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Social structures in *Pan paniscus*: testing the female bonding hypothesis

Abstract Based on previous research in captivity, bonobos, *Pan paniscus*, have been called a female-bonded species. However, genetic and behavioural data indicate that wild females migrate. Bonding between these unrelated females would then be in contradiction with socio-ecological models. It has been argued that female bonding has been overemphasized in captive bonobos. We examine patterns of proximity, grooming and support behaviour in six well established captive groups of bonobos. We find that female bonding was not a typical characteristic of all captive bonobo groups. In only two groups there was a trend for females to prefer proximity with other females over association with males. We found no evidence that following or grooming between females was more frequent than between males and unrelated females or between males. Only in coalitions, females supported each other more than male–female or male–male dyads. We also investigated five mother–son pairs. Grooming was more frequent among mothers and sons than in any other dyad, but sons did not groom their mothers more than males groomed unrelated females. Mothers groomed their sons, or provided more support to them than females groomed or supported unrelated males. Thus, while bonds between females were clearly present, intersexual relations between males and either unrelated females or their mothers are of more, or equal importance.

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Introduction

Socio-ecological models predict that when females migrate, bonds between them will be less developed than in species where females are philopatric (Wrangham 1980; Van Schaik 1989; Sterck et al. 1997). These female bonded species are characterised by "highly differentiated networks of social relationships within groups, based on grooming, aggression and other interactions" (Wrangham 1980, p. 263). While this is true for many species, especially cercopithecine monkeys (Smuts et al. 1987), bonobos, *Pan paniscus*, seem to be an exception to this rule. In the wild, females are the migrating sex and are generally unrelated to other females in their community (Kano 1982, 1992; Furuichi 1989; Hashimoto et al. 1996; Furuichi et al. 1998; Gerloff et al. 1999; Hohmann et al. 1999; Hohmann and Fruth 2002). However, several studies have reported that close bonds develop between these females (Badrian and Badrian 1984; White 1988; Furuichi 1989; Parish 1996). On the other hand, bonds between the philopatric males are relatively weak (Ihobe 1992; Furuichi and Ihobe 1994; Kano 1992). A study in captivity revealed that females prefer to affiliate and associate with other females over contact with males (Parish 1996). Females in captivity also groom each other often (Franz 1999) and form coalitions (Parish 1994; Vervaecke et al. 2000a, b). Therefore, the species has been called a 'female-bonded' species (de Waal 1995; Parish 1996; Parish and de Waal 2000).

However, it has been stated that this tendency of female bonding in bonobos may be a side effect of captivity (Stanford 1998; Franz 1999; Hohmann et al. 1999), similar to the stronger female bonding of captive chimpanzees (de Waal 1994; Baker and Smuts 1994). Although female–female relations are indeed well

developed in wild bonobos, several studies found that intersexual bonds are stronger (Kuroda 1979, 1980; Kano 1982; Furuichi and Ihobe 1994; Muroyama and Sugiyama 1994; Hohmann et al. 1999). Since bonds between mothers and their grown sons are very close (Kano 1982, 1992; Furuichi 1989, 1997; Ihobe 1992), this effect is partly due to relatedness. When excluding mother–son relationships, Furuichi and Ihobe (1994) found that proximity between unrelated females was more pronounced than between unrelated males and females. Grooming, on the other hand, was more frequent among unrelated males and females than among unrelated females. Hohmann and Fruth (2002) found that, even when controlled for mother–son dyads, grooming and proximity relations between unrelated adults were equally well developed as female–female bonds. Thus, it has been suggested that, in the wild, bonds between female bonobos are present, but are not equivalent to the strong male–male bonding in chimpanzees. Instead, bonobos live in a society based on interactions between females and their grown sons, and between males and unrelated females (Fruth et al. 1999; Hohmann et al. 1999).

In this paper, we aim to describe social relations in five well-established captive groups of bonobos. Here, we analyse patterns of spatial proximity, proximity maintenance, grooming and support in conflicts. We compare the frequencies of these behaviours between the following sex classes: female–female, male–male, female–male (and male–female, for asymmetric behaviours such as following, grooming and support), mother–son (and son–mother for asymmetric behaviours) and compare our data with what has been previously published on wild and captive bonobos.

