# Fission–fusion species under restricted living conditions: a comparative study of dyadic interactions and physical proximity in captive bonobos and Bornean orangutans

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**The present study investigates how the 'fission–fusion-adapted' bonobos and Bornean orangutans manage social relationships when kept under permanent group-living conditions. Our results showed that the bonobos and orangutans did not differ in the overall frequency of dyadic interactions. The orangutans evidently realized a potential to interact with partners, which on a surface did not differ from what was found in the bonobos. However, the bonobos spent more time on sociopositive interactions, especially on grooming and sit in contact, whereas the orangutans agonistically interacted with each other more often. Though frequencies of approaching were similar between the two species, orangutans actively left the proximity to a partner more often than the bonobos, which in turn were more often in spatial proximity. The three groups of bonobos housed under different conditions differed from each other for sociopositive and agonistic interactions. The orangutans differed for agonistic but not for sociopositive interactions. As a striking difference between the species, it appeared that between subadult/adult orangutans, behaviours which required prolonged body contact occurred only rarely and briefly. Differences in bonding patterns have been discussed as a possible explanatory factor. The 'short and distant nature' of interactions between adult orangutans suggests the existence of social relationships, the management of which requires less 'servicing behaviours'. Subadult/adult orangutans may be less attracted by each other than individuals in more gregarious species: they may have the cognitive skills to interact, but may not be motivated to stay together for long.**

**Keywords:** Bonobo, orangutan, dyadic interactions, fission–fusion species, spatial proximity.

IN comparison to other mammals, in primates a particularly large variety of social systems has evolved[1]. A few species have a solitary way of living; others live in neighbourhood systems or pairwise systems. Many species are group-living[1,2]. There is a great diversity in species-specific group-demography referring to size, sex ratio and temporal stability (for detailed classification see, Vogel[2]). In some species, spatiotemporal group cohesion is strong and permanent (e.g. *Macaca* spp.)[1]. Especially in these species, social bonds among individuals support or even 'establish' group cohesion[3]. In others, individuals are associated more loosely in 'open communities'. Such flexible social systems can split into smaller temporary subunits (parties) of variable size and composition, which merge again ('fission–fusion' organization[4]). Two types of fission–fusion are identified: 'group-based'[4] (e.g. in hamadryas baboons) and 'individual based'. The latter is described for human societies, a few simian primate species[5] (e.g. spider monkeys) and (at least) for chimpanzees[6] and bonobos[7]. Orangutans, with their more solitary way of living, are hypothesized to be 'candidates' of fission–fusion[8], though evidences on the existence of loose communities around flanged males have been reported[9].

Recently, Aureli *et al.*[10] suggested to integrate Kummer's[4] approach towards fission–fusion systems into a broader concept. According to them, any social system can be described in terms of the extent to which it expresses fission–fusion. The authors postulate that temporal variations in spatial cohesion among group members, subgroup size and subgroup composition, which together constitute fission–fusion dynamics, influence the opportunities for group members to interact with each other and, ultimately, the resulting social system.

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Whereas a number of field studies both in bonobos and orangutans describe patterns of fission–fusion of individuals or subgroups in terms of time and space, and subgroup composition[11,12], investigations on a proximate level about the nature of social relationships in fission–fusion societies of apes based on the analysis of social interactions are rare. Especially studies which investigate the patterns, mechanisms and possible intrinsic determinants of fission–fusion on the individual level are missing. The possible cognitive and social challenges emerging from a lack of information about partners which an individual may meet occasionally and briefly are discussed with reference to possible inhibitory control systems which evolved in relation to an enhancement of cognitive skills[13]. These might enable individuals to suppress prepotent but ineffective responses (e.g. aggressive behaviour) in a changing and more or less unpredictable social environment. The limited and unpredictable presence of individuals and partner combinations (in subgroups) an observer in the wild is confronted with evidently makes it difficult to study these aspects quantitatively. Consequently, results from captive studies play an important role here[14].

Usually the sociality of chimpanzees and bonobos is compared[15]. Comparative studies on proximate aspects of social relationships and sociality between ape species, especially between genera, however, are rare. The present study aims to contribute here.

Captive studies were carried out on animals which live under restricted and largely constant conditions. The lack of temporal variation in terms of spatial cohesion, subgroup size and composition as typical for apes under captive conditions may hinder the occurrence of species-specific behavioural patterns and may occasionally lead to behavioural problems[16,17]. This constellation, though limiting the range of research questions to be answered, is used as a quasi-experimental set-up in our study. It allows us to comparatively ask how the 'fission–fusion-adapted' bonobos and Bornean orangutans manage social relationships when kept in stable groups with permanently present group mates. Results might allow drawing inferences about species-specific differences in sociality and adaptive potential[18].

In this study, we compared structural aspects of social behaviour in bonobos and Bornean orangutans as indicators of sociality. Specifically, we compared the quality and the strength (i.e. frequency and duration) of inter-individual interactions, physical contacts, and physical proximity: (a) between the species and (b) within the species among groups with different keeping systems: in one group each, individuals were kept in different subgroups temporarily and in the others, individuals were kept under stable group composition. We expected that these comparisons would yield species-specific differences pertaining to the relatively more gregarious living in bonobos than in orangutans[7,9,11,19–22].

We expected that the bonobos would interact with and physically contact each other to a greater extent than the orangutans, and would show relatively greater spatial proximity. We expected that the bonobos and not the orangutans would interact with and physically contact each other to a greater extent when kept in different subgroups than the individuals of the groups with stable group composition, and would show relatively greater spatial proximity.

According to the individual-based fission–fusion sociality in orangutans[8] with their high individual variation in the social behaviour observed in the wild[9,11,23], we expected the individual variability to be more pronounced among the orangutans (and possibly masking group-specific differences) than in the bonobos.

Some of the within-species comparisons have been carried out earlier by Kiessling[24] for bonobos, and Classen[25] for orangutans. We aim to combine these results and provide additional analyses.

