on the social behavior of several captive groups of bonobos. We examine our earlier published results and provide new additional data about the relationship between dominance, age, and sociosexual behavior of bonobos in captivity. We specifically investigate to what extent the image of bonobos as female-dominated, egalitarian, female-bonded and peaceful is manifest in different captive groups and to describe possible differences among groups. To test some of the current contradictions about dominance and bonding patterns in bonobos, we studied four multimale, multifemale groups, which is the largest study sample of captive bonobos.

## Methods

### *Study Groups and Housing*

We studied four captive groups of bonobos. Although each group contained one or more infants or juveniles, younger than 7 years, these are not included in the analyses. Each group contained at least three males, older than 7 years. Although some of these males are only adolescent (Kano 1992), DNA analyses have shown that each of these adolescent males was able to successfully reproduce (Marvan et al. 2006, P Galbusera unpublished data). Three of the study groups contained at least one adult or adolescent male who that mother reared. Except for one mother-daughter pair at Twycross, all females within groups are unrelated. Furthermore, most of the groups had been stable for at least a few years before our study. Table 1.1 is an overview of all adult and adolescent bonobos, their respective ages, relationships and dominance ranks.

Stevens studied the group at Wuppertal Zoo for 203 hours on 23 days between August and September 1999. It comprised four adult and adolescent males, two adult females, and one juvenile. Female LL was the mother of adolescent male BD and of the juvenile female. LL and LM were raised together, and were joined in 1988 by MT, who sired both BG and BD. In 1996 another female (EJ) joined the group. Haas (1983) described their housing.

Stevens observed the group in Apenheul Primate Park for 490 hours on 74 days between February and May 2001. The group included three adult males, five adult females (older than 8 years old), and three juveniles. All adults were unrelated and had been housed together since March 1998, three years before the study period. Gold (2001) described their housing conditions and group formation.

Stevens studied the group at Twycross Zoo for 263 hours on 34 days in November and December 2001 and in February 2002 for 228 hours on 28 days. The group comprised three males, three females, one juvenile, and one infant. DT was the mother of female KC and male KE. KA was the father of KE. All other group

**Table 1.1** Group composition and individual characteristics of the study groups and animals

| Group | Code | Full Name | Sex | Age | Parents | Rank |
|---|---|---|---|---|---|---|
| Wuppertal | LL | Lisala | F | 19 | Masikini × Catherine | 6 |
| | LM | Lusambo | M | 19 | Masikini × Kombote | 5 |
| | BG | Birogu | M | 10 | Mato × Catherine | 4 |
| | EJ | Eja | F | 9 | Bono × Daniella | 3 |
| | BD | Bondo | M | 8 | Lisala × Catherine | 2 |
| | MT | Mato | M | 36 | Camillo × Margrit | 1 |
| Apenheul | JI | Jill | F | 17 | Bosondjo × Laura | 8 |
| | ZU | Zuani | F | [11] | Wild | 7 |
| | RO | Rosie | F | [11] | Wild | 6 |
| | ML | Molaso | F | [17] | Wild | 5 |
| | HA | Hani | M | 11 | Wild | 4 |
| | LO | Lomela | F | 9 | Bono × Salonga | 3 |
| | MB | Mobikisi | M | [21] | Wild | 2 |
| | MW | Mwindu | M | [17] | Wild | 1 |
| Twycross | DT | Diatou | F | 24 | Masikini × Catherine | 6 |
| | KA | Kakowet II | M | 21 | Kakowet × Linda | 5 |
| | KC | Kichele | F | 12 | Masikini × Diatou | 4 |
| | BY | Banya | F | 11 | ? × Bonnie | 3 |
| | KE | Ke-Ke | M | 7 | Kakowet II × Diatou | 2 |
| | JS | Jasongo | M | 11 | Mato × Lisala | 1 |
| Planckendael | DZ | Dzeeta[1] | F | [27] / – | Wild | 7/– |
| | HE | Hermien[1,2] | F | [21] / [24] | Wild | 6/6 |
| | HO | Hortense[1,2] | F | [21] / [24] | Wild | 5/5 |
| | DE | Desmond[1] | M | [28] / – | Wild | 4/– |
| | RE | Redy[1,2] | M | 9 / 12 | Desmond × Hortense | 3/4 |
| | KO | Kosana[1] | F | [19] / – | Wild | 2/– |
| | KI | Kidogo II [1,2] | M | 16 / 19 | Masikini × Catherine | 1/3 |
| | DJ | Djanoa[2] | F | – / 7 | Santi × Yala | –/2 |
| | VI | Vifijo[2] | M | – / 8 | Kidogo II × Hortense | –/1 |

Age is given in years; numbers between brackets represent estimated ages, following Leus & Van Puijenbroeck (2005). Animals present in Planckendael during the 1999 study period are marked with [1], animals present in the second period in 2002 are marked with [2], their respective ages and ranks are separated with a /. Ranks are taken from Stevens et al. (in press) and are based on the occurrence of "fleeing upon aggression," with the highest rank number given to the most dominant member of the group.

members were unrelated. The group was formed in 1992, when DT and her daughter KC joined males KA and JS. Data from the two periods were pooled, since no changes in group composition occurred. We used matrix correlations to compare behavioral frequencies of the two periods and no significant differences were found.

Stevens observed the group at Planckendael for 190 hours on 24 days in November and December 1999, when the group comprised four adult females, three males, and four infants and juveniles. Except for the mother-son pair HO-RE, all adults and adolescents are unrelated. Stevens studied them again on 73 days for 505 hours between

November 2002 and February 2003, when there were three males three females, and two juveniles. One of the females (DJ) joined the group three months before the onset of the study. Females HE and HO and males RE and KI, were present during the previous study. One male (VI) had reached adolescence by the second period. Apart from the newly introduced female DJ, all other members had been together since 1992 or since they were born into the group. RE and VI were maternal half-brothers and had their mother (HO) in the group. KI was the father of male VI. All other members are unrelated. Stevens et al. (2003) provided more details regarding housing conditions and changes in group composition.

## *Behavioral Observations, Categories and Analyses*

We used a standardized ethogram, based on those by de Waal (1988) and Vervaecke et al. (2000a). Stevens conducted continuous observations throughout the day, starting in the morning and ending at dusk, when social interactions between the bonobos generally ceased. Frequent night observations at Planckendael revealed that no substantial social interactions occur after nest building or before feeding in the morning. Observations halted only when the bonobos were separated for cage cleaning or management purposes. Between 4 and 8 hours of observations occurred daily.