Methods

Study groups

We studied five captive groups of bonobos for a total of 1,871 study hours. Table 1 lists observation periods, the number of study hours per group and group composition. For the analyses, only animals older than 7 years were considered, which resulted in a total of 29 different individuals (14 males and 15 females; Table 1). The study groups contained four mother–son pairs: Ho-Re

and Ho-Vi in Planckendael, Ll-Bd in Wuppertal and Dt-Ke in Twycross. There was only one mother–adult daughter pair: Dt-Kc in Twycross. All other female–female dyads within groups were unrelated. Further details on group relatedness and background of the individuals in different study groups can be found in Vervaecke et al. (2003) and Stevens et al. (2003).

The Planckendael study group was observed twice, and some individuals were present during more than one period. Since group composition and age distribution of this group differed considerably between periods, we considered them as separate groups. Planckendael-1 refers to the study period in 1999, while Planckendael-2 refers to the group in 2002–2003. For details regarding changes in group composition at Planckendael see Stevens et al. (2003). In all institutions, the bonobos were all housed together day and night, and only separated during cleaning of the enclosure, or in case of serious illness.

Data collection

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

Spatial proximity was scored by instantaneous scan sampling (Altmann 1974). Every 15 min it was noted for every individual whether it was in close proximity (less than 3 m, following Furuichi and Ihobe 1994) of any other individual. For analyses, seven data points were chosen at random per observation day, to avoid interdependency of these data (Martin and Bateson 1993). This resulted in 100, 511, 100, 428, 341 scans for Planckendael-1, Planckendael-2, Wuppertal, Apenheul and Twycross, respectively.

Proximity maintenance, grooming bouts and support were all scored using "all occurrence sampling" (Altmann 1974). Proximity maintenance was scored by all occurrence sampling of following, which was defined as closely walking behind another animal. In each grooming bout the participation of each partner was

Table 1 Observation periods on captive groups of bonobos, *Pan paniscus*. Males are indicated in bold. Numbers in parentheses refer to the individuals' age in years (after Leus and Van Puijenbroeck 2003)

Pldael-1 (193 h)	Pldael-2 (505 h)	Wuppertal (203 h)	Apenheul (493 h)	Twycross (490 h)
He (21)	He (24)	Ll (19)	Ji (17)	Dt (24)
Dz (29)	Ho (24)	**Lm (19)**	Zu (11)	**Ka (21)**
Ho (21)	**Re (12)**	**Bg (10)**	Ro (11)	Kc (12)
De (28)	**Ki (19)**	Ej (9)	Ml (17)	By (11)
Re (9)	Dj (7)	**Bd (8)**	**Ha (11)**	**Ke (7)**
Ko (19)	**Vi (8)**	Mt (36)	Lo (9)	**Js (11)**
Ki (16)	–	–	**Mb (21)**	–
–	–	–	**Mw (17)**	–

scored once. Subsequent switches between the active and passive role where not counted as new bouts (Vervaecke et al. 2000a). Support was defined as all instances where an individual A intervenes with an aggression within 30 s in an agonistic interaction between two other individuals B and C to aid in attack or in defence (de Waal 1978). We only studied triadic interventions: when more individuals joined in support, these were not considered. All aggressions from individual C towards B were considered as opportunities for support, regardless of the reaction of the victim B. We then corrected for the opportunity for individual A to provide support to B in a conflict with C, by dividing the total number of supports between A and B by the total number of conflicts involving A and B, with the exception of the conflicts they had with each other, and then multiplied this number by 100 (Hemelrijk and Ek 1991; Vervaecke et al. 2000a, b).

Analyses and statistics

For each of the behaviours, we calculated individual values as follows. The total frequency of individual x with all individuals from a certain "class" (female–female, female–male, male–female, male–male, mother–son, son–mother) was divided by the observation time and by the number of individuals belonging to the class the individual could interact with. This resulted in an individual measure, corrected for the number of observation hours and for the number of interaction partners.

