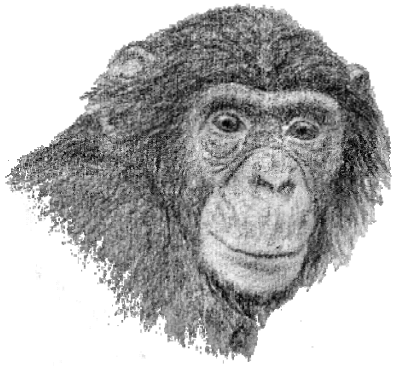
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Social relationships in zoo-living bonobos, *Pan paniscus*



Dissertation

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vorgelegt von

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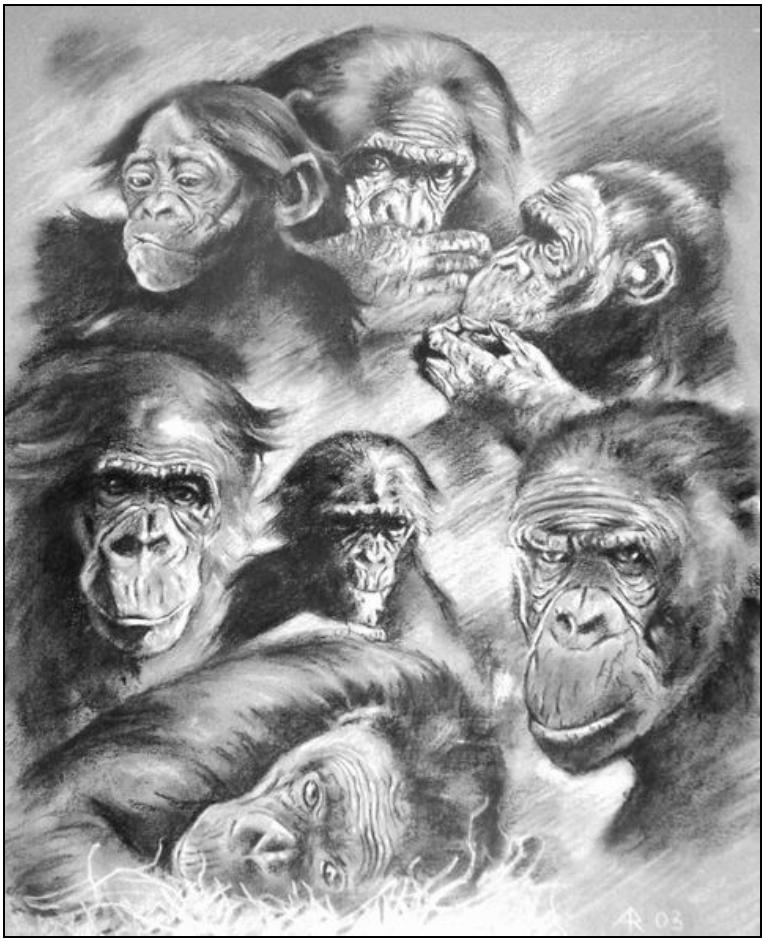
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Front cover: Bonobo female Bonnie, Cologne Zoo (drawing by Dorothee Claßen)



Impressions of the bonobo group in Frankfurt
(drawing by Alexander Rebik, 2003)

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1. Introduction

Primates belong to the most social of all mammals (Dunbar, 1988). Most primate social systems are considerably diverse and complex and many primate species form various kinds of long-term social relationships (Cheney et al., 1987).

This study investigates aspects of the social relationships of bonobos (*Pan paniscus*). Bonobos are still the least studied of the great apes (Stanford, 1998). They live in complex fission-fusion social systems in the wild (Kano, 1992) with their social lives being shaped by flexible grouping patterns. Only a few studies exist with regard to patterns and proximate causes of the observed grouping patterns in free-ranging bonobos, basically referring to ecological pressures (Kuroda, 1979; White, 1988; Hohmann & Fruth, 2002).

Zoo-living bonobos are mainly kept in small, long-term stable groups (Stevens et al. 2008), often lacking the experience of changes in grouping for several years. Little investigations about the impact of partner changes on their social relationships were carried out so far, primarily associated with integration processes (Pfalzer & Ehret, 1995; Haase 2002).

The present study analyses and describes the social relationships in 3 groups of zoo-living bonobos, one of which is kept in an artificial fission-fusion system. It thereby focuses on possible effects of the more flexible keeping strategy on the social lives of captive bonobos. The results may help to detect hints with regard to intrinsic motivations and social needs of fission-fusion primate species apart from food supply and other ecological factors.

1.1 Social relationships

According to Hinde (1975), a social structure arises from content, quality and patterning of relationships, and relationships are in turn seen as the content, quality and patterning of interactions. Patterns of interactions are brought about by the frequency of different types of interactions and their mutual impact. A relationship only occurs over time and can not be defined in a snap-shot. Stability (the maintenance of a steady state within limits) plays a major role, but a relationship must also be dynamic to a certain extent (interactions are affected by preceding interactions and affect subsequent interactions, and physical environments may change). Additionally, each relationship an individual has is affected by other relationships it has and the relationships of its partners (Hinde, 1979).

To get a picture of the structure of a complex social group it is essential to understand its social network by investigating the different social relationships between its members.

Relatively simple interactions among group members may coordinate much of complex group behaviour ("self-organization theory", Couzin & Krause, 2003). Structures, affecting the social relationships of primates on a daily, proximate level are often related with dominance and inhibition (Kummer, 1984) and with mechanisms to manage and overcome conflicts, like cooperation and reconciliation (Muller & Mitani, 2005; de Waal, 2000).