The observations comprised a combination of focal animal sampling, all occurrence sampling of agonistic, affiliative and sociosexual behaviors and instantaneous scan sampling for proximity. Stevens recorded observations manually and later entered them in the Observer software (Noldus), or entered them directly in the Observer. When social interactions were very frequent, e.g. during feeding bouts, he made video recordings and analyzed them later.

## *Dominance Relationships*

We determined dominance relationships only on the outcome of decided agonistic interactions, using fleeing upon aggression as a behavioral marker for dominance (Vervaecke et al. 2000a), and analyzed the dominance matrix with MatMan software (de Vries et al. 1993). We calculated Landau's linearity index, corrected for unknown relationships, and tested whether the value of h' differs significantly from the value that is expected under the null hypothesis of random dominance relations (de Vries 1995). When we found significant dominance hierarchies, we reordered the matrices following the I & SI methods, minimizing the number of inconsistencies (I) and the strength of inconsistencies (SI) to reorder the matrix in a manner most consistent with the linear hierarchy (de Vries 1998).

Based on the same marker for dominance, i.e. fleeing upon aggression, we calculated the individual's David's scores (David 1988), a cardinal rank measure which gives a dominance value for each individual, based on the relative numbers of winning and losing conflicts. David's scores have been shown to be more accurate than the index used by Clutton Brock et al. (1979) because 1) they are not disproportionately affected by minor deviations from the main dominance direction within dyads and 2) an individual's rank is independent of interactions in which he was not involved (Gammell et al. 2003). By performing a simple linear regression on individual David's scores, after they have been normalized to control for differences in group size, a measure for the steepness of a dominance hierarchy can be calculated (de Vries et al. 2006). The steepness varies from 0, a complete egalitarian, or shallow hierarchy, to 1, a steep or despotic hierarchy (de Vries et al. 2006).

We briefly reviewed our earlier findings on the linearity and steepness of dominance hierarchies in each of the study groups (Stevens et al. 2007). Furthermore, we correlated dominance with age, testing the idea that dominance and age are not correlated (Vervaecke et al. 2000a, Paoli and Palagi this volume). Patterns of social bonding:

- *Proximity*: every 15 minutes we scored which individuals were within arm's reach of one another (ca. 3 meter, following Furuichi and Ihobe 1994) by means of instantaneous scan sampling (Altmann 1974). From the samples, we took seven random scans for each day to avoid statistical interdependence of the data (Martin and Bateson 1993).
- *Grooming*: we scored grooming bouts by all occurrence sampling (Altmann 1974). In each grooming bout we scored the participation of each partner once. We did not count subsequent switches between the active and passive role as new bouts (Vervaecke et al. 2000b). For intergroup comparisons, we expressed dyadic grooming frequencies as number of bouts per hour.
- *Coalitions*: we scored coalitions per terminology and criteria of de Waal (1978, 1984). A brief overview of our results concerning the direction of support against likely winners or losers is also given.

Previously, we analyzed bonding patterns by lumping data across all groups to look for general trends (Stevens et al. 2006). Here we elaborate on these findings and analyze bonding patterns per group, to look for between groups using matrix comparisons, an approach which has also been used for wild bonobos (White and Burgman 1990). We used a Mantel test (Schnell et al. 1985) to compare each symmetrical matrix of behavioral interactions (spatial association, symmetrical matrices for grooming and for support) with three hypothesis matrices. For each hypothesis, we constructed a matrix, filling in values of 1 for all dyads important for the respective hypothesis, and values of 0 for all the other dyads. *Hypothesis 1*: structure of proximity, grooming or support was caused by preferential female-female associations; *Hypothesis 2*: structure of proximity, grooming or support was caused by preferential association among individual males; *Hypothesis 3*: structure was caused by preferential associations between males and unrelated females. For more details on this approach, see White and Burgman (1990). As we were mainly interested in intersexual bonding between unrelated males and females, we controlled for mother-son dyads by correcting the original data matrix. In the cells containing data on mother-son dyads, we filled in values that would be expected on the basis of the marginal totals of the matrices. We then correlated these adjusted data matrices with each of the hypothesis matrices, via a Mantel test in MatMan (de Vries et al. 1993).

While the Mantel test gives an idea for each group separately whether bonding is caused by preferential female-female, male-female or male-male bonding, we used a Fisher Combination test (Fisher 1954, Sokal and Rohlf 1981,780) to study the effects across groups. Hereto we combined the p-values of all individual Mantel tests. If the null hypotheses are true, the quantity $-2\Sigma \ln P$ is expected to be distributed as $\chi 2$ with degrees of freedom= 2 * the number of separate tests and probabilities. Values of $-2\Sigma \ln P$ greater than the corresponding $\chi 2$ value allow one to reject the null hypothesis of no effect.

### Sociosexual Behavior

We calculated individual sexuality scores for rough comparison with data presented by de Waal (1998, 2001). We used the same definitions and criteria of sociosexual behavior, between all individuals 7 years or older (similar to de Waal's (1998, 2001) adult group).

- *Sex present*: Presenting genital area (penis or anogenital swelling) towards another individual. May or may not be followed by further sexual interactions.
- *Sexual inspection*: Inspecting genital area of another individual by looking at, licking, touching or sniffing it. This category also includes de Waal's (1988) genital massage and oral genital massage.
- *Copulation*: All sexual interactions between mature (> 7 years) heterosexual dyads, which included intromission of the penis and clear thrusting of the pelvis (Furuichi 1997).
- *Non-copulatory mount*: Any sexual interaction involving a) homosexual dyads; b) immature subjects; or c) mature male-female dyads without observations of thrusting or intromission of the penis. Thus this category includes, rump-rump-rubbing, GG-rubbing and any mounting activity.