To decide whether we could lump data from different groups, we performed a 2-way ANOVA on the behavioural frequencies, with individual as random factor. When frequencies were normally distributed, as was the case for proximity (Shapiro Wilks test: $W = 0.95$), we could use a simple 2-way ANOVA. When data were not normally distributed, in the case of following ($W = 0.41$), grooming ($W = 0.86$) and support ($W = 0.48$) we used a General Linear Model to modulate the behavioural frequencies. We then used the ANOVA procedure to test whether the differences between "classes" depended on the "group", by studying the interaction between these two effects. If this interaction was not significant, data could be lumped, and we analysed the main effects of differences between groups and between classes. When significant differences were found between groups or classes, we performed post hoc Tukey–Kramer tests, to compare groups or classes two by two. If the interaction between groups and classes was significant, as in the case of the proximity data, there were significant differences between groups in the effect of classes on the distribution of behaviour.

All analyses were performed using SAS software (release 8.01). The critical significance level was set at 0.05. Significance levels between 0.05 and 0.10 are considered as trends.

Results

Spatial proximity

We found a significant interaction between the factors 'group' and 'class' [$F_{\text{interaction (8,25.8)}} = 8.94$, $P < 0.0001$], indicating that differences between classes varied among groups. Therefore, we analysed each group separately. As a consequence, we could not compare proximity between mothers and sons to any other dyads, since the number of mother–son dyads per group was too small for analysis.

Post hoc Tukey tests showed there was no significant difference between any of the classes in Planckendael-2, Wuppertal and Twycross. Proximity between females was higher than between females and unrelated males, both in Planckendael-1 ($t = 6.40$, $df = 21.8$, $P < 0.0001$) and Apenheul ($t = 4.39$, $df = 21.8$, $P = 0.01$) (see Fig. 1). Proximity between females was also significantly higher than proximity between males in Planckendael-1 ($t = 6.86$, $df = 35$, $P < 0.0001$) and Apenheul ($t = 6.74$, $df = 34.9$, $P < 0.0001$). Thus, in two out of five groups (Planckendael-1 and Apenheul), we found that females preferred spatial proximity over association with unrelated males.

Proximity maintenance

There was no significant interaction between group and class [$F_{\text{interaction(1,18)}} = 1.66$, $P = 0.55$]. The difference between groups in the frequencies of following was not significant [$F_{(4,25.8)} = 0.60$, $P = 0.66$] so we lumped data of all groups. We found an overall significant effect of 'class' on the distribution of following [$F_{(5,50.1)} = 5.80$, $P = 0.0003$]. Following was most common between males and unrelated females. The frequencies of following between all other dyads were more or less similar (Fig. 2). Males followed unrelated females more often than sons followed their mothers ($t = 3.54$, $df = 42.2$, $P = 0.01$) or than males followed other males ($t = 4.55$, $df = 41.5$, $P = 0.0005$). All other differences were non-significant. Thus, females did not significantly follow other females more frequently than they followed unrelated males or members of any other category. Mothers did not follow their sons more frequently than females followed unrelated males ($t = 0.16$, $df = 47.5$, 1.00).

Grooming

The effect of classes on grooming frequencies did not differ between groups [$F_{\text{interaction (19,36.5)}} = 1.10$, $P = 0.15$]. However, there was a main effect of the factor 'group' [$F_{(4,28.8)} = 3.57$, $P = 0.02$]. Indeed, post hoc Tukey test revealed that grooming rates were higher in Twycross compared to Planckendael-1 ($t = 3.37$, $df = 29.3$,