1.2 Primate social systems

Evolutionary processes resulted in a great diversity of social systems found within the primate order. Kappeler & van Schaik (2002) distinguish between 3 basic elements of primate social systems, which had been recognized and identified as fundamental and distinct components earlier, although they have been named and used interchangeably by means of different terms and labels (van Schaik & van Hooff, 1983; Wrangham, 1987, Dunbar, 1988):

1. The social organisation, which describes the size, sexual composition and spatiotemporal cohesion of a society (3 fundamental types: solitary, pair-living, and group-living species).
2. The mating system, including a social and a genetic component (monogamy, polygyny, polyandry and polygyandry).
3. The social structure, which refers to the pattern of social interactions and the resulting relationships among the members of a society (interfemale, intermale and intersexual relationships).

These 3 elements can be considered in isolation but they are highly interrelated. The social organisation e.g. determines which animals are available for relationships but, from an evolutionary point of view, the benefits of the formation of particular kinds of alliances (elements of the social structure) may have led to a particular kind of social organisation (Kappeler & van Schaik, 2002).

Most primate species live in social groups. A group can be regarded as a set of individuals in a closed social network (Struhsaker, 1969). Kummer (1971) defines a primate group as "…a number of animals, which remain together in or separate from a larger unit and mostly interact with each other".

According to van Schaik & van Hooff (1983), groups will form where basic requirements (obtaining food, avoiding predators and reproducing) are best pursued in the company of others. For a detailed essay about the reasons why primates might form groups see Dunbar (1988). The classic socio-ecological paradigm links ecological factors (resources and risks) to

female distribution and relationships, whereas mating opportunities (access to fertile females) are linked to male distribution and relationships (Emlen & Oring, 1977). The distinction between a single-male or a multi-male system, according to van Schaik & van Hooff (1983), is ultimately dependent on the varying ability of a male to monopolize access to a breeding group of females, which in turn depends on group cohesiveness, determined by feeding strategies and predation pressure.

Competition for food can be of the contest or of the scramble type, and can occur both, within and between groups (van Schaik, 1989). The contest type of competition is found if an individual (or a group) is able to monopolize an exclusive feeding patch, e.g. trees with seasonally ripe fruits. Behaviours, related to dominance are advantageous in this case. The scramble type is found when resource patches are highly dispersed, of low quality or to large to monopolize (no restricted access, e.g. leaves). Dominance behaviour has no direct beneficial value in this case. The majority of frugivores and omnivores belong to the contest type, whereas in folivores the scramble type is more abundant (van Schaik, 1989), but the competition experienced by a group-living animal is generally a mix of both kinds (van Schaik, 1989; Sterck et al., 1997).

Despite ecological factors, which are said to play a more important role in the evolution of female associations, several other factors are discussed to affect the formation of association patterns and social relationships within and between the genders in nonhuman primates. Some of the social factors, mentioned and discussed in this regard are e.g. infanticide avoidance, male sexual strategies, coalitions and mate choice (Smuts, 1987; van Schaik, 1996; Sterck et al., 1997; Koenig, 2002).

A great variety exists among the primate order regarding different types of social organization, ranging from mainly solitary primates with only some gregarious tendencies (e.g. lorises, bushbabies and tarsiers; Bearder, 1987) and family groups of pair-living primates (e.g. gibbons; Leighton, 1987) to bigger social units as found with most catarrhine primates (Vogel, 1975). The last author provided one of the first classifications of different types of social organization in catarrhine primates (Old World monkeys and apes). Regarding groups, containing multiple males and females, usually called multi-male groups because polyandry is very rare in mammals, Vogel differentiated between more “closed” groups and so called “open communities”. In the first case, group cohesion widely remains constant (separated all-male troops or solitary males may additionally exist), whereas the latter reflect flexible societies with a, to some extent, uncommitted change in composition (Vogel, 1975; fig. 1.1).

Members of different subgroups meet each other and may separate again in an altered composition. The phenomenon of "temporary associations" was already described by Goodall in 1965, when studying chimpanzees in Gombe. The type of social organization, in which members of a community forage and travel in varying subgroups is described by the term fission-fusion society today.

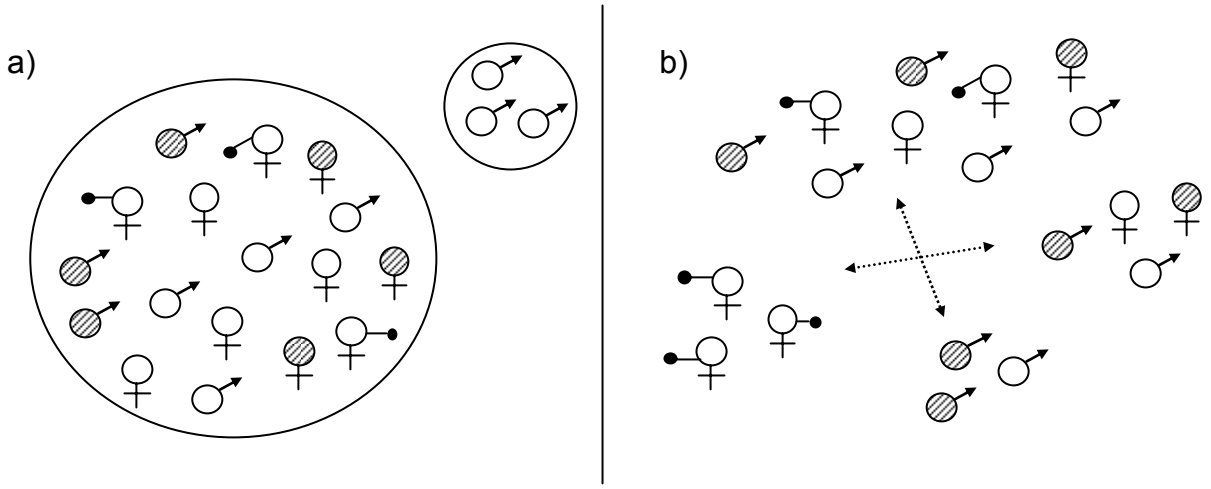


Fig. 1.1: Two different types of social organization found in multi-male primate groups (based on type VI and type VIII of Vogel's classification from 1975: a) Closed multi-male group with possible loosely attached all-male troop; b) "Open community" with alternating subgroup memberships (fission-fusion society); ♀=female, ♂=male, ●=infant, striped=juveniles

1.3 Fission-fusion societies

A crucial attribute of fission-fusion societies is that social units are variable in respect of size and composition. Different species of mammals are known to live in this kind of dynamic groups, in which members merge and split regularly. Mammals, said to live in fission-fusion social systems are e.g. African elephants (*Loxodonta africana*; Couzin, 2006), bottlenose dolphins (*Tursiops truncatus*; Connor et al., 2000), spotted hyenas (*Crocuta crocuta*; Smith et al., 2007) and several primate species (see below). Animals belonging to one community can only rarely be observed all together because they forage and travel in flexible subgroups.