## Methods

### *Subjects and housing conditions*

Tables 1 and 2 provide an overview of the study subjects and a brief description of their housing conditions.

### *Bonobos*

The subjects were 21 bonobos housed at the Cologne, Frankfurt and Planckendael zoos (Table 1). The Cologne group comprised of five individuals, and the Frankfurt and the Planckendael groups eight individuals each. While in the Cologne and Planckendael groups, the bonobos were kept together, in the Frankfurt group, they were mainly kept in two different subgroups, the compositions of which were altered by the colony keepers on an optional basis ('separation management', details described in Kiessling[24]). There were no bonobo transfers, births or deaths in any group during the study period.

### *Orangutans*

The subjects were 23 Bornean orangutans housed at the Apenheul, Chester and Cologne zoos (Table 2). The Apenheul group comprised of ten individuals, the Chester group five individuals, and the Cologne group eight individuals. In the Chester and Cologne groups, the orangutans were kept together in one and two groups respectively, whereas in the Apenheul group, the orangutans were mainly kept in two–three subgroups. The composition of these subgroups was altered daily by the colony keepers based on the preferences of the individuals ('separation management', details described in Classen[25]). Other than the transfer of one subadult male to another zoo and the

**Table 1.** Bonobos of the Cologne, Frankfurt and Planckendael groups

| Group | Individual | Age-class | Sex | Date of birth (DD/MM/YYYY) | Parents (father × mother) | Rearing |
|---|---|---|---|---|---|---|
| Cologne: housed in an indoor enclosure (area: ca. 145 sq. m) | | | | | | |
| | Clyde | Adult | Male | ca. 1978 | Unknown | Unknown |
| | Kindu | Adult | Male | 23/09/1984 | Clyde × Bonnie | Mother |
| | Bolombo | Subadult | Male | 07/11/1997 | Yenge × Kosana | Hand |
| | Bonnie | Adult | Female | ca. 1976 | Unknown | Unknown |
| | Binti | Adult | Female | 14/08/1995 | Bono × Ukela | Mother |
| Frankfurt: housed in three indoor enclosures (area: ca. 15, 27 and 32 sq. m) respectively with access to at least one outdoor enclosure (area: ca. 19 to 36 sq. m) | | | | | | |
| | Ludwig | Adult | Male | 26/08/1984 | Desmond × Dzeeta | Hand |
| | Heri | Infant | Male | 23/01/2001 | Ludwig × Natalie | Mother |
| | Margrit | Adult | Female | ca. 1951 | Unknown | Unknown |
| | Natalie | Adult | Female | ca. 1964 | Unknown | Mother |
| | Salonga | Adult | Female | 02/05/1973 | Camillo × Margrit | Mother |
| | Ukela | Adult | Female | 19/12/1985 | Bono × Natalie | Mother |
| | Kamiti | Adult | Female | 21/01/1987 | Masikini × Kombote | Unknown |
| | Haiba | Infant | Female | 16/11/2001 | Ludwig × Ukela | Mother |
| Planckendael: housed in an indoor enclosure (area: ca. 77 sq. m) with access to a huge outdoor enclosure (area: ca. 3000 sq. m) | | | | | | |
| | Kidogo | Adult | Female | 28/02/1983 | Masikini × Catherine | Hand |
| | Redy | Adult | Female | 24/11/1990 | Desmond × Hortense | Mother |
| | Vifijo | Adult | Female | 23/07/1994 | Kidogo × Hortense | Mother |
| | Zamba | Juvenile | Female | 16/04/1998 | Kidogo × Hortense | Mother |
| | Hermien | Adult | Female | ca. 1978 | Unknown | Unknown |
| | Hortense | Adult | Female | ca. 1978 | Unknown | Unknown |
| | Djanoa | Subadult | Female | 27/03/1995 | Santi × Yala | Mother |
| | Zomi | Juvenile | Female | 28/01/1998 | Kidogo × Hermien | Mother |

death of an adult female (both in the Cologne group), there were no orangutan transfers, births or deaths in any group during the study period.

### *Data collection*

Kiessling[24] observed the bonobos of the Cologne group for a total duration of 85 h (i.e. 17 h per individual), spread over a three-month span, i.e. November 2004–January 2005; the Frankfurt group, 584 h (i.e. 73 h per individual), spread over two, two-month and two, three-month spans between April 2003 and March 2004; the Planckendael group, 168 h (i.e. 21 h per individual), spread over a three-month span: July–September 2004.

Classen[25] observed the orangutans of the Apenheul group for a total duration of 270 h (i.e. 30 h per individual), spread over a two-month span: August–October 2005; the Chester group, 164 h: the all-female-group for 144 h (i.e. 48 h per individual) and the male–female-group for 20 h (i.e. 10 h per individual) spread over a two-month span: May–June 2004; the Cologne group, 828 h (i.e. 120 h per individual, except the subadult male, Sandai, observed for 6 h and the adult female, Suka, observed for 102 h), spread over ten, two-month spans between June 2002 and July 2005.

The observation hours fell between 0800 and 1630 h for the bonobos, and 1000 and 1600 h for the orangutans, balanced over time and focal animals each. During observational hours, Kiessling and Classen recorded the various aspects of social behaviour among the bonobos and the orangutans (Table 3) using focal animal sampling with continuous recording[26]; 10-min units were used as focal animal time in all settings. For social interactions, the observers recorded the identity of the actor and the recipient. To examine the socio-spatial patterns, in all groups the inter-individual distances were recorded using instantaneous scan sampling at 10-min intervals before and after each focal observation[26].