Fig. 1 Proximity index of bonobos, *Pan paniscus*: per class *x* we calculated for each individual *i* how often it was in close spatial proximity (i.e. less than 3 m away, Furuichi and Ihobe 1994) of members of a class *x*, and divided this frequency by the number of scan samples and by the number of members of class *x* with whom individual *i* could interact. Because of small sample sizes (one dyad per group), mother–son proximity was not analysed statistically, but is shown in the figure only for reference. *Asterisks* indicate significant differences between classes, based on post hoc Tukey–Kramer tests ($P < 0.05$)
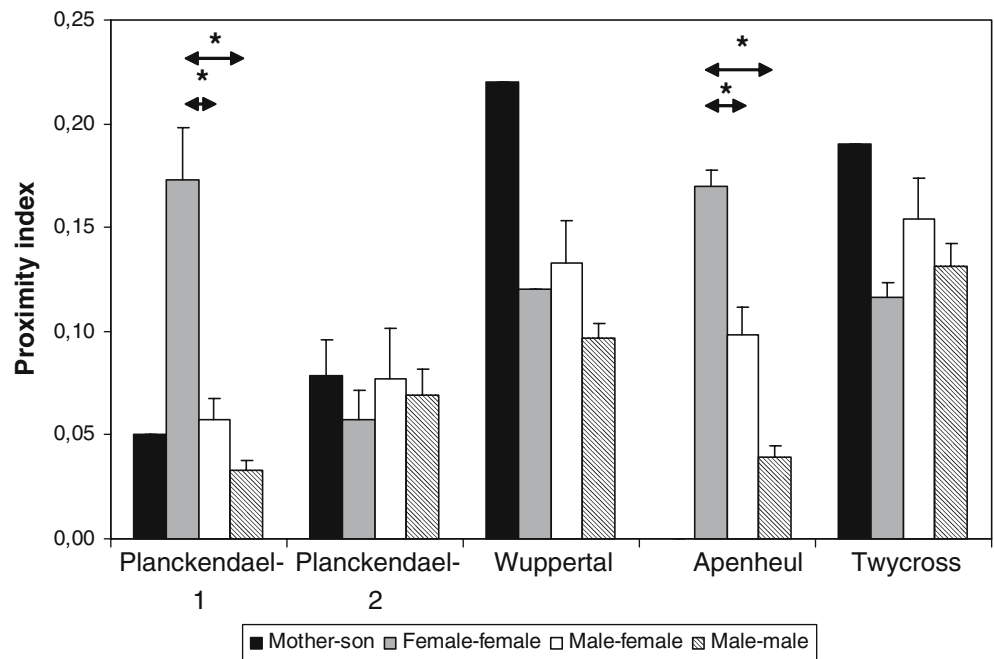
$P = 0.02$) and Apenheul ($t = 2.93$, $df = 28.3$, $P = 0.05$). All other intergroup differences were non-significant. We also found a significant effect of the factor 'class' [$F_{(5,56.6)} = 4.02$, $P = 0.004$]. Grooming occurred most frequently between sons and their mothers and vice versa, followed by grooming frequencies of unrelated males to females, between females, and female–male grooming. Grooming was least frequent in male–male dyads (see Fig. 3).

The post hoc Tukey tests showed that grooming between females was not significantly more frequent than grooming between females and unrelated males ($t = 0.81$, $df = 45.1$, $P = 0.96$) or than grooming between males ($t = 1.26$, $df = 54.2$, $P = 0.81$).