Two types of fission-fusion societies were differentiated by van Schaik (1999) among nonhuman primates: Species living in more persistent, unaltered subgroups or bands, which regularly come together as a herd or community e.g. at sleeping sites, represent the group-based or nested fission-fusion type (e.g. hamadryas baboons, *Papio hamadryas*; Kummer, 1971; Zinner et al., 2001). By contrast, some species live in communities whose subgroups or parties (term established by Sugiyama, 1968) are not rigidly structured, so that party membership can change from day to day or even from hour to hour (McFarland-Symington,

1990). According to van Schaik (1999), this organisation form can be called individual-based fission-fusion.

It seems likely, that the flexible nature of the fission-fusion system requires well developed intellectual capacities like a long-term memory (Tutin et al., 1983). Particularly separating and reuniting beyond the limits of persistent social units is assumed to require complex social skills (Kummer, 1971). It can be found among large, arboreal frugivores, like spider monkeys (*Ateles spec.*; Wallace, 2008) and within 3 out of the 4 great ape species: chimpanzees and bonobos (*Pan troglodytes* and *Pan paniscus*; Stanford, 1998) and, to a certain extent, orang-utans (*Pongo spec.*; van Schaik, 1999).

Generally, flexible grouping patterns are assumed to be an adaptation to specific ecological conditions (Kummer, 1971; McFarland Symington, 1990; Ramos-Fernandez et al., 2006). On a more proximate level, various factors were found to be possible determinants regarding the fission-fusion patterns of a given society:

Food availability and/or the number of oestrous females present in subgroups was said to explain large parts of variation observed in party sizes of chimpanzee and bonobo communities (Mitani et al., 2002; Anderson et al., 2002; Kuroda, 1979, White, 1998). Contrarily, some researchers stated that neither the number of receptive females nor feeding competition could explain the observed party size variations in this great ape species (Hohmann & Fruth, 2002; Lehmann & Boesch, 2004). Hohmann & Fruth (2002) found that only the adult sex ratio changed in favour of males when oestrus females were present in bonobo parties. Additionally, male membership per party was larger in their study, on days following intercommunity encounters, which may have had protection functions. Lehmann & Boesch (2004) stated that chimpanzee subgroups lasted longer and were larger with decreased community size (also mentioned by Hohmann & Fruth, 2002), indicating that demographic variables play an important role in the fission-fusion fluidity. However, parties still altered within minutes or hours in their study after community size decreased. Additionally, a possible "need" to encounter all community members on a regular basis was guessed by Lehmann & Boesch (2004) for chimpanzees and a "need" to obtain information at least on food resources was also supposed to partly drive the bonobo fission-fusion dynamic (Fruth & Hohmann, 1996).

Thus, apart from its evolutionary history, the fission-fusion social system seems to be driven by many parameters, including demographic, ecological and social components which are highly interweaved. It may be that one parameter gets more apparent if the constraint of another one is more relaxed, e.g. in times of food abundance social factors may progressively

become more important (Newton-Fisher et al., 2000). To identify factors which drive cognitively complex organisms like great apes, interacting in a highly flexible social system like the fission-fusion one, remains challenging. But, investigating and understanding the social behaviour of these species, and how anthropogenic changes within their environment (e.g. habitat fragmentation) may impact their social lives, may prove critical also for future conservation efforts (Couzin, 2006).

1.4 The bonobo, *Pan paniscus*

The bonobo was first described by Schwarz as a "new race" of chimpanzee in 1929 and classified as a distinct species by Coolidge in 1933. Compared to the second species of the genus *Pan*, the chimpanzee (*Pan troglodytes*), the bonobo is somewhat lighter, has a slender body, with longer legs and smaller head and shoulders (Kano, 1990). For further anatomical distinctions see Coolidge (1933) and Kano (1992). In addition to a totally different vocal repertoire (de Waal, 1988), the two species are distinct regarding their behaviour and social structure (Doran et al., 2002).

Distribution and feeding ecology

Bonobos can only be found in the Democratic Republic of Congo (formally Zaire). They inhabit the lowland rainforests of the Congo Basin, south of the Congo River (fig. 1.2). According to Kano (1984), the distribution of bonobos is concentrated in an area of 900 km east to west and 600 km north to south. The size of the whole range of distribution is considered to be less than 200,000 km^2 (Kano, 1992). Their range is declining rapidly, due to human presence (uncontrolled hunting and habitat loss), making the bonobo one of the most threatened species of African primates (Oates, 1996). About 50,000 individuals were estimated by Kano (1992) to still live in the wild, but the actual population size remains unclear due to their patchy distribution, the inaccessibility of parts of their range and periodic political crisis in the country (Kortlandt, 1995; Reinartz et al., 2006). De Waal (1995) guessed that perhaps fewer than 10.000 bonobos survive in the wild. Reinartz et al. (2006) found a significant negative correlation between bonobo density and human presence and claimed immediate protection of the remaining free-living individuals.