We averaged the 10-min units of focal sampling per each dyadic pair of bonobos and orangutans to determine the median frequency (number of interactions per hour) and the median duration (minutes per hour) of sociopositive and sexual interaction per dyad, and the frequency of agonistic interactions, approaching and leaving behaviour as we considered them as events, rather than states. As two pivotal elements of sociopositive interactions, we determined for each dyad the median frequency and duration partners spent on allogrooming and sitting in physical contact. We also calculated the frequency and duration for several other interactions per dyad for the overall comparison (Table 3), but did not analyse them separately. We did not include triadic interactions in the analyses; these are, however, described by Kiessling[24] and Classen[25]. The calculation of median values per hour was controlled for the time partners of a given dyad were

**Table 2.** Orangutans of the Apenheul, Chester and Cologne groups

| Group | Individual | Age-class | Sex | Date of birth (DD/MM/YYYY) | Parents (father × mother) | Rearing |
|---|---|---|---|---|---|---|
| Apenheul: housed in four indoor enclosures (area: ca. 58 sq. m each) with access to an outdoor enclosure (area: ca. 254–358 sq. m each) from each of them | | | | | | |
| | Karl | Adult | Male | ca. 1961 | Unknown | Unknown |
| | Willie | Juvenile | Male | 17/04/2002 | Karl × Radja | Mother |
| | Radja | Adult | Female | ca. 1963 | Unknown | Unknown |
| | Silvia | Adult | Female | ca. 1965 | Unknown | Unknown |
| | Sandakan | Adult | Female | 19/04/1982 | Giles × Bali | Unknown |
| | Ralfina | Adult | Female | ca. 1986 | Unknown | Unknown |
| | Jose | Adult | Female | 15/09/1992 | Pi-ku × Barbara | Unknown |
| | Katja | Subadult | Female | 17/05/1997 | Karl × Radja | Mother |
| | Binti | Juvenile | Female | 11/12/2000 | Tuan × Ralfina | Hand |
| | Samboja | Infant | Female | 09/06/2005 | Karl × Sandakan | Mother |
| Chester: housed in three in-line indoor enclosures (area: ca. 116, 116 and 172 sq. m respectively) with access to outdoor islands? from the last two (area: ca. 391 and 282 sq. m respectively) | | | | | | |
| | Matu | Subadult | Male | 26/11/1995 | Anark × Sarikei | Mother |
| | Martha | Adult | Female | ca. 1964 | Unknown | Unknown |
| | Sarikei | Adult | Female | 26/11/1983 | Dennis × Martha | Unknown |
| | Pundu | Adult | Female | 20/04/1989 | Anark × Lola | Mother |
| | Leia | Subadult | Female | 06/02/1996 | Anark × Martha | Mother |
| Cologne: housed in an indoor enclosure (area: ca. 245 sq. m) which can be divided into two separate enclosures (area: ca. 100 and 145 sq. m respectively) with access to a larger outdoor enclosure (area: ca. 485 sq. m) | | | | | | |
| | Bornie | Adult | Male | 18/03/1984 | Pi-ku × Barbara | Unknown |
| | Sandai | Subadult | Male | 20/08/1993 | Tuan × Lotti | Hand |
| | Barito | Juvenile | Male | 16/02/2000 | Bornie × Nony | Mother |
| | Bunyu | Juvenile | Male | 05/03/2000 | Bornie × Tjintah | Mother |
| | Lotti | Adult | Female | 29/01/1971 | Eddi × Petra | Hand |
| | Tjintah | Adult | Female | 01/05/1984 | Maias × Tjantike | Hand |
| | Suka | Adult | Female | 09/05/1984 | Yogi × Lotti | Hand |
| | Nony | Adult | Female | 28/10/1985 | Jonny × Nonja | Hand |

kept in the same subgroup for settings with altering subgroup compositions.

As a measure of socio-spatial cohesion, we calculated the proximity index (PI)[27] for each dyad, which could range from 0 to 1. PI was determined by the number of 10-min scans in which the two partners were found within a distance of 1 m from each other, divided by the total number of scans the two individuals were in sight and kept in the same (sub-) group.

We included only dyads composed of adult and subadult individuals in our analyses (Table 4). The engagement of the juvenile and infant individuals in the bonobo and orangutan groups has been previously investigated by Kiessling[24] and Classen[25] respectively.

### *Statistical analyses*

We performed all statistical analysis using two-tailed tests in SPSS 20. Median values per dyad for a given behavioural element were averaged to determine the median dyadic value per species, and per bonobo and orangutan group respectively. We used Mann–Whitney *U* tests to compare the dyadic values of behavioural elements between the two species. We applied Kruskal–Wallis one-way ANOVAs with post-hoc Mann–Whitney *U* tests in case of significant difference to compare the dyadic values for the behaviour of interest among the different groups per species with their different keeping conditions. For comparison between the species, we considered the outcomes of the tests significant at values $P < 0.05$. For comparisons of groups within the species, we applied Bonferroni correction for post-hoc multiple comparison and considered the test results as significant at alpha values $P < 0.0167$.

## Results

### *Between-species comparisons*

With regard to an average dyad composed of subadult/adult partners, the bonobos and orangutans did not differ in their overall frequency of dyadic interactions (median values: bonobos: 2.47 interactions/h, orangutans: 3.22 interactions/h; Mann–Whitney *U* test, $P$ = n.s., Appendix, Table A1). However, partners in a bonobo dyad spent four times longer duration on social interactions than

orangutan partners did (median values: bonobos: 2.12 min/h; orangutans: 0.27 min/h; Mann–Whitney *U* test, $P < 0.001$).