## Results

### Dominance Relationships

#### Linearity and Steepness of Dominance Hierarchies

Based on the outcome of decided agonistic interactions, we found a significantly linear dominance hierarchy in each of the study groups (Stevens et al. 2007). Linearity indices varied from 0.86 at Planckendael in 1999 up to the maximum

**Table 1.2** Correlation between rank and age in different groups of bonobos

| Group | Adult group size | Dominance-rank & age | |
|---|---|---|---|
| | N | Kendall tau | $P_r$ |
| Planckendael-1999 | 7 | 0.48 | 0.13 |
| Planckendael-2002 | 6 | 0.69 | 0.05 |
| Wuppertal | 6 | 0.27 | 0.43 |
| Apenheul | 8 | –0.08 | 0.78 |
| Twycross | 6 | 0.82 | 0.02 |

value of 1 in Planckendael in 2002 and in Wuppertal. The individual dominance ranks are provided in Table 1.1. Although females occupied the highest-ranking position in each group, and the lowest-ranking position was always taken by a male, at least one male in every group could dominate at least one female, resulting in non-exclusive female dominance.

We measured the steepness of dominance hierarchies based on the outcome of agonistic interactions (measured by fleeing upon an aggression), and found that groups varied slightly in the steepness of their dominance hierarchy, with steepness values between 0.66 (Apenheul) and 0.81 (Planckendael-1992) (Stevens et al. in press). In general we found that hierarchies between males are steeper than those between females (Stevens et al. 2007).

### Dominance and Age

There is a significant correlation between age and rank only in Twycross zoo and in Planckendael 2002 (Table 1.2), where older bonobos tended to occupy the highest ranking positions in the hierarchy. In all other groups, dominance was not correlated with age.

## *Social Bonding*

### Patterns of Social Bonding

- *Proximity*: Mantel tests showed that females preferred the proximity of other females only in Planckendael-1999 and Apenheul, but the significance level only reached a trend (Table 1.3). In Planckendael-2002, females avoided the company of other females. Female-female preference could not be tested in Wuppertal, because there was only one female-female dyad in the group. When we combined the correlation coefficients of different groups, female preference for other females was not significant (Fisher combination test, $p = 0.23$). Between unrelated males and females, there are both positive (Planckendael-2002, Wuppertal, and Twycross) and negative (Planckendael-1999 and Apenheul)

**Table 1.3** Results of Mantel's Z correlation tests in which observed patterns of proximity were compared with three hypothetical matrices, assuming 1) bonding between females (f-f), 2) bonding between unrelated males and females (m-f), and 3) bonding between males (m-m)

| | f-f | m-f | m-m |
|---|---|---|---|
| Planckendael-1999 | 0.74° | –0.46° | –0.30 |
| Planckendael-2002 | –0.22 | 0.25 | –0.08 |
| Wuppertal | – | 0.41 | –0.41 |
| Apenheul | 0.63° | –0.33 | –0.45* |
| Twycross | 0.13 | 0.08 | –0.24 |
| Fisher combination test | P = 0.23 | P = 0.08 | P = 0.14 |

* $p<0.05$; °: $0.05 < p < 0.10$.

–: testing for female-female preference was impossible in Wuppertal, because of the low number (n=1) of female dyads.

**Table 1.4** Results of Mantel's Z correlation tests in which observed patterns of grooming were compared with three hypothetical matrices, assuming 1) bonding between females (f-f), 2) bonding between unrelated males and females (m-f), and 3) bonding between males (m-m)

| | f-f | m-f | m-m |
|---|---|---|---|
| Planckendael-1999 | 0.11 | 0.08 | –0.25 |
| Planckendael-2002 | –0.22 | –0.05 | 0.28 |
| Wuppertal | – | 0.36 | –0.35 |
| Apenheul | 0.04 | 0.15 | –0.31 |
| Twycross | 0.12 | 0.14 | –0.29 |
| Fisher combination | P = 0.99 | P = 0.83 | P = 0.31 |

–: testing for female-female preference was impossible in Wuppertal, because of the low number (n=1) of female dyads.

correlations. The Fisher combination test reached a trend (p = 0.08), indicating that overall, male-female proximity might influence overall group structure. The negative values for male-male proximity indicate that males in all groups tended to avoid proximity to other males, but the effect is only significant in Apenheul. Combining the results of different groups, there is no significant effect (Fisher combination test p= 0.13).

- *Grooming*: In general, grooming relationships between mothers and their adolescent or adult sons were most common, though the difference with grooming between unrelated males and females is not significant (Stevens et al. 2006). Testing against the three hypothesis matrices resulted in no significant effect (Table 1.4). In general, males tended to avoid grooming other males; the relations are always negative, with the exception of Planckendael-2002, but this effect never reached the significance level (Fisher combination test: p = 0.32). Female-female grooming, and grooming between unrelated males and females resulted in both negative and positive correlations, but they did not reach significance (Fisher combination test: female-male p= 0.84; female-females p= 0.99).

**Table 1.5** Results of Mantel's Z correlation tests in which observed patterns of support were compared with three hypothetical matrices, assuming 1) bonding between females (f-f), 2) bonding between unrelated males and females (m-f), and 3) bonding between males (m-m)

| | f-f | m-f | m-m |
|---|---|---|---|
| Planckendael-1999 | 0.67° | –0.44$^{**}$ | –0.24 |
| Planckendael-2002 | 0.74$^{**}$ | –0.39$^{**}$ | –0.26 |
| Wuppertal | – | 0.12 | –0.05 |
| Apenheul | 0.59$^{*}$ | –0.42$^{*}$ | –0.23 |
| Twycross | 0.37 | –0.20 | –0.21 |
| Fisher combination | P < 0.01 | P < 0.001 | P = 0.82 |

$^{**}$ p< 0.01; $^{*}$: p< 0.05; °: 0.05 < p < 0.10.

–: testing for female-female preference was impossible in Wuppertal, because of the low number (n=1) of female dyads.

- *Coalitionary support*: Overall, coalitions between females were significantly more common than coalitions between females and unrelated males, or coalitions between males (Stevens et al. 2006). When analyzed per group, support was significantly more common in female-female dyads than among other dyads in Planckendael-2002 and Apenheul, and there is a positive trend in Planckendael-1999 (Table 1.5). There is no evidence for preferential female-female support in Twycross or Wuppertal. When data from all groups were combined, the effect proved significant (Fisher combination test, p < 0.01), confirming our earlier findings. Comparison of the symmetrical support matrix with the hypothetical matrix for unrelated female-male preference resulted in significantly negative correlations for Planckendael-1999, Planckendael-2002 and Apenheul, suggesting that females and males avoided providing support to members of the other sex. When the results for all groups were combined, this negative effect proved significant (Fisher combination test: p < 0.0001). Male-male relations also resulted in negative correlations, but they never reached statistical significance (Fisher combination test: p = 0.82).