Fig. 1.2: Range of bonobo distribution. Lo (Lomako), Wa (Wamba), Lu (Lukuru): bonobo study sites, referred to in the text; dotted area: Salonga National Park, the only federally recognized national park where bonobos occur
source of map: http://www.bonobo.org/wheredobonobolive.html; Copyright © 2002 The Bonobo Conservation Initiative

Bonobos mainly feed on fruits and seeds with fibrous foods (e.g. leaves, roots, pith, sprouts) being the second important food resource, which particularly becomes more important in times of ripe fruit scarcity (Kano, 1992). The consumption of animal food is meager in bonobos (1-1.5%, Kano; 1992), but they are known to eat invertebrates and some species of vertebrates occasionally (Horn, 1980; Badrian et al., 1981; Kano, 1992, Ihobe, 1992a; Fruth & Hohmann, 2002).

Grouping patterns and social behaviour

Bonobos live in bigger social units ("unit-groups", Nishida, 1968; "communities", western scientists), whose members all know each other and who share a common home range. Ranges vary from approx. 22 km^2 at the Lomako study site to 40-50 km^2 at the Wamba study

site (Nishida & Hiraiwa-Hasegawa, 1987). Individuals forage and travel in subgroups (parties) which congregate (fusion) and split (fission) with changing constituents. Different parties are therefore the only observable units of a community. Community size seems to vary between 50-120 individuals, with party size varying between 2-50 individuals (Badrian & Badrian, 1984). Mean party sizes, computed at different study sites were: 6.7 and 4.9 animals respectively for the Lomako study site (White, 1998; Hohmann & Fruth, 2002), 6.4 animals for the Lukuru study site (Myers Thompson, 2002) and 19 and 14 animals respectively for the Wamba study site (Kano, 1982, 1992). Only in Wamba, artificial provisioning was performed regularly to habituate the bonobos, which may have resulted in larger party sizes (White, 1992).

According to Kano (1992), mixed-sex parties are much more common than uni-sex parties, pure mother-offspring parties or lone individuals. The relative adult sex ratio within mixed-sex parties is about 1:1, although it can deviate in some parties (Kano, 1982, 1992). No significant difference could be found between the frequencies with which each sex joined or left a party (White, 1988). Also Kuroda (1979) concluded that there is little difference in the nomadic style between males and females. According to White (1988), only the tendency to leave a party alone was significantly higher in males. The mean time until a change in party composition occurred was 145 min (range 24-398 min; White, 1988), during long time party sightings (>6 hr) at the Lomako study site.

Bonobo males remain in their natal community, whereas females leave their natal group upon adolescence (first signs of genital swelling, approx. 7-9 years) and migrate to another community (Kano, 1987; Furuichi, 1989). Between 1976 and 1988 a total of 7 secure female transfers and 9 temporary visits could be documented within a known community (Furuichi, 1989). Analysis of genetic relationships done by Gerloff et al. (1999), approved the notion that migration is female biased. No records of inter-group transfers by males were made at the Wamba study site, but Hohmann (2001) reported about two strange males joining a community at the Lomako study site. Hohmann & Fruth (2002) therefore suggested that patterns of dispersal may be more flexible than assumed.

Encounters with members of neighbouring communities are described as diverse but more peaceful than in chimpanzees (Kano, 1992). Different communities tend to avoid each other and group encounters can also develop into conflicts, but bonobos have rarely been found to severely attack each other and they have not been found to kill a conspecific so far. Kano

(1992) reported about group encounters at Wamba, involving frequent sexual and friendly interactions, apart from agonistic ones. Agonistic behaviours during community encounters also occurred at the Lomako study site, but social grooming and mating could also be observed at times (Hohmann & Fruth, 2002). Compared to those findings, in chimpanzees, several authors report severe, hostile attacks during community encounters, sometimes having fatal consequences for an individual (Muller, 2002; Wilson et al., 2004; Boesch et al., 2007, 2008).

Encounters of different parties, belonging to the same community, tend to increase the social arousal as well, but with a predominantly friendly keynote. Aggressive interactions (like chasing) were found only infrequently (Badrian & Badrian, 1984). According to the authors, the level of social excitement varied with party sizes, with encounters between larger groups being more likely to involve loud vocalization, displaying and an increased sexual behaviour. All party encounters observed by Kano (1982) resulted in fusion of the parties within a few to some ten minutes.

Agonistic interactions in free-living animals were mostly observed between males (Idani, 1991; Kano, 1992; Furuichi, 1997; Hohmann & Fruth, 2003). According to Idani, Kano and Furuichi, they occurred least frequently between females, but when calculating the rate of incidents per animal dyad, Furuichi found a nearly equal rate of agonistic interactions for the male-female and the female-female class. When separating the male-female class regarding the direction of aggression, Hohmann & Fruth (2003) found female aggression towards males to be more prominent than vice versa.

In zoo-living animals, Palagi et al. (2004) found no significant differences between the adult sex-class combinations concerning agonistic dyadic contacts. Regarding the quality of conflicts, Vervaecke et al. (2000a) found that males predominantly “pestered” females, whereas females predominantly chased males.

Kano (1992) assumed that a female has about the same rank as a male in the bonobo society, although females seem to have prior access to food. According to Furuichi (1989), males first appeared at the artificial feeding sites, but left, as soon as the females gathered around the provided sugarcane.

When trying to determine male rank orders in free-ranging bonobos by using the outcome of agonistic interactions, Kano (1992) failed to find linear correlations. Even after ten years of study he failed to determine how rank is established among males, because although

dominant-subordinate interactions randomly occurred in certain associations, they did not occur in others. Furuichi (1997) also stated that dominance rank orders seemed to exist among males, but a linear hierarchy remained unclear. In contrast to chimpanzees, lower-ranking males were e.g. found to copulate relatively freely in the presence of higher-ranking males (Furuichi & Ihobe, 1994; Furuichi, 1997). However, some age-related dominance relations seem to be more important: Ihobe (1992a) pointed out that adult males were clearly dominant over adolescent males and Kano (1992) stated that the older brother was always the most dominant individual among adult male siblings.