### *Sociopositive, agonistic and sexual interactions*

The median frequency of sociopositive interactions between partners was similar in both species (medians, bonobos: 0.82 interactions/h, orangutans: 0.68 interactions/h; Mann–Whitney *U* test, $P$ = n.s; Figure 1 *a*; Appendix, Table A1), but varied greatly among the dyads ranging up to a maximum of 7.33 interactions/h between orangutans and maximally 4.20 events/h in the bonobos. Individuals of both species interacted more often sociopositively among each other than agonistically, wherein the median frequency of dyadic agonistic interactions was six times higher in the orangutans than in the bonobos (medians, bonobos: 0.03 interactions/h, orangutans: 0.18 interactions/h; Mann–Whitney *U* test, $P < 0.001$; Figure 1 *a*). However, absolute frequencies of agonistic interactions per time unit were low in both species. The frequency of sexual interactions per dyad were even lower in both species, i.e. less than 0.06 events/h, and in both species partners spent only seconds on these interactions (Figure 1; Appendix, Table A1, Mann–Whitney *U* test, $P$ = n.s).

Regarding the duration of sociopositive interactions, there was a clear difference between the species with bonobos partners participating about ten times longer in sociopositive interactions as orangutan partners did (medians, bonobos: 1.89 min/h, orangutans: 0.20 min/h; Mann–Whitney *U* test, $P < 0.001$; Figure 1 *b*; Appendix, Table A1).

**Table 3.** Dyadic interactions among the bonobos and orangutans (asterisks indicates the behaviour for which the duration was recorded)

| |
|---|
| Sociopositive interactions |
| Allogroom* |
| Beg |
| Embrace* |
| Graze |
| Invite to play |
| Kiss |
| Make contact |
| Peer* |
| Play socially (contact or w/o contact)* |
| Share food |
| Sit/or be in physical contact (including lean arm on)* |
| Tandem* |
| Touch gently |
| Agonistic interactions |
| Attack |
| Chase/direct charge |
| Displace |
| Draw |
| Flee* |
| Flinch |
| Give |
| Grasp |
| Hit |
| Precede |
| Push back (contact or w/o contact) |
| Retreat/evade |
| Scuffle |
| Shrink back |
| Take away food/object |
| Tease |
| Threaten |
| Sexual interactions |
| Inspect genitals (contact or w/o contact)* |
| Copulate* |
| Position* |
| Present itself* |
| Rape* |
| Rub genitals* |
| Try to copulate* |
| Approach/come close (in normal pace) |
| Leave/go away (without any proceeding agonistic interaction) |
| Other interactions |
| Advance |
| Drink urine |
| Follow* |
| Pass by |
| Hold out hand* |
| Watch conspecific* |

### *Allogrooming and sit in contact*

The analyses of two sociopositive elements which imply staying in body contact revealed that grooming and sit in contact occurred only briefly between orangutan partners in general and lasted on average for seconds per hour only, though the variability among dyads was higher in the bonobos compared to the orangutans (grooming, bonobo dyads: min–max: 0.00–3.08 events/h and 0.00–8.21 min/h, orangutans dyads: min–max: 0.00–1.56 events/h and 0.00–5.58 min/h). In a bonobos dyad, partners groomed each other multiple times more often (0.39 times/h) and longer (1.34 min/h) than individuals of an orangutan dyad (median, 0.0 events/h and 0.01 min/h; Mann–Whitney *U* test, Appendix, $P < 0.001$, Appendix,

**Table 4.** The total number of dyads per bonobo and orangutan group and the number of dyads composed of adult and sub-adult/adult individuals used for comparative analysis

| Species<br>Group | Total no. of dyads | No. of dyads observed |
|---|---|---|
| Bonobos | 66 | 40 |
| Cologne | 10 | 10 |
| Frankfurt | 28 | 15 |
| Planckendael | 28 | 15 |
| Orangutan | 65 | 38 |
| Apenheul | 33 | 19 |
| Chester | 4 | 4 |
| Cologne | 28 | 15 |

Table A1). Bonobo partners also sat more often in contact with each other compared to orangutan partners, but differences did not reach significance (medians, orangutan: 0.08 times/h, bonobos: 0.21 times/h; Mann–Whitney *U* test, *P* = n.s; Figure 2 *a*; Appendix, Table A1). Referring to the duration, bonobo partners spent ten times more duration on sitting in body contact (Mann–Whitney *U* test, $P < 0.001$; Figure 2 *b*), i.e. 0.21 min/h, whereas the orangutans sat in contact for only 0.02 min/h.

### *Approaching, leaving and spatial proximity*

In both species, partners of an average dyad came close to each other once per hour (median, bonobos: 0.96 times/h, orangutans: 1.00 times/h; Mann–Whitney *U* test, *P* = n.s; Figure 3; Appendix, Table A1). Orangutan individuals also actively left the proximity to a partner in median once per hour, whereas bonobo partners rarely did (Mann–Whitney *U* test, $P < 0.001$).

The analyses of PI revealed that subadult/adult bonobos were on average four times more often in each other's proximity compared to orangutan partners (median, PI bonobos = 0.09, PI orangutans = 0.02; Mann–Whitney *U* test, $P < 0.001$; Figure 4; Appendix, Table A1).

### *Within-species comparisons*

*Bonobos:* The comparison among groups revealed that the bonobo groups differed in most of the socio-spatial aspects analysed, but not in the frequency of agonistic interactions (Appendix, Tables A2 and A3). Differences were mainly found between the individuals kept under flexible grouping conditions at Frankfurt and those kept under constant grouping, but spacious conditions at Planckendael.