Our further analyses of the use and function of coalitions have shown that females provided significantly more support than males did, but females did not receive more support than males did. Furthermore, males were the usual targets of coalitions (Vervaecke et al. 2000c; unpublished data). Both males and females showed the same marked tendency to support likely winners in conflicts (females and males: 84% in support of likely winners), thus most coalitions were conservative (Chapais 1995). In some cases a lower ranking supporter would opportunistically provide support to a high ranking initial aggressor against an opponent that ranked in between the so-called "bridging alliances." Revolutionary alliances, in which two lower-ranking individuals support one another against a higher-ranking opponent, were extremely rare. This suggests that coalitions in bonobos mainly serve to maintain and reinforce existing dominance hierarchies.

## *Sociosexual Behavior*

We found differences in sociosexual activity between groups. The frequency of sociosexual behavior was remarkably low at Planckendael in 1999, with only 0.13 interactions per hour, a value that lies very close to the value given by de Waal (1998, 2001) for common chimpanzees. In the other bonobo groups, sexual activity was lower than, but close to those observed among the adult group at San Diego (Fig. 1.1).

To explain the low activity at Planckendael in 1999, we looked at the mean age of individuals in the different groups. de Waal's (1988, 1998, 2001) adult group in San Diego was in fact composed of two subgroups. One group comprised one male of 14 years, a 10 year old female, and an adolescent male of 7 years old. The second group included an adult female of 11.5 years, an adolescent male of 8 years old, and an infant. This resulted in a mean individual age of 10 yrs, for the two subgroups combined. In Planckendael, the mean individual age was 20 years.

There is a strong correlation for female individual age to sociosexual activity per hour (Spearman rank rs = –0.63 N = 15, p = 0.01). For males the correlation is slightly weaker but still significant (rs = –0.55 N = 14 p = 0.04, Fig. 1.2). Thus the relatively low frequencies of sexual interactions at Planckendael-1 and Planckendael-2 could be attributed to the presence of several older females, which were less sexually active, though regularly cycling.

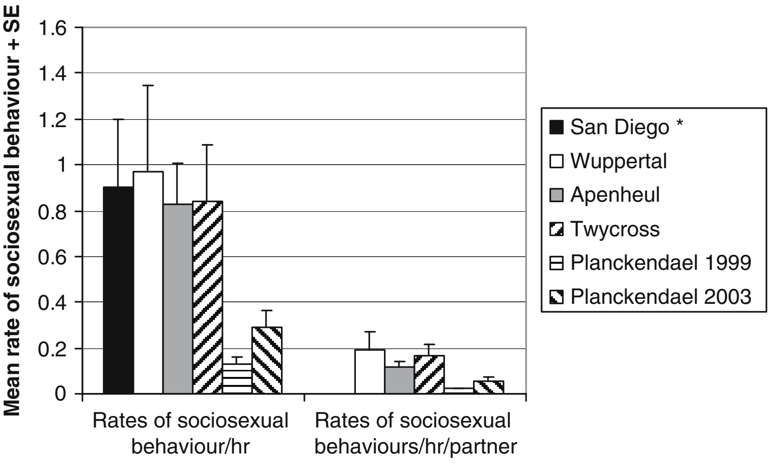

**Fig. 1.1** Mean rates of sociosexual behavior per hour for different groups of bonobo in captivity + SE. Data from San Diego are taken from de Waal (1998; 2001) but were not controlled for the number of partners available.

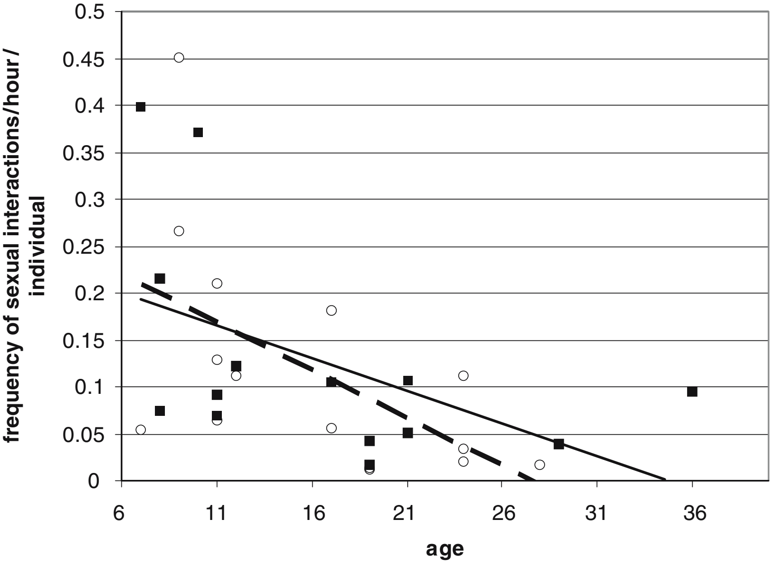

**Fig. 1.2** Correlations between individual age (years) and the frequency of sociosexual interactions per hour and per available partner across all study groups. Males (black squares, black trendline: $r_s = -0.55$, N = 14, p = 0.04) and females (white circles, broken trendline: $r_s = -0.63$, N= 15, p=0.01).

Elsewhere, we showed that mating success (measured as number of copulation bouts, excluding all other forms of sociosexual behavior) between males is not equally distributed. In Apenheul, the highest-ranking male HA obtained the highest mating success (Stevens et al. subm., cf. Paoli and Palagi in press). However, both in Planckendael-2002 and in Twycross, the alpha male did not have the highest overall mating success, with regularly cycling females or with the presumably cycling females when they were in estrus. Although alpha males in each group tried to aggressively monopolize females when they were in estrus by aggressively chasing away lower-ranking males, the younger and lower-ranking males had the highest mating success in Planckendael-1999 and Twycross (Stevens et al. subm.) and also sired offspring (Marvan et al. 2006).