Also in females, dominance relationships are apparently hard to observe in free-living animals. According to Kano (1992), they are even underdeveloped compared to that of males. An animal's age seems to play a role in female dominance relationships as well, as older individuals tended to be dominant over younger ones (Furuichi, 1997).

For zoo-living animals, rank order is usually determined by the outcome of agonistic interactions, like "fleeing upon aggression" (Vervaecke et al., 2000b; Stevens et al., 2007). Vervaecke et al. (2000b) pointed out, that the investigated dominance hierarchy showed significant and strong linearity, with females occupying the highest ranks and males occupying the lowest. But one male could outrank a female agonistically, so the authors created the term "nonexclusive female dominance", which was also used by Stevens et al. (2007, 2008). As in the wild, in competitive situations, adult females seem to control food access and mostly acquired more food than other group members (Vervaecke et al., 2000b; Parish, 1994). Interestingly, when Vervaecke et al. (1999) investigated the outcomes of competitive feeding in an experimental set up, they found that for some pairs of individuals, the strength of the competitive feeding dominance over another was dependent on the presence or absence of other individuals. Generally, the expression of dominance seems to be more rigid in captivity and dominance styles may be more despotic than those found in the wild, because there are only a few competitors that are almost always in the vicinity (Stevens et al., 2008).

In contrast to chimpanzees, free-living as well as captive male bonobos rarely form alliances (Kano, 1992; Ihobe, 1992a; Furuichi & Ihobe, 1994, Stevens et al., 2006, 2008), whereas females sometimes do (Kano, 1992; Furuichi, 1997; Vervaecke et al., 2000a; Stevens et al., 2006, 2008). Vervaecke et al., (2000a) assumed that coalitions fulfil a crucial role in the maintenance of the power of high ranking females over males, while captive low ranking males were even found to serve as "scapegoats", being the victims of allied females quite

often, not even being involved in the original conflict. Females, cooperating against males who did not confront them, were also observed in free-living bonobos (Furuichi, 1997).

In the wild, female bonobos are described as very sociable and they normally forage in close vicinity of each other (Furuichi, 1989; Kano, 1992). This led to the assumption that females are the core of bonobo society, with males associating with them (Badrian & Badrian, 1984). Additionally, White & Chapman (1994) and Hohmann & Fruth (2002) found smallest nearest-neighbour distances and close dyadic associations respectively, to be most prominent between females. De Waal (1995) argued, that bonobos can be said to be secondarily female-bonded because their bonding is not linked with kinship like assumed by Wrangham (1980) for female-bonded primate groups. However, strong female associations could not always be found in captive groups of bonobos. Stevens et al. (2008) found preferred spatial proximity between females in only 2 out of 5 captive settings and some female-female bonds were equally strong as bonds between unrelated males and females.

With reaching adolescence, females leave their natal group and "wander around" between different communities, before settling down in one of them (Kano, 1992). Young, immigrated females eagerly approach older, resident ones and frequently initiate friendly contacts with them (Furuichi, 1989; Idani, 1991; Kano, 1992). Close associations with these experienced, higher-ranking females ("specific senior females", SSF) seem to help the immigrant to attain a more stable position in the community (Furuichi, 1989; Idani, 1991). Via her SSF, the immigrant female attends the female centre of the society and Furuichi (1997) found that even recently immigrated young females could have priority to food access if they stayed in the proximity of other females. In captivity, after studying the integration process of a bonobo mother and her dependent daughter into a new group, Pfalzer & Ehret (1995) also found evidence for the existence and mediating function of a SSF for the new female, although this immigrant already raised offspring herself.

Regarding sexual behaviours, bonobos are known to show some exceptional patterns. Whereas most other primates copulate dorso-ventrally, free-living and captive bonobos also frequently copulate ventro-ventrally (Kano, 1992; de Waal, 1989). The most sexually active members in free-living communities were found to be young, nulliparous females (Kano, 1992) and young, immigrated females (Idani, 1991). Besides mating with the other gender, bonobos are also known to frequently show homosexual behaviours, particularly females

show "genito-genital rubbing" (GG rubbing). According to Kano (1990, 1992) and Hohmann & Fruth (2000), homosexual behaviour in the bonobo society appears to have multiple social functions and can serve e.g. as a greeting, or to appease and reassure. It frequently occures when social tension is high, e.g. when parties join together (Kano, 1992). Badrian & Badrian (1984), Furuichi (1989) and Idani (1991) reported that GG rubbing occurred most often during feeding sessions. The relation between food and sex is quite conspicuous, also in captivity (de Waal, 1989). The last author coined the term "sociosexual behaviour" and supposed an induced state of arousal, which can "spark over" into sexual arousal. Furuichi & Ihobe (1994) found that bonobos were also frequently engaged in mounting or rump contact immediately following agonistic interactions, which ceased the conflict in that case.

One of the most observed affiliative behaviours in bonobos is allogrooming. Participants of social grooming include both sexes and all age-sex classes (Badrian & Badrian, 1984) and grooming occurs irrespective of being involved in a sexual relationship (Kano, 1992). According to the latter author, the frequency of grooming between males and females is extremely high, but grooming between females is also common. Also other authors, studying free-living bonobos, found that male-female grooming could be observed most frequently, whereas grooming between males was found least frequently (Badrian & Badrian, 1984; Kuroda, 1980). Regarding zoo-living individuals, Palagi et al. (2004) observed that female dyads showed the highest frequency for grooming interactions. Contrarily Stevens et al. (2006) found that grooming between sons and their mothers occurred most frequently, which was also stated by Kano (1992) for free-ranging animals, when separating the mother-son dyads from the male-female ones.
High-ranking adult females received most allogrooming, within each investigated captive group observed by Franz (1999). Idani (1991) found that immigrant females in the wild tended to groom other individuals rather than to be groomed.