Post-hoc comparison revealed that partners of a given dyad at Frankfurt interacted above three times more often and for longer duration by sociopositive and sexual

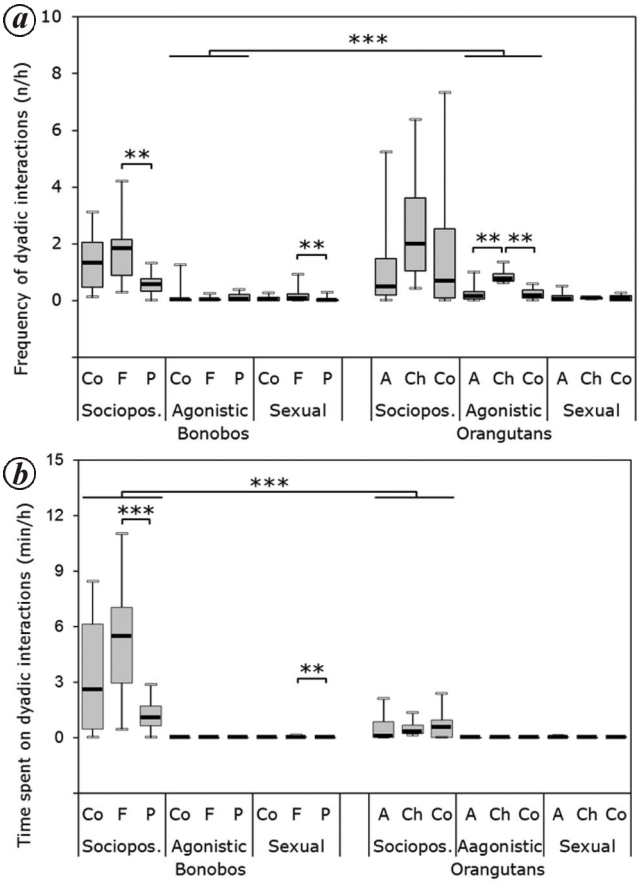


**Figure 1.** Median (***a***) frequency of and (***b***) time spent on sociopositive (sociopos.), agonistic, and sexual interactions among bonobos of the Cologne (Co; number of dyads = 10), Frankfurt (F; number of dyads = 15) and Planckendael (P; number of dyads = 15) groups, and orangutans of the Apenheul (A; number of dyads = 19), Chester (Ch; number of dyads = 4) and Cologne groups (Co; number of dyads = 15). $^{**}P < 0.005$, $^{***}P < 0.001$.

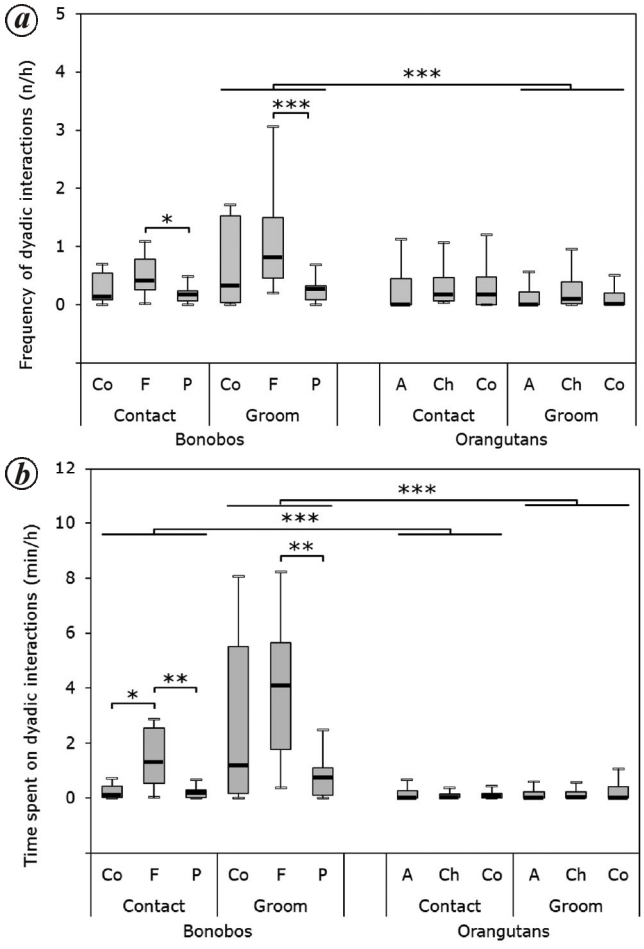


**Figure 2.** Median (***a***) frequency of and (***b***) time spent on grooming and sitting in contact among bonobos of the Cologne (number of dyads = 10), Frankfurt (number of dyads = 15) and Planckendael (number of dyads = 15) groups, and orangutans of the Apenheul (number of dyads = 19), Chester (number of dyads = 4) and Cologne groups (number of dyads = 15). $^{*}P < 0.01$, $^{**}P < 0.005$, $^{***}P < 0.001$.

interactions than dyadic partners at Planckendael (post-hoc Mann–Whitney *U* tests: frequency sociopositive: $P = 0.001$, sexual: $P = 0.003$; duration spent on: sociopositive: $P < 0.001$, sexual: $P = 0.002$). Differences between the Cologne and the Frankfurt groups, and Cologne and Planckendael respectively, did not reach significance (Appendix, Tables A2 and A3).

Median values of grooming (0.81 bouts/h and 4.91 min/h; Figure 2) were also found to be about five times higher at Frankfurt compared to those at Planckendael (post-hoc Mann–Whitney *U,* frequency: $P < 0.001$; duration: $P < 0.001$; Appendix, Table A2), and sitting in contact was three times higher for individuals for a given dyad at Frankfurt (post-hoc Mann–Whitney *U*, frequency: F vs P: $P = 0.006$, F vs Co: $P =$ n.s.; duration: F vs Pl: $P = 0.001$; F vs Co: $P = 0.004$).

Regarding approaches and leavings, bonobo partners at Frankfurt and Cologne came close to and went away from each other more often than bonobos of an average dyad at Planckendael (Figure 3; post-hoc Mann–Whitney *U,* approach: F vs P: $P < 0.001$, F vs Co: $P =$ n.s, Co vs P: $P = 0.002$; leave: F vs P: $P < 0.001$, F vs Co, Co vs. P: $P =$ n.s). Under the spacious conditions at Planckendael, partners were found least often in close proximity with an average PI = 0.04 compared to the pronounced proximity at Frankfurt (PI = 0.22; Figure 4, post-hoc Mann–Whitney *U*, F vs P: $P = 0.008$, F vs Co: $P =$ n.s, Co vs P: $P < 0.001$).