## Discussions

Like wild bonobos (Kano 1992, Kano 1996, Furuichi 1997), in our captive groups, relationships between males are characterized by strongly asymmetric dominance relationships. Dominance hierarchies among captive males are extremely linear, probably because the number of males per group is very small (3–4 males per group), making despotic dominance relationships easier. Both in captivity and in the wild, males can compete over access to females, as is apparent from regular dominance displays and frequencies of male mating harassment (Kano 1992, 1996, Hohmann and Fruth 2003b). Affiliative bonds between males are relatively weak versus those in other dyads; males are rarely near one another and groom each other infrequently. Like wild bonobos (Kuroda 1980, Ihobe 1992, Furuichi and Ihobe 1994, Kano 1992), support between males is very rare, but not completely absent.

Dominance relationships between females are asymmetric, albeit somewhat less overtly expressed than among males (Furuichi 1997; Paoli and Palagi in press, Stevens et al. in press). Rank distances between females are often smaller compared to those between males (Stevens et al. 2007). Competition between females may be less overt, but is not absent, as evident from female mating harassment and abduction of infants, both in the wild and in captivity (Vervaecke and Van Elsacker 2000; Vervaecke et al. 2003; Hohmann and Fruth 2002, 2003b), which confirms the findings for wild bonobos at Lomako (Fruth et al. 1999, Hohmann et al. 1999, Hohmann and Fruth 2002). In two groups, we found a tendency for females to associate preferably with other females, but grooming was not more pronounced between them, which also corresponds to findings by Furuichi & Ihobe (1994) at Wamba, where association between females is pronounced, but grooming is not. Our finding that female-female support is more common than support between the sexes, or support between males, also confirms earlier reports on coalitions (Parish 1994, 1996, Vervaecke et al. 2000 b,c).

While most females could dominate males, female dominance is not complete. In each group, at least one male could dominate one or more females, and females were only able to evoke submission from males in 61% of the conflicts (Stevens et al. 2007). Female dominance was not complete, which we term non-exclusive female dominance (Vervaecke et al. 2000a, Stevens et al. 2007). For wild bonobos, it has been stated that females have about the same rank as males, and that there is a close dominance status between the sexes (Furuichi 1992, 1997, Kano 1992). The term co-dominance, used for wild bonobo males and females (Fruth et al. 1999) and sometimes in captive studies (Paoli et al. 2006, Paoli and Palagi this volume), also suggests that both sexes occupy similar cardinal rank positions, which contradicts our findings.

Bonds between unrelated males and females were equally strong as some female-female bonds, which confirms the findings for bonobos at Wamba and Lomako. Grooming was most frequent between mothers and their sons, but unrelated males also groom females more frequently than female-female grooming. Females support both related and unrelated males in conflict, albeit less frequently than they support other females. Males occasionally provide support to unrelated females. Since females often dominate males, it may pay for unrelated males to invest in long-term friendship relations with dominant females (Furuichi 1989, 1997, Kano 1992, Fruth et al. 1999, Hohmann et al. 1999, Hohmann and Fruth 2002).

The mean number of copulations per hour for each male in our study is 0.19 copulations/hour (range 0.01–0.36), which is similar to that reported for wild bonobos (Takahata et al. 1996: mean of 0.11, range of 0.10–0.20 copulations/hour;

Furuichi and Hashimoto, 2002: mean of 0.13 and 0.18 copulations/hour), thereby dispelling the idea of captive bonobos as being supersexual.

In general, the alleged difference between wild and captive groups of bonobos in term of bonding patterns is less pronounced than in earlier studies. The patterns of social bonding we observed are similar to those in wild bonobos, which confirms the bonobos as a female-centered species with bonds not only between females, but also between males and females instead of female bonded, with primary bonds between females. In contrast to chimpanzees, wherein female relationships seem influenced by captivity and male relations are comparable between the wild and captive conditions (de Waal 1994), we found that bonding patterns among captive bonobos largely resemble those in the wild.

In contrast to affiliative patterns, which may be more intense in captivity, but whose proportional distribution is largely similar to those of wild bonobos, the expression of dominance will undoubtedly be more rigid in captivity, where there are fewer competitors that are nearly always in the vicinity. Similarly, dominance styles may be more despotic compared to those in the wild. Coalitionary support may occur more frequently due to the general higher degree of spatial crowding and the consequent increased potential for occurrence of conflicts.

In contrast to studies by Paoli and colleagues (Paoli et al. 2006, Paoli and Palagi this volume), we consistently found significantly linear dominance hierarchies in all focal groups (Stevens et al. 2007). The difference in results may be due in part to a different behavioral measure. The studies by Paoli and colleagues used a combination of decided agonistic interactions and displace/yielding to measure dominance. Vervaecke et al. (2000a) found that yielding resulted in hierarchies with low linearity and directional consistency indices. This may be partly due to motivations of individuals, which need not concur with dominance ranks. For example, females can retreat to avoid sexually interested lower-ranking males (Vervaecke et al. 2000a). Franz (1999), who also used a combination of fleeing upon aggression and yielding, found significant linear hierarchies nonetheless in the bonobo groups of Stuttgart, Wuppertal and Planckendael. Further, the relation between dominance and age differed strongly among the groups.

Patterns of social bonding differed somewhat between groups, with some of them being more female-bonded than others. For example, in Apenheul and Planckendael-1999, females spent more time in proximity of other females, while this was not the case in the other groups. A combination of the results of all groups failed to confirm traditional assumptions of bonobo grooming patterns: there is no significant female bonding or intra-sexual grooming. Conversely, coalitionary support confirms expectations: female-female support was most common, while support among males was extremely rare.

The most impressive differences between groups are in the rates of sociosexual interactions, most notably at Planckendael, where the frequency of these interactions was much lower than previously reported for bonobos (de Waal 1998, 2001). The age composition of the group may determine the frequency of sexual interactions, because older individuals show a significant decline in sexual activity. There is no consistent pattern regarding male mating success in relation to dominance. The highest-ranking male acquired most copulations in only one of the focal groups. The relationship between male rank and mating success probably is largely influenced by female mate choice: when female choice runs concurrently with male dominance rank (as in Apenheul), dominance predicts mating success. When females show preferences for lower-ranking males, e.g. in Twycross and Planckendael-2002, dominance effects on mating are less clear.