It seems that in bonobos, an accentuated relationship between mothers and their adult sons is striking. According to Kano (1992), mothers and sons are linked by continuous strong bonds and males tend to stay close to their mothers and spend a great deal of time with them. Hohmann & Fruth (2002) found that mother-adult son dyads were responsible for a higher association index than expected in the male-female class, and long-term associations (lasting for more than two field seasons) existed only between two mother-son pairs (Hohmann et al., 1999). Most authors suggest that the mother's presence in the community is an important

factor which enhances the social status of a male (Furuichi, 1989; Kano, 1992; Ihobe, 1992b; Furuichi & Ihobe, 1994; Furuichi, 1997) and allows him to roam in the centre of a party (Furuichi, 1989, 1997). There are even findings that mothers support their sons directly during agonistic encounters (Kano, 1992; Furuichi, 1997) and that sons of high-ranking females have a higher paternity success (Gerloff et al., 1999). Therefore, bonobo males may depend critically on the membership of their mothers in the group and in some cases even on their immediate presence (Fortunato & Berman, 2002).

According to Kano (1992), female bonobos are very indulgent mothers who do not punish or threaten their offspring. Infants gradually decrease the time spent close to their mothers when getting older, and during adolescence, the mother-daughter relationship in contrast to the mother-son relationship is usually completely severed (Kano, 1992).
The behaviour of elders towards juveniles and infants is characterized by a great tolerance (Kano, 1992). Male-infant interactions were observed frequently in bonobos and, unlike chimpanzee males, captive bonobo males were found to carry infants occasionally (Patterson, 1979). Enomoto (1990) suggests that the presence of play between different generations may facilitate the acquisition of traditional signals employed in various social interactions. Youngsters may also play an important role as facilitators between adults and between residents and new group members. In their study about an integration process in a captive colony, Pfalzer & Ehret (1995) found that two juveniles were most active in initiating contacts with the new group members. This seemed to catalyze social interactions between their mothers and the newcomers. Also in free-ranging animals, immigrant females and immature animals were found to be the most frequent participants in play (Idani, 1991).

In summary, what emerges from the data and the accumulated impressions of the social life of bonobos is that it seems to be shaped by predominantly peaceful, even-tempered relationships between the members of a community. Mechanisms to manage and overcome conflicts seem to be more pronounced than dominance concepts. Females seem to be more bonded with each other than males. Especially mothers and elderly females are assumed to constitute the centres of bonobo societies, although females do not exclusively keep in touch with each other. Strong male-female associations are also observable which seems to be especially true regarding mothers and their adult sons. Animals of a given community are connected via a fluid, individual based fission-fusion framework. Such a scheme offers the possibility for a greater flexibility regarding different ecological pressures. It also allows for an ongoing

exchange of information and the maintenance of a bigger social unit, without forcing the costs of foraging in a big group. But, the animals must be capable of dealing with an ongoing social change without loosing sight of the social network including all its members and relationships.

Although any conclusions about the ultimate function of fission-fusion mechanisms must remain tentative, this variable system can be assumed to directly affect the social life of bonobos on a proximate level. It is therefore plausible to conclude that a loss of flexibility will have an observable impact on their social relationships. Comparisons with zoo-living animals may be instructive in this regard.

A series of studies about captive bonobos has been carried out so far, often focussing on specific aspects of the social structure, like female relationships or reproductive patterns, with many of them referring to only a few groups and settings. Investigations about the effects of alterations within the partner spectrum were hardly carried out so far and only a few institutions are keeping their bonobos in an artificial fission-fusion system (e.g. the Zoological Garden of Frankfurt and the Milwaukee County Zoo).

1.5 Aim of the study

The background for this study was that bonobos in zoos are often kept in small, long-term constant groups which presumably are not existent in free-living animals. Hardly any investigations of zoo-living bonobos with reference to their supposed fission-fusion nature have been carried out so far. There were hints that long-term stable grouping may have been a reason (or at least an intensifier) for social problems in some captive settings (chapter 4.2.3).

The basic approach of this study was to investigate patterns of social relationships in different groups of zoo-living bonobos, kept under different conditions. A stable group at Cologne Zoo, a stable group with a lot of space at Planckendael Zoo and a group at Frankfurt Zoo, kept in an artificial fission-fusion system, were chosen.

The study addressed the following topics and corresponding hypothesis:

1. Patterns of social relationships in zoo-living bonobos and comparisons with literature, mainly considering studies of free-ranging bonobos

→ The individuals of a group differ regarding their dyadic relationships (differences in type and patterning). Some analogue patterns can be found in all 3 settings regarding

different age and sex combinations of animals and general behavioural traits. Similar traits were also found in free-living bonobos and/or other captive settings.

2. Comparison of different keeping conditions

→The groups differ in terms of vitality. The group which is kept in an artificial fission-fusion system (Frankfurt) is the liveliest, resulting in higher rates of social and spatial proximity between its members. The bonobos kept within the most spacious conditions (Planckendael) show certain fission-fusion tendencies themselves, resulting in higher rates compared to the other constant setting with more limited spatial conditions (Cologne).

3. Influence of artificial fission-fusion conditions (separation management)

→ Separation management schedules have a perceivable effect on the social relationships of zoo-living bonobos. An alteration within the partner spectrum will increase the vitality of a group, resulting in higher rates of social and spatial proximity between the individuals (without an increase in agonistic behaviour). Social and spatial proximity will decrease after a while of staying as a party of a given composition, indicating splitting tendencies.

Comparative studies like the present one, analysing and describing patterns of social relationships within different groups of zoo-living bonobos will help to enhance the knowledge about the social potential of these least-known great ape species. All captive settings studied kept reasonably social groupings, so that interactions between the social partners can inform meaningfully about the species fundamental sociality (King, 2004).

A key question of the study was, whether there are traits or changes in the interactive and spatial behaviour of bonobos in captivity which indicate an intrinsic motivation for fission-fusion structures. As fission-fusion attributes are assumed to be an integral part of their social relationships in the wild, it was expected that a separation management, mimicking at least basic patterns of the natural conditions should have a positive effect which can quantitatively be measured.