*Orangutans:* The comparison among the zoo groups revealed that the orangutan groups did not differ significantly in almost any of the socio-spatial aspects analysed (Appendix, Tables A2 and A3).

Regarding the frequency of interactions, partners of a given dyad kept in the constant small-sized groups at Chester interacted sociopositively and agonistically, and approached and left each other about three times more often each compared to partners of an average dyad at Cologne and Apenheul living under more spacious conditions and in larger-sized, or flexible groupings respectively (Figure 1 *a*, 3). At Chester, partners were also found more often within close spatial proximity (median PI = 0.05) compared to the other groups.

In contrast, referring to the duration (Figure 1 *b* and 2 *b*), partners at Chester spent on average least time per time unit on sociopositive interactions. Dyads at Chester ranged at the lower end in particular regarding the duration of grooming and sit in contact compared to individuals with more different partners available at Apenheul and Cologne. In the latter group, highest values for grooming were found in some dyads (Figure 2).

However, the variation at all socio-spatial aspects was high among the dyads in all groupings and none of the differences reached statistical significance (Kruskal–Wallis tests, $P =$ n.s.; Appendix, Tables A2 and A3), with the exception of agonistic interactions (post-hoc Mann–Whitney *U* tests, A vs Ch: $P = 0.002$; Ch vs Co: $P < 0.001$).

## Discussion

Our study aimed to comparatively investigate the sociality of captive bonobos and Bornean orangutans by analysing structural aspects of their social behaviour. The captive conditions were used as a quasi-experimental set-up to examine how the 'fission–fusion-adapted' bonobos and Bornean orangutans manage social relationships when kept in groups with permanently present group mates. Captive conditions were expected to facilitate

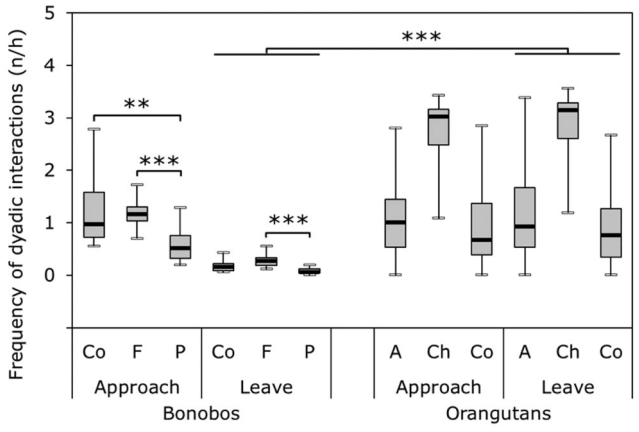


**Figure 3.** Median frequency of approaching and leaving interactions among bonobos of the Cologne (number of dyads = 10), Frankfurt (number of dyads = 15) and Planckendael (number of dyads = 15) groups, and the orangutans of the Apenheul (number of dyads = 19), Chester (number of dyads = 4) and Cologne groups (number of dyads = 15). $^{**}P < 0.005$, $^{***}P < 0.001$.

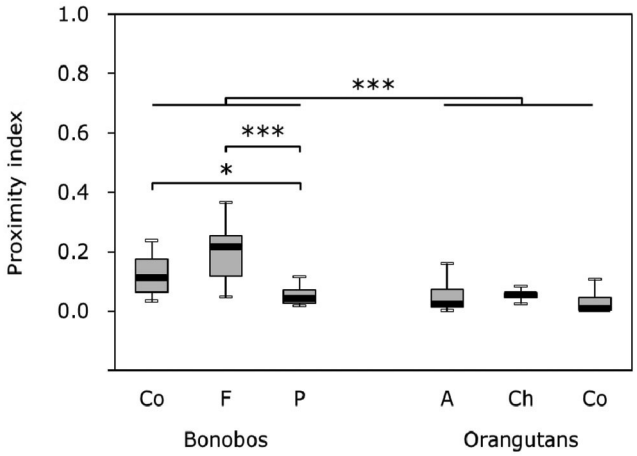


**Figure 4.** Median proximity index values for bonobos of the Cologne (number of dyads = 10), Frankfurt (number of dyads = 15) and Planckendael (number of dyads = 15) groups, and orangutans of the Apenheul (number of dyads = 19), Chester (number of dyads = 4) and Cologne groups (number of dyads = 15). $^{*}P < 0.01$, $^{***}P < 0.001$.

inferences about species-specific differences in sociality and adaptive potential.

Under these conditions, we expected the supposedly more gregarious bonobos to interact with and physically contact each other more frequently and longer compared to the orangutans, and to show greater spatial proximity. Since in both species one of the study groups was kept under 'separation management', which in a limited way mimicked fission–fusion conditions as described for the wild, a comparison between the two types of groups allowed assessing the influence of the management system on the social behaviour of the study animals. Against our expectations the two species did not differ significantly referring to the overall frequency of interactions: the supposedly less gregarious orangutans showed an even higher median value per hour than the bonobos. In both species interactions were predominantly of a socio-positive nature; agonistic interactions were rare, but occurred more often in the orangutans. The time spent on interactions, however, was higher in the bonobos. This was specifically the case for allogrooming, which occurred much more rarely and only briefly in the orangutans. A tendency in the orangutans to be engaged only little in prolonged body contact as required for allogrooming was also indicated by lower frequencies and less time spent in sitting in body contact.

In both species partners approached each other with a similar frequency; leaving a partner, however, occurred significantly more often in the orangutans. Sexual interactions occurred rarely in both species. In the bonobos more than in the orangutans, however, the results on sexual interactions are biased by the exclusion of infants and juveniles as they used to be involved in a decent proportion of them. The overall frequency of sexual interactions on group level therefore was higher in the bonobos[24].