Fig. 2 Following index: per class we calculated for each individual *i* how often it followed members of a class *x*, and divided this frequency by the number of study hours and by the number of members of class *x* with whom individual *i* could interact. *Asterisks* indicate significant differences between classes, based on post hoc Tukey–Kramer tests ($P < 0.05$)
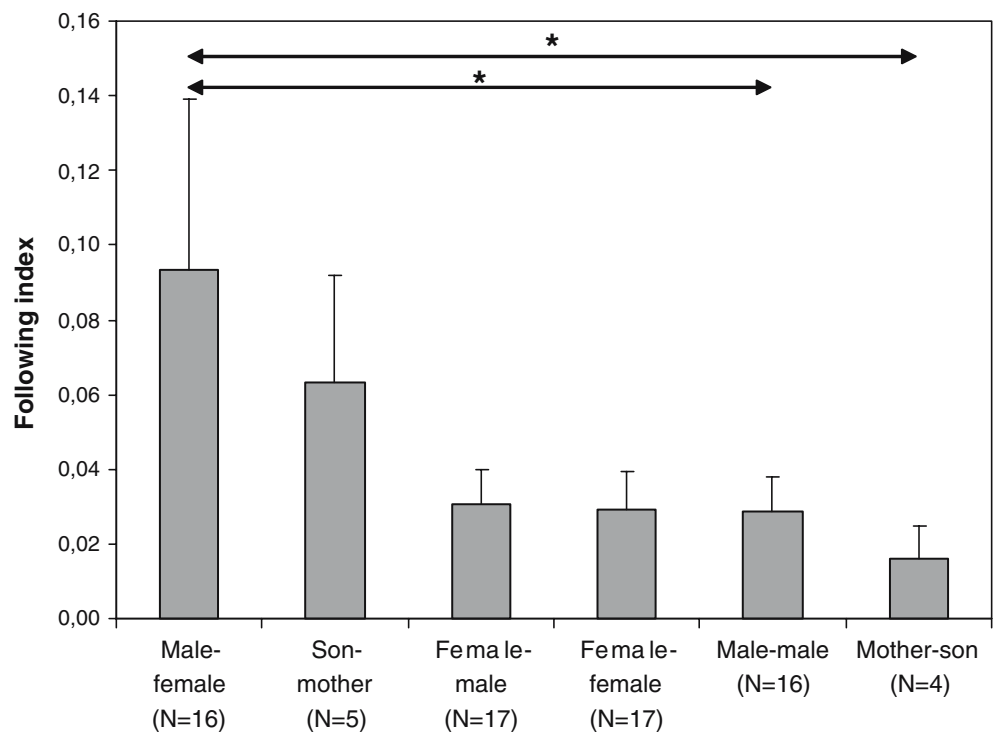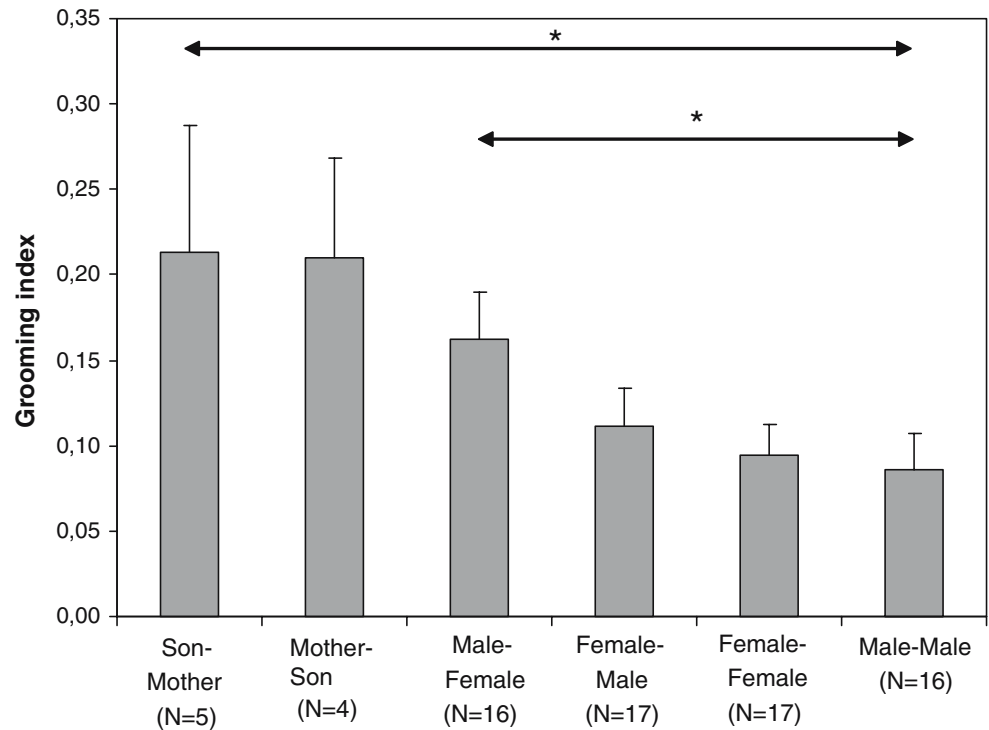
Fig. 3 Grooming index: per class x we calculated for each individual i how often it groomed members of a class x, and divided this frequency by the number of study hours and by the number of members of class x with whom individual i could interact. *Asterisks* indicate significant differences between classes, based on post hoc Tukey–Kramer tests ($P < 0.05$)