Group dynamic processes may also explain why earlier research found higher degrees of female social bonding in captive groups of bonobos. Parish (1996) conducted the study in San Diego Wild Animal Park during captive group formation. In the wild, when young females migrate to new communities, they look for contacts with resident females (Furuichi 1989, Idani 1991). Later, when they have offspring, the relations with other females weaken, as relationships with their offspring gain importance (Furuichi 1989). Therefore, in newly-formed groups in captivity, females may at first seek contact with other females, while intersexual bonds may take longer to develop. We predict that the importance of female bonding will decrease as groups stabilize. Anecdotic data from 10 years of study at Planckendael support this. When the colony was founded, it comprised three unrelated females, three unrelated males, and one male offspring. Female bonding was more pronounced, with many female-female coalitions directed against the unrelated, lower-ranking males (Vervaecke et al. 2000b). Typically, the females supported each other unconditionally in conflicts with these males. Ten years later, two of the original females have had several offspring. The close bonds between them have weakened, as more conflicts arise between the females and the offspring of their former allies. In these conflicts, support is less unconditional and mothers are only rarely inclined to support their female friends. Instead, they withdraw or make appeasement gestures to both parties of the conflict.

Apart from the differences between bonobo groups in dominance behavior, bonding patterns and sexual behavior, cultural differences have been described for captive bonobo groups. De Waal (1988) described clapping behavior during grooming in the bonobos of San Diego Zoo. Later, Thompson (1994) showed how clapping had spread to other American zoos, where bonobos from San Diego Zoo had been transferred. A bonobo in our study groups, the adult male KA, which was one of the original bonobos studied by de Waal (1988), clapped during grooming. This behavior seemed to be adopted by at least two of the younger bonobos (KE and KC) at Twycross. Similar processes had been reported for other colonies with San Diego Zoo (Parish, cited in de Waal 1994) and seem to indicate social learning as a mechanism of cultural transmission. Apart from clapping behavior, Pika et al. (2005) described two group-specific gestures among young bonobos at Planckendael and Apenheul.

According to de Waal (1994), the capacity to adjust to new conditions is also a good indicator for the study of adaptive potential. He specifically refers to the flexibility of chimpanzees at Arnhem zoo, which coped with crowded winter conditions by increasing friendly grooming behavior to counterbalance an increase in the frequency, but not the intensity, of aggression (Nieuwenhuijsen and de Waal 1982). In Planckendael, we also compared behavior of bonobos in the winter, when they are confined to $600m^3$ indoor quarters, while in the summer they have access to a

3000m$^2$ island. Van Dyck et al. (2003) found that bonobos at Planckendael groom each other more frequently during winter periods, possibly as a mechanism to cope with the increase in certain types of aggressive behavior during the same study periods (Sannen et al. 2004).

## General Conclusions

In general, our study warns against generalizations derived from studies on a single bonobo group. For instance, the typical bonobo-pattern of female bondedness (Parish 1996) is confirmed by the data on coalitionary support in several groups, but not by the grooming patterns. Further, the dominance related bonding patterns described in the Planckendael group of 1999 (Vervaecke et al. 2000b) no longer persist in the changed group. In some groups, dominant individuals received more grooming or support than subordinates, and in other groups support or grooming was reciprocal (Stevens et al. 2005). However, this variation could be related to variation in dominance steepness, as predicted by biological market theories, wherein one expects reciprocal exchange in groups with a shallow dominance hierarchy, and up-the-hierarchy grooming and interchange of commodities in groups with a more steep dominance gradient (Barrett et al. 1999). Grooming was indeed more reciprocal in groups with a shallow dominance hierarchy, and in relatively steep hierarchies, grooming was not consistently directed at higher-ranking individuals and not interchanged against support or tolerance more frequently (Stevens et al. 2005).

Contrary to the common view derived from single-group studies, we found many variants from the presumed conciliatory, peaceful, and egalitarian bonobo. Bonobos exhibit relatively low conciliatory tendencies. Furthermore, serious aggression occurs. Intersexual aggression is especially common; females gang together against lower-ranking males (Parish 1996). We observed fierce female attacks on lower-ranking males in Planckendael, Twycross, Apenheul, Wuppertal and Frankfurt Zoo. Often they result in the temporary or permanent removal of the target males, though lethal aggression that occurs among chimpanzees (de Waal 1986) is not recorded. The orphan males, which have been hand-reared, have no mother to back them up during conflicts, and may lack social skills to cope with the attacks, are typical scapegoats of redirected aggression and suffer most from violent female attacks. But mothers do not always support their sons in conflicts, and may opt to provide support to the party opposing their own offspring (Stevens et al. subm.). Coalitionary attacks on sons of high-ranking mothers are rarer, but not absent. Furthermore, we also recorded a marked tendency for female bonobos to kidnap or harass offspring of other females (Vervaecke et al. 2003). Although the precise meaning of these interferences is unclear, similar cases of infant abduction in chimpanzees are considered a sign of female competition (Pusey et al. 1997). A wild female bonobo carried another female's newborn offspring, which subsequently died (Hohmann and Fruth 2002).

We did not confirm egalitarianism in dominance relationships in the diverse study groups. Overall, bonobo behavior is so variable and flexible, that studies over longer periods and on multiple groups are a prerequisite to any generalization. Researchers with single groups should reflect cautiously on possible context-related determining factors of observed behavioral patterns. The expectations that have been created by previous bonobo studies should also be put in this perspective in order to observe them without bias.

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

## References

Altmann J (1974) Observational study of behavior: sampling methods. Behaviour 49: 227–267

Baker KC, Smuts BB (1994) Social relationships of female chimpanzees: diversity between captive social groups. In: Wrangham RW, McGrew WC, de Waal FBM, Heltne PG (eds) Chimpanzee Cultures, Harvard University Press, Cambridge Massachusets and London, pp 227–242

Barrett L, Henzi SP, Weingrill T, Lycett JE, Hill RA (1999) Market forces predict grooming reciprocity in female baboons. Proc Roy Soc London B266:665–670

Boesch C (2002) Behavioural diversity in *Pan*. In: Boesch C, Hohmann G, Marchant LF (eds) Behavioural Diversity in Chimpanzees and Bonobos, Cambridge University Press, Cambridge, pp 1–8

Chapais B (1995) Alliances as a means of competition in primates; evolutionary, developmental and cognitive aspects. Yearbook of Physical Anthropology 38: 115–136

Clutton-Brock T H, Albon S D, Gibson R M, Guinness F E (1979) The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus* L.). Animal Behaviour, 27, 211–225

David HA (1988) The method of paired comparisons. London: Charles Griffin

Fisher RA (1954) Statistical methods for Research Workers. 12th ed. Oliver & Boyd, Edinburgh