The study particularly serves to obtain and improve hypothesis and model conceptions about important aspects of the social life of bonobos, which may deserve further investigations, including zoo and field studies. The study may also be useful regarding future management concepts about preserving vital groups of bonobos in zoological institutions.

2. Animals and Methods

Social relationships were described via analysing the interactive behaviour (including the time and frequency spent in physical contact) and the spatial behaviour of bonobos in three different zoo-living colonies. The datasets were used for comparisons between the groups and for a "close-up" view of the Frankfurt group, kept in an artificial fission-fusion system (separation management). The study comprises a long term observation of the Frankfurt colony, and observations for shorter periods of time in Planckendael and Cologne.

2.1 Animals and keeping conditions

Three groups of zoo-living animals were observed. The individuals in Planckendael and Cologne lived in permanent groups. The Frankfurt colony was kept in two different subgroups mainly, the compositions of which were changed by the keepers on an optional basis. No animal transfers, deaths or births occurred in any of the groups during the observation periods.

a) Frankfurt

The bonobos in Frankfurt had access to a total of three indoor enclosures ($15m^2$, $27m^2$, $32m^2$) and four outdoor ones ($18.5m^2$, $36m^2$, $21m^2$, $21m^2$) resulting in a population density of $21.31m^2$/individual. For a plan of the enclosures (used for scan sampling) see Appendix (fig. 8.3). When separated into two subgroups (as in the majority of cases), each group had access to at least one indoor and one outdoor enclosure. The inside enclosures were heated constantly and air moistening was provided regularly resulting in an average temperature of 21.5°C (range: 20-25°C) and an average humidity of 68.7% (range: 52-86%). Mean outside temperature and humidity were 22.7°C (range: 9-33°C) and 45.5% (range: 25-76%). Measurements were done by the observer (digital thermometer) and within the whole study period (April 2003-March 2004). Inside and outside measurements were altered, depending on whether the animals were only kept inside (normally below 10°C) or could also enter their outside enclosures.
The Frankfurt colony consisted of 8 individuals during the observation periods: 1 adult male, 5 adult females and 2 infants. All animals are listed in table 2.1.

name	EEP number	sex	date of birth	origin	mother present	reared
Ludwig (Lu)	126	m	26.08.1984	Planckendael*	no	hand
Margrit (Ma)	31	f	approx. 1951	wild	no	?
Natalie (Na)	46	f	approx. 1964	wild	no	?
Salonga (Sa)	52	f	02.05.1973	Frankfurt	yes (Ma)	mother
Ukela (Uk)	132	f	19.12.1985	Frankfurt	yes (Na)	mother
Kamiti (Ka)	138	f	21.01.1987	Stuttgart	no	mother
Heri (He)	274	m	23.01.2001	Frankfurt	yes (Na)	mother
Haiba (Ha)	281	f	16.11.2001	Frankfurt	yes (Uk)	mother

Table 2.1: Composition of the bonobo group at Frankfurt Zoo: m=male; f=female; *=the animal was born in Antwerp but was transferred to a new facility in Planckendael in 1992; EEP=European Endangered Species Program

Cleaning of the in- and outdoor cages was usually done in the early morning between 07:30 and 09:00 a.m. During cleaning, the animals were confined to the neighbouring enclosures, the outdoor enclosures or to separate cages behind public viewing and they were fed different kinds of porridge with food supplements individually. After cleaning, the animals were fed their morning meal, which consisted of different kinds of vegetables and salad. This meal was normally provided scattered in the cleaned indoor enclosures. The second meal was provided in the afternoon (between 03:30 and 04:30 p.m.) and consisted of fruits. This meal was also scattered in the indoor enclosures or thrown over the grid of the roof, causing the animals to climb and pick up most of the pieces through the grid. Most vegetables and fruits were left uncut or just split into bigger pieces. Some additional food items were offered alternately during the day: monkey pellets, cooked rice, eggs, potatoes, fresh branches, seeds, nuts, dry fruits, honey and raisins and small pieces of cooked meat. Some of these food items were hidden inside different enrichment constructs or given as a reward in the context of medical health training. Water was always accessible ad libitum and hand-made drinks (apple juice, cocoa etc.) were offered through the front grid in the afternoon on a regular basis.

b) Planckendael

The individuals of the Planckendael colony had access to one inside enclosure and a huge outdoor island (77m^2/ 3000m^2) resulting in a population density of 384.63m^2/individual. For a plan of the enclosures (used for scan sampling) see Appendix (fig. 8.4).The animals were kept together constantly and just confined to different “nightquarters” behind the public viewing zone during cleaning of the enclosures (1-4 animals per cage, depending on the animal’s intention).

The indoor hall was heated constantly but the Planckendael group was only observed in summer time, when the animals mainly stayed on their outside island during the day, so only outside temperature and humidity were measured. This resulted in an average temperature of 22.5°C (range: 16-29°C) and an average humidity of 65% (42-91%).Measurements were done within the whole study period, between July and September 2004.
The group consisted of eight individuals during the observation period: 3 adult males, 2 adult females, 1 subadult female and 2 juveniles. Detailed group composition is shown in the following (table 2.2).

name	EEP number	sex	date of birth	origin	mother present	reared
Kidogo II (Ki)	113	m	28.02.1983	Stuttgart	no	hand
Redy (Re)	161	m	24.11.1990	Planckendael	yes (Ho)	mother
Vifijo (Vi)	197	m	23.07.1994	Planckendael	yes (Ho)	mother
Hermien (He)	88	f	approx. 1978	wild	no	?
Hortense (Ho)	91	f	approx. 1978	wild	no	?
Djanoa (Dj)	203	f	27.03.1995	Berlin	no	mother
Zomi (Zo)	240	f	28.01.1998	Planckendael	yes (He)	mother
Zamba (Za)	243	m	16.04.1998	Planckendael	yes (Ho)	mother

Table 2.2: Composition of the bonobo group at Dierenpark Planckendael: m=male; f=female; EEP=European Endangered Species Program