On the level of analysing sociality as chosen here, it is evident that the presumably more solitary and less gregarious Bornean orangutans under conditions of permanent spatial closeness and presence of group mates did realize a potential to interact (peacefully) with partners and to manage social relationships, which on a surface did not differ much from what was found in the bonobos. As a striking difference between the species, however, appeared that between subadult/adult orangutans behaviours which required prolonged body contact, especially like allogrooming occurred only rarely and briefly. This is in accordance with what is reported from field studies: in free-ranging orangutans, social interactions (excluding mother–infant dyads), especially interactions with physical contact, seem to be rare[23,28–30]. Grooming is reported anecdotally to occur between adolescent females[31], but it is described to be uncommon[23] or virtually absent between adult individuals[31]. Feeding and resting in spatial proximity, e.g. near or in richly fruiting trees ('social feeding', 'social resting'), however, is regarded as an indicator for affiliate relationships[22,28,32,33].

Other captive studies on orangutans revealed higher frequencies in social interactions and grooming than assumed for free-ranging individuals. This is tentatively attributed to the favourable ecological conditions and a higher density of potential social partners in captivity[34–40].

The patterns of interactions and the spatial patterns indicate that our orangutan study groups were less cohesive than the bonobo groups. Other patterns of spatial behaviour in the orangutans described by Classen[25], furthermore indicated large and highly variable inter-individual distances, small nearest neighbour distances, and frequent changes of partners within the nearest surroundings in all three groupings. At Cologne, individuals tended to be more widely dispersed under conditions of more available space. Since there were large differences between individual dyads across the orangutan groups, however, it is likely that the interactive and spatial behaviour were less influenced by their group/zoo-specific physical and social living conditions, but tended to be expressed in an individualistic manner. Even the 'separation management' practised with the Apenheul orangutans did not lead to group-specific patterns there. This finding contrasts strongly with the significant differences of the intergroup comparison found in the bonobos. The 'separation management' as practiced at Frankfurt Zoo was accompanied by the highest frequencies and most time spent on interactions in this group, though in terms of available space these individuals lived under the most limited conditions of our study groups. The results on the bonobos fit well with those provided by other authors[14] revealing significant differences among groups in a number of parameters for six study groups kept in different zoos. Our results also reveal the influence and resulting importance of social and spatial living conditions in captive bonobos.

Our comparative approach moreover allowed obtaining further insight into the sociality of orangutans and their evolution. It reveals that the nature of the social relationships might be a critical component of orangutan sociallity.

As a possible underlying explanatory factor for the differences between the species, our results suggest considering species-specific differences in bonding patterns. According to van Schaik *et al.*[32], there is not much evidence for clear social bonds between adult orangutans in the field. In bonobos, both field and captive studies demonstrated the existence and importance of social bonds[41,42]. Following Lehmann *et al.*[43] the maintenance of social bonds in primates requires interactions and, in particular, grooming. The orangutans of our study groups interacted but did not spend much time on it. The 'short and distant nature' of interactions between subadults/adults and their limited physical component suggests the existence of social relationships, the maintenance and

management of which require less servicing behaviours sensu Lehmann *et al.*[43]. Whether this is linked to or even a result of the absence of social bonds between adults remains questionable (for a general discussion on the use of the term 'bond' see Silk *et al.*[44]). According to Cords[45], the term 'friendship' or 'bond' usually implies affiliation in the form of extraordinary proximity or grooming, or both. The ecological conditions under which the orangutan system may have evolved might have required more extreme fission–fusion patterns leading to an almost solitary way of living with competitive structures between adult females in overlapping areas of their home ranges[22]. Under these conditions and possibly under the condition of low predation pressure, the maintenance of social bonds, including strong mutual (physical) attraction was possibly not supported[43]. As a consequence adult orangutans may be less attracted to each other than individuals in more gregarious species. If they meet they may have the cognitive tools and skills to interact, but they may not be motivated to stay together for long. This overall pattern would be compatible with the 'Route B' of the evolution of fission–fusion dynamics as proposed by Aureli *et al.*[10]. This patterning towards the evolution of a higher degree of fission–fusion dynamics 'does not require that differentiated social relationships become increasingly valuable as gregariousness intensifies, and associations may have been short-lived and random or opportunistic'. As the structure of social relationships among the orangutans of our study reflected these traits also under the conditions of optimal ecological conditions and high density of potential partners, our results indicate this tendency to be a species-specific feature.

Our study also intended to investigate whether under captive conditions the fission–fusion adapted study species can cope with the permanent presence of partners, The results of the study suggest that they do have the potential inhibitory control systems might play an important role here too. For the discussion of whether keeping orangutans and bonobos respectively, in permanent groups is appropriate when taking into account their way of living in the wild our study shows that they have at least some coping potential. There are pointers, however, that on a larger timescale and on the captive population level at least some individuals are beyond their coping potential leading to behavioural disturbances and breeding problems, e.g. almost 40% of the orangutan females did not breed successfully[48]. Aberrant behaviours like regurgitation, hair pulling and other behavioural disturbances have been reported from captive groups[25,46]. Furthermore, hormonal analyses indicated that female Bornean orangutans tend to show a stress response when housed in permanent groups, whereas Sumatrans do not[47].

The analysis of the historical European bonobo population[48] showed a moderate growth and that about 82% of the adult females bred. For this more gregarious species, however, there are evidences on the occurrence of behavioural problems too (e.g. increase in certain types of aggression under more crowded conditions in winter[17], hair pulling[46]). On the other hand, van Dyck *et al.*[49] found more frequent grooming during this period. An earlier study[50] on the Cologne group showed that after a 15-year period without any change in group composition and no breeding, a change in group composition was followed by an increase in social and especially sexual behaviours and successful breeding. Stevens *et al.*[14] also found a higher level of interactions in newly formed groups. Separations and reunifications are therefore assumed to have a positive effect on the affiliation in bonobos.

Our study compared the interactive behaviour of bonobos and Bornean orangutans on a rough and structural level. This approach revealed surprisingly clear similarities on the overall adaptive potential of the two species supposed to incorporate a similar type of fission–fusion system, and at the same time indicated species-specific differences in the characteristic of social relationships as the underlying basis of the system.