Franz C (1999) Allogrooming behavior and grooming site preferences in captive bonobos (*Pan paniscus*): association with female dominance. International Journal of Primatology 20: 525–546

Fruth B, Hohmann G, McGrew WC (1999) The *Pan* species. In: Dolhinow P, Fuentes A (ed) The Nonhuman Primates. Mayfield Publishing Company, London, pp 64–72

Furuichi T (1989) Social interactions and the life history of female *Pan paniscus* in Wamba, Zaire. International Journal of Primatology 10: 173–197

Furuichi T (1992) The prolonged estrus of females and factors influencing mating in a wild group of bonobos (*Pan paniscus*) in Wamba, Zaire. In: Itoigawa N, Sugiyama Y, Sackett GP, Thompson RK (eds) Topics in Primatology, Vol. 2: Behavior, Ecology and Conservation. Tokyo: University of Tokyo Press. pp 179–190

Furuichi T (1997) Agonistic interactions and matrifocal dominance rank of wild bonobos (*Pan paniscus*) at Wamba. Folia Primatologica 18: 855–875

Furuichi T, Hashimoto C (2002) Why female bonobos have a lower copulation rate during estrus than chimpanzees. In: Boesch C, Hohmann G, Marquardt L (eds) Behavioral diversity of chimpanzees and bonobos. Cambridge Univ Press, New York, pp 156–167

Furuichi T, Ihobe H (1994) Variation in male relationships in bonobos and chimpanzees. Behaviour 130: 212–228

Gammell MP, De Vries H, Jennings DJ, Carlin CM, Hayden TJ (2003) David's score: a more appropriate dominance ranking method than Clutton-Brock et al.'s index. Animal Behaviour 66: 601–605

Gold KC (2001) Group formation in captive bonobos: sex as a bonding strategy. In: The Apes: Challenges for 21st Century, Brookfield Zoo, Brookfield, pp 90–93

Haas G (1983) Neue menschenaffenanlage im Zoo Wuppertal. Der Zoologischer Garten, N.F. 53: 93–101

Hashimoto C, Yasuko T, Hibino E, Mulavwa M, Yangozene K, Furuichi T, Idani G, Takenaka O (in press) Longitudinal structure of a unit-group of bonobos: male philopatry and possible fusion of unit-groups. In: Furuichi T, Thompson J (eds) Bonobos: behavior, ecology, and conservation. Springer, New York, pp 107–119

Hohmann G, Fruth B (2002) Dynamics in social organization of bonobos (*Pan paniscus*). In: Boesch C, Hohmann,G, Marchant L F (eds) Behavioural Diversity in Chimpanzees and Bonobos. Cambridge, Cambridge University Press. pp 138–150

Hohmann G, Fruth B (2003a) Culture in bonobos? Between-species and within-species variation in behavior. Current Anthopology 44: 563–571

Hohmann G, Fruth B (2003b) Intra-and inter-sexual aggression by bonobos in the context of mating. Behaviour 140: 1389–1413

Hohmann G, Gerloff U, Fruth B (1999) Social bonds and genetic tests: kinship, association and affiliation in a community of bonobos (*Pan paniscus*). Behaviour 136: 1219–1235

Idani G (1991) Social relationships between immigrant and resident bonobo (*Pan paniscus*) females at Wamba. Folia Primatol 57:83–95

Ihobe H (1992) Male-male relationships among wild bonobos (*Pan paniscus*) at Wamba, Republic of Zaïire. Primates 33:163–179

Kano T (1992) The last ape: pygmy chimpanzee behavior and ecology. Stanford California, Stanford University Press

Kano T (1996) Male rank order and copulation rate in a unit-group of bonobos at Wamba, Zadre. In: McGrew WC, Marchant LA, Nishida T (eds) Great Ape Societies. Cambridge: Cambridge University Press. pp 135–145

Kuroda S (1980). Social behavior of pygmy chimpanzees. Primates 21: 181–197

Martin P, Bateson P (1993) Measuring Behaviour: an introductory guide (second edition). Cambridge, Cambridge University Press

Marvan R, Stevens JMG, Roeder AD, Mazura I, Bruford MW, de Ruiter JR (2006) Male dominance rank, mating and reproductive success in captive bonobos. Folia Primatologica 77: 364–376

Mills J, Reinartz G, De Bois H, Van Elsacker L, Van Puijenbroeck B (1997) The care and management of bonobos (*Pan paniscus*) in captive environments. The Zoological Society of Milwaukee County, Milwaukee

Nieuwenhuijsen K, de Waal FBM (1982) Effects of spatial crowding on social behavior in a chimpanzee colony. Zoo Biol 1:5–28

Palagi E, Paoli T, Tarli SB (2004) Reconciliation and consolation in captive bonobos (*Pan paniscus*). American Journal of Primatology 62: 15–30

Paoli T, Palagi E, Borgognini, Tarli SMB (2006) Reevaluation of dominance hierarchy in bonobos (*Pan paniscus*). American Journal of Physical Anthropology xx

Parish AR (1994) Sex and food control in the "uncommon chimpanzee": how bonobo females overcome a phylogenetic legacy of male dominance. Ethology and Sociobiology 15: 157–179

Parish AR (1996) Female relationships in bonobos (*Pan paniscus*). Human Nature 7: 61–96

Parish AR, de Waal FBM (2000) The other "closest living relative": how bonobos (*Pan paniscus*) challenge traditional assumptions about females, dominance, intra- and inter-sexual interactions, and hominid evolution. Annals of the New York Academy of Sciences 907: 97–113

Pika S, Liebal K, Tomasello M (2005) Gestural communication in subadult bonobos (*Pan paniscus*): repertoire and use. Amer J Primatol 65:39–61

Pusey A, Williams J, Goodall J (1997) The influence of dominance rank on the reproductive success of female chimpanzees. Science 277:828–831

Sannen A, van Elsacker L, Eens M (2004) Effect of spatial crowding on aggressive behavior in a bonobo colony. Zoo Biol 23:383–395

Schnell G, Watt D, Douglas M (1985) Statistical comparison of proximity matrices: applications in animal behaviour. Animal Behaviour 33, 239–253

Sokal RR, Rohlf FJ (1981) Biometry, 2nd edition. Freeman, San Francisco

Stanford CB(1998) The social behavior of chimpanzees and bonobos. Current Anthropol 39: 399–420