Cleaning of the indoor hall and the outdoor island was usually done in the early morning between 07:30 and 09:00 a.m. During this time the animals were confined to the "night cages", where they were fed individually (milk containing food supplements, fruits). Sometimes, a medical health training was performed at this time as well. The morning meal for the complete group was scattered over the outdoor island and consisted of different kinds of vegetables and salad (mainly whole pieces). In the afternoon (around 06:00 p.a. in summer) they were again confined in the "night cages" for a few minutes and fed individually (monkey pellets, fruits and vegetables) and vegetables were also distributed in the indoor enclosure. Some additional food items were offered alternately during the day, mainly involved in enrichment procedures: eggs, honey, nuts, seeds, raisins etc. Fresh branches were provided regularly and the animals could also eat from the growing vegetation on the outdoor island and the surrounding moat. Water was always accessible ad libitum.

c) Cologne

As the observations in Cologne took place in winter, the bonobo group was housed only in the indoor enclosure (145m^2) resulting in a population density of 29m^2/individual. For a plan of the enclosure (used for scan sampling) see Appendix (fig. 8.5). Additionally to the indoor

hall, animals had access to some "night cages" sometimes, which were secluded from public viewing (19m^2 in total). The "Urwaldhaus", containing the indoor hall, was heated constantly and air moistening was provided regularly. Temperature and humidity were measured inside at alternate times. This resulted in an average temperature of 21.4°C (range: 19.4-23°C) and an average humidity of 84.1% (range: 67-97%). Measurements were done within the whole study period (November 2004 to January 2005).
During the observation period the group consisted of five individuals: 2 adult males, 2 adult females and one subadult male. Detailed group composition is shown in table 2.3.

name	EEP number	sex	date of birth	origin	mother present	reared
Clyde (Cl)	97	m	approx. 1978	wild	no	?
Kindu (Ki)	130	m	23.09.1984	Cologne	yes (Bo)	mother
Bolombo (Bol)	225	m	07.11.1997	Leipzig	no	hand
Bonnie (Bo)	86	f	approx. 1976	wild	no	?
Binti (Bi)	208	f	14.08.1995	Frankfurt	no	mother

Table 2.3: Composition of the bonobo group at Cologne Zoo: m=male; f=female; EEP=European Endangered Species Program

Cleaning of the indoor enclosure was done between 08:00 and 09:30 in the morning. While the enclosure was cleaned the animals were confined to the "night cages", where they got some special porridge (containing cooked meat, curd cheese, dried dog food, monkey pellets cooked potatoes, cooked rice, cooked eggs, etc.) and something to drink (milk or tea with food supplements). After cleaning, different kinds of chopped vegetables and fruits were distributed all over the inside hall and the night cages were closed. A second feeding time was around noon which again consisted of chopped vegetables and fruits, this time thrown into the enclosure through the grid roof. In the afternoon (around 04:30 p.m.) the group was confined to the night cages again as the third main feeding items were spread all over the enclosure. Some fruit items were fed individually again. After the afternoon feeding session, the night cages remained open for the rest of the evening and for the night. Additional feeding sessions occurred alternately, sometimes involved in enrichment tasks. Also different kinds of foliage were offered regularly. Water was only provided by the keepers in the "night cages".

2.2 Data collection

The observations in Frankfurt took place between April 2003 and March 2004 during 4 observation periods, resulting in a total of 128 observation days. The Planckendael group was observed between July and September 2004, resulting in a total of 48 days. In Cologne, the

observations started in November 2004 and lasted until January 2005, resulting in a total of 30 observation days. Due to management reasons, in Cologne two animals were separated from the rest of the group on the last 4 observation days and therefore only 26 days were taken into account for the analysis.

Animals were observed for most of their active daytime. In total the time between 08:30 a.m. and 04:30 p.m. (04:50 in Cologne) was covered. Starting time was altered: At one day the observation started at 08:30 and ended in the early afternoon (01:50 respectively 02:20 in Cologne) with one break in between. The following day started at the previous pause time (11:10 respectively 11:00 in Cologne) and ended in the late afternoon with an appropriate break in between.

Observations methods were taken from Martin & Bateson (1993): Continuous focal animal sampling was used for 10-minute units and instantaneous scan sampling was done between the units. Protocols were noted on paper sheets. Focal animal order was randomized but balanced (to assure that the individuals were observed in varying orders of appearance but equally often at the same time of the day). Additionally, in some cases, when all individuals were kept together in Frankfurt, ad libitum focal group sampling was used for the first 10-30 minutes with the aid of a voice recorder.

In total, the data collection resulted in 812 observation hours and 5278 scan samplings.

2.3 Ethogram

The ethogram was established after personal pre-observations using mutually exclusive behaviours and following inter alia Kano (1980), Mori (1984), Vervaecke & van Elsacker (2000) and Vervaecke et al. (2000b). During most of the social interactions one individual was the sender and the other one the receiver of a given behaviour, which was noted with the aid of arrows within the datasheets. The following ethogram describes the behaviours always from an actor's point of view.

Interactive behaviour

1. Physical contact: being in body contact to another individual without being involved in a grooming bout with this individual

Sociopositive

2. Social play: playing with another individual

3. Share food: taking a piece or whole food item from an individual, without any signs of antagonism
4. Peer: fixed but calm looking into the face of another individual from not more than an arm's length distance
5. Touch: directed touching of another individual with a hand or foot
6. Allogroom unidirectional: grooming a conspecific
7. Allogroom bidirectional: being involved in mutual grooming

Sexual

8. Sexual contacts: including copulation with a conspecific (with and without intromission) and homosexual interactions
9. Present itself: clearly showing the genitals to another individual

Agonistic

10. Chase: tensed running after another individual
11. Displace: directly approaching another individual and taking its place
12. Attack: any form of hitting, biting and kicking another individual
13. Direct charge: tensed running in the obvious direction of or closely passing by another individual, sometimes while pushing an object

Submissive

14. Evade: forgoing