## Appendix

**Table A1.** Results of Mann–Whitney *U* tests comparing the median frequency of dyadic interactions and proximity index values between the bonobos (number of dyads = 40) and orangutans (number of dyads = 38)

| | Frequency | | Duration | |
|---|---|---|---|---|
| Dyadic interactions | *U* | *P* | *U* | *P* |
| All interactions | 585.0 | 0.080 | 256.0 | < 0.001 |
| Sociopositive | 704.0 | 0.576 | 278.0 | < 0.001 |
| Agonistic | 343.0 | < 0.001 | – | – |
| Sexual | 682.0 | 0.423 | 636.0 | 0.203 |
| Contact | 616.0 | 0.148 | 390.0 | < 0.001 |
| Grooming | 313.0 | < 0.001 | 245.0 | < 0.001 |
| Approach | 712.0 | 0.631 | – | – |
| Leave | 181.0 | < 0.001 | – | – |
| Proximity index | 339.5 | < 0.001 | – | – |

**Table A2.** Results of Kruskal–Wallis tests with post-host Mann–Whitney *U* tests comparing the median frequency of dyadic interactions and proximity index values among different groups of bonobos (number of dyads: Cologne, Co = 10; Frankfurt, F = 15; Planckendael, P = 15) and orangutans (number of dyads: Apenheul, A = 19; Chester, Ch = 4; Cologne, Co = 15)

| | Bonobos | | | | | | | | Orangutans | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Co vs F vs P | | Co vs F | | Co vs P | | F vs P | | A vs Ch vs Co | | A vs Ch | | A vs Co | | Ch vs Co | |
| | $\chi^2$ | *P* | *U* | *P* | *U* | *P* | *U* | *P* | $\chi^2$ | *P* | *U* | *P* | *U* | *P* | *U* | *P* |
| All interactions | 16.630 | <0.001 | 62.0 | 0.495 | 26.0 | 0.005 | 18.0 | <0.001 | 4.761 | 0.092 | – | – | – | – | – | – |
| Sociopositive | 9.856 | 0.007 | 62.0 | 0.495 | 42.0 | 0.071 | 37.0 | 0.001 | 1.705 | 0.426 | – | – | – | – | – | – |
| Agonistic | 1.116 | 0.572 | – | – | – | – | – | – | 9.685 | 0.008 | 3.0 | 0.002 | 130.5 | 0.681 | 0.0 | <0.001 |
| Sexual | 9.129 | 0.010 | 43.5 | 0.080 | 62.0 | 0.495 | 43.0 | 0.003 | 0.112 | 0.945 | – | – | – | – | – | – |
| Sit in contact | 7.420 | 0.024 | 45.0 | 0.103 | 67.5 | 0.683 | 47.0 | 0.006 | 1.849 | 0.379 | – | – | – | – | – | – |
| Grooming | 11.934 | 0.003 | 50.0 | 0.177 | 61.0 | 0.461 | 22.0 | <0.001 | 1.412 | 0.494 | – | – | – | – | – | – |
| Approach | 17.468 | <0.001 | 61.0 | 0.461 | 22.0 | 0.002 | 18.0 | <0.001 | 5.593 | 0.061 | – | – | – | – | – | – |
| Leave | 19.125 | <0.001 | 35.0 | 0.026 | 36.0 | 0.031 | 12.0 | <0.001 | 5.477 | 0.065 | – | – | – | – | – | – |
| Proximity index | 20.614 | 0.001 | 34.0 | 0.023 | 11.0 | < 0.001 | 28.5 | 0.008 | 3.634 | 0.097 | – | – | – | – | – | – |

**Table A3.** Results of Kruskal–Wallis tests with post-host Mann–Whitney *U* tests comparing the median duration of dyadic interactions among different groups of bonobos (number of dyads: Cologne = 10; Frankfurt = 15; Planckendael = 15) and orangutans (number of dyads: Apenheul, A = 19; Chester, Ch = 4; Cologne, Co = 15)

| | Bonobos | | | | | | | | Orangutans | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Co vs F vs P | | Co vs F | | Co vs P | | F vs P | | A vs Ch vs Co | | A vs Ch | | A vs Co | | Ch vs Co | |
| | $\chi^2$ | *P* | *U* | *P* | *U* | *P* | *U* | *P* | $\chi^2$ | *P* | *U* | *P* | *U* | *P* | *U* | *P* |
| All interactions | 13.473 | 0.001 | 50.0 | 0.177 | 48.0 | 0.144 | 21.0 | < 0.001 | 0.762 | 0.683 | – | – | – | – | – | – |
| Sociopositive | 13.473 | 0.001 | 49.0 | 0.160 | 56.0 | 0.311 | 22.0 | < 0.001 | 0.878 | 0.645 | – | – | – | – | – | – |
| Agonistic* | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Sexual | 10.688 | 0.005 | 34.5 | 0.023 | 66.0 | 0.643 | 41.0 | 0.002 | 0.003 | 0.998 | – | – | – | – | – | – |
| Sit in contact | 12.509 | 0.002 | 24.0 | 0.004 | 71.5 | 0.849 | 37.0 | 0.001 | 2.593 | 0.276 | – | – | – | – | – | – |
| Grooming | 11.611 | 0.003 | 55.0 | 0.285 | 58.00 | 0.367 | 22.0 | < 0.001 | 1.028 | 0.598 | – | – | – | – | – | – |
| Approach* | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Leave* | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Proximity index* | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |

*No duration.

Due to the limited scope of the study, aspects such as the behaviour and role of infants, polyadic interactions which are indicated to be rare in orangutans but common in bonobos, details of the sexual behaviour and vocalizations have been not included here. The inclusion of these aspects and behavioural systems in future studies might provide a better picture, probably revealing more species-specific behavioural traits.


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