Mothers groomed their sons significantly more than females groomed unrelated males ($t = 2.31$, $df = 57.6$, $P = 0.02$) and than males groomed other males ($t = 2.52$, $df = 59.6$, $P = 0.01$). Mothers also groomed their sons more frequently than females groomed other females, but the difference reached only a trend ($t = 1.78$, $df = 58.1$, $P = 0.08$). Sons did not groom their mothers significantly more than males groomed unrelated females ($t = 1.11$, $df = 57$, $P = 0.27$). Grooming between sons and their mothers was also more frequent than grooming among females, but the difference reached only a trend ($t = 1.95$, $df = 55.9$, $P = 0.06$).

Support

We found no significant interaction between the effects of group and class on the corrected frequencies of support [$F_{\text{interaction } (14,1)} = 2.87$, $P = 0.43$]. There was no significant effect of the factor 'group' [$F_{(4,26.7)} = 1.72$, $P = 0.18$]. Thus, data from all groups were lumped. We then found a significant difference between 'classes' [$F_{(5,49.7)} = 10.46$, $P < 0.001$].

Support occurred far more frequently between females than between members of other classes (Fig. 3). Females provided significantly more support to other females than to unrelated males ($t = 6.33$, $df = 43.4$, $P < 0.0001$) and than males supported other males ($t = 3.79$, $df = 40.2$, $P = 0.01$). Females also supported each other more frequently than sons supported their mothers, but this difference reached only a trend ($t = 2.72$, $df = 63.5$, $P = 0.09$). There were also trends for mothers to support their sons more frequently than

females supported unrelated males ($t = 2.83$, $df = 46.6$, $P = 0.07$) and than males supported other males ($t = 2.71$, $df = 56.1$, $P = 0.09$) (Fig. 4).

Discussion

Although female–female association (proximity) and affiliation (grooming) were clearly present and well expressed in most groups, our analyses showed that these bonds were on the whole not significantly stronger than association and grooming between unrelated males and females. On the other hand, coalitionary support was more pronounced among females than among males or among males and females.

In other words, some female–female bonds were strong, but others were equally strong as bonds between unrelated males and females. This 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 these females. This also corresponds to findings by Furuichi and Ihobe (1994) in 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. 2000a, b).

We also found that male–female bonds were well developed in all groups. Since females often dominate males, it may pay for unrelated males to invest in