Stevens J, Vervaecke H, Melens W, Huyghe M, De Ridder P, Van Elsacker L (2003) Much ado about bonobos: ten years of management and research at Planckendael Wild Animal Park, Belgium. In: Gilbert TC, (ed) Proceedings of the Fifth Annual Symposium on Zoo Research, 7–8 July 2003, Marwell, Marwell Zoological Park, pp114–125

Stevens JMG, Vervaecke H, De Vries H, Van Elsacker L (2005) The influence of steepness of dominance relations on reciprocity and interchange in captive bonobos (*Pan paniscus*). Behaviour 142: 941–960

Stevens JMG, Vervaecke H, De Vries H, Van Elsacker L (2006) Social structures in *Pan paniscus*: Testing the female bonding hypothesis. Primates 47: 210–217

Stevens JMG, Vervaecke H, De Vries H, Van Elsacker L (2007) Sex differences in steepness of dominance hierarchies in captive groups of bonobos International Journal of Primatology DOI 10.1007/s10764-007-9186-9

Takahata Y, Ihobe H, Idani G (1996) Comparing copulations of chimpanzees and bonobos: do females exhibit proceptivity or receptivity. In: McGrew WC, Marchant LF, Nishida T (eds) Great ape societies. Cambridge Univ Press, Cambridge

Thompson JA Myers (1994) Cultural diversity in the behavior of *Pan*. In: Quiatt D, Itani J (eds) Hominid culture in primate perspective. Univ Press of Colorado, Niwot, pp 95–115

Thompson JA Myers (2002) Bonobos of the Lukuru Wildlife Research Station. In: Boesch C, Hohmann G, Marchant LF. (eds) Behavioural Diversity in Chimpanzees and Bonobos, Cambridge University Press, Cambridge, pp 61–70

Van Dyck S, Stevens J, Meuleman B, Van Elsacker L (2003) Effects of the change in accommodation and group composition on the affinitive behaviour of a captive bonobo group (*Pan paniscus*). In: Gilbert TC (ed) Proceedings of the Fifth Annual Symposium on Zoo Research, 7–8 July 2003, Marwell Zoological Park, Marwell, pp 205–210

Van Elsacker L, Claes G, Melens W, Struyf K, Vervaecke H, Walraven V (1993) New outdoor exhibit for a bonobo group at Planckendael: design and introduction procedures. Bonobo Tidings: 35–47

Van Elsacker L, Vervaecke H, Verheyen RF (1995) A review of terminology on aggregation patterns in bonobos (*Pan paniscus*). International Journal of Primatology 16: 37–52

Vervaecke H, Van Elsacker L (2000) Sexual competition in a group of captive bonobos (*Pan paniscus*). Primates 41: 109–115

Vervaecke H, de Vries H, Van Elsacker L (1999) An experimental evaluation of the consistency of competitive ability and agonistic dominance in different social contexts in captive bonobos. Behaviour 136, 423–442

Vervaecke H, de Vries, H, Van Elsacker L (2000a) Dominance and its behavioral measures in a captive group of bonobos (*Pan paniscus*). International Journal of Primatology 21: 47–68

Vervaecke H, de Vries H, Van Elsacker L (2000b) The pivotal role of rank in grooming and support behavior in a captive group of bonobos (*Pan paniscus*). Behaviour 137: 1463–1485

Vervaecke H, de Vries H, Van Elsacker L (2000c) Function and distribution of coalitions in captive bonobos (*Pan paniscus*). Primates 41: 249–265

Vervaecke H, Stevens J, Van Elsacker L (2003) Interfering with others: female-female reproductive competition in *Pan paniscus*. In: Jones CB (ed) Sexual Selection and Reproductive Competition in primates: new perspectives and directions, American Society of Primatologists, pp 1235–1246 de Vries H (1995) An improved test of linearity in dominance hierarchies containing unknown or tied relationships. Animal Behaviour 50: 1375–1389

de Vries H (1998) Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. Animal Behaviour 55: 827–843

de Vries H, Netto WJ, Hanegraaf PLH (1993) Matman: a program for the analysis of sociometric matrices and behavioural transition matrices. Behaviour 125: 157–175

de Vries H, Stevens JMG, Vervaecke H (2006) Measuring the steepness of a dominance hierarchy based on normalised David's score and the dyadic dominance index corrected for chance. Animal Behaviour 585–592

de Waal FBM (1978) Exploitative and familiarity dependent support strategies in a colony of semi-free living chimpanzees. Behaviour 66: 268–312

de Waal, FBM (1982) Chimpanzee Politics: power and sex among apes. London, Jonathan Cape Ltd

de Waal, FBM (1984) Sex differences in the formation of coalitions among chimpanzees. Ethology and Sociobiology 5: 239–255

de Waal FBM (1986) The brutal elimination of a rival among captive male chimpanzees. Ethology and Sociobiology 7: 237–251

de Waal FBM (1988) The communicative repertoire of captive bonobos (*Pan paniscus*) compared to that of chimpanzees. Behaviour 106: 183–251

de Waal FBM (1994) Chimpanzee's adaptive potential. In: Wrangham RW, McGrew WC, de Waal FBM, Heltne PG. (eds) Chimpanzee Cultures, Harvard University Press, Cambridge Massachusets and London, pp 243–260

de Waal FBM (1995) Bonobo sex and society. Scientific American 272: 58–64

de Waal FBM (1998) Comment on CB Stanford The social behavior of chimpanzees and bonobos. Current Anthropology 39: 407–408.

de Waal FBM (2001) Apes from Venus: bonobos and human social evolution. In: de Waal FBM, (ed) Tree of Origin: What Primate Behavior Can Tell Us about Human Social Evolution, Harvard University Press, Cambridge, Massachusetts & London, England pp 41–68

de Waal F, Lanting FL (1997) Bonobo, The Forgotten Ape. Berkeley and Los Angeles: University of California Press

White FJ, Burgman MA (1990) Social organization of the pygmy chimpanzee (*Pan paniscus*): Multivariate analysis of intracommunity association. American Journal of Physical Anthropology 83: 193–201

Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham RW, Boesch C (1999) Cultures in chimpanzees. Nature 399: 682–685

Wrangham RW, McGrew WC, de Waal FBM, Heltne, PG (1994) Chimpanzee Cultures. Harvard University Press, Cambridge Massachusets and London