Fig. 4 Support index: per class *x* we calculated for each individual *i* how often it supported members of a class *x* (corrected for the opportunity to provide support—by dividing the number of interventions of individual A in conflicts between B and C, by the number of conflicts between B and C), and divided this frequency by the number of study hours and by the number of members of class *x* with whom individual i could interact. *Asterisks* indicate significant differences between classes, based on post hoc Tukey–Kramer tests ($P < 0.05$)
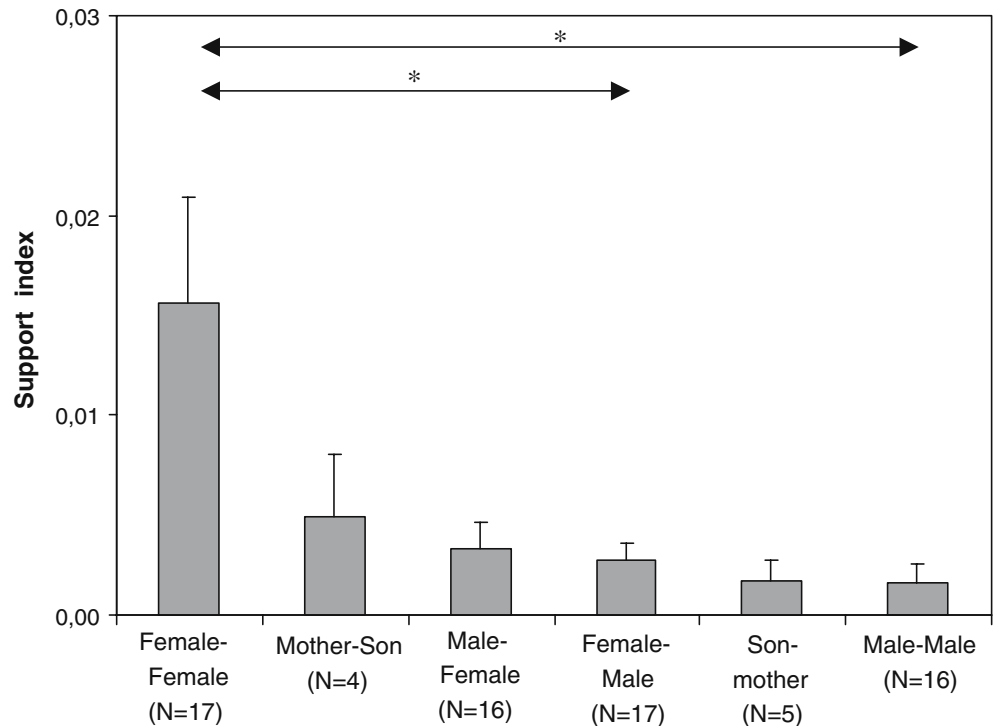
long-term friendship relations with dominant females (Furuichi 1992, 1997; Fruth et al. 1999; Hohmann et al. 1999). Future research will have to reveal whether this increases the mating success for these males.

It has been suggested that the relations between males and unrelated females have evolved as a side effect of strong relations between female bonobos and their sons (Hohmann et al. 1999). Although we could only study four mothers and five sons, we found clear evidence that in captivity, too, bonds between mothers and their (sub-)adult sons are very strong. This was most clear in grooming relations. Grooming between sons and their mothers was most common. Mothers supported their sons more frequently than they supported unrelated males, but they received very little support from them in return, and sons did not support their mothers more than males supported unrelated females. However, the participation of males in coalitions is in any case low.

Male–male relations were in general weak. Males were rarely in each others' proximity and rarely followed, groomed or supported each other. This corresponds with several findings from wild studies (Kuroda 1980; Ihobe 1992; Furuichi and Ihobe 1994; Kano 1992; White 1991).

Our results of proximity and grooming between females are in contrast with earlier findings that have emphasised female–female bonding in captive bonobos (Parish 1994, 1996; Franz 1999). Several reasons for this can be proposed. First of all, sex ratio may have influenced bonding patterns. In the Stuttgart group (Parish 1994; Franz 1999) and the Frankfurt group (Parish 1996), there was only one adult male and several adult females. In this situation, females are more likely to

choose other males as bonding partners. Furthermore, earlier studies focussed on relatively recently formed groups, which may have overemphasised female bonding. The study in San Diego Wild Animal Park was conducted during captive group formation (Parish 1996). When females migrate to new communities in the wild, they look for contacts with resident females (Furuichi 1989; Idani 1991). Later, when these young females have offspring, the relations with other females weaken as relationships with their offspring gain importance (Furuichi 1989). So, 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 stabilise. Anecdotal data from 10 years of study at the Planckendael study group 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. Rather they withdraw, or make appeasement gestures to both parties of the conflict.

The reported discrepancy between bonding patterns in wild and captive populations (Stanford 1998;

Hohmann et al. 1999) was less pronounced in our study than in earlier reports. The results from captive studies should be interpreted cautiously, as captivity influences many aspects of behaviour, such as time spent grooming (Franz 1999). On the other hand, as it becomes clear that bonobos in the wild occupy a range of habitats, ranging from savannah woodland to dense rainforest (Boesch et al. 2002) and exhibit local cultures (Hohmann and Fruth 2003), captive studies can shed light on this species' adaptive potential (de Waal 1994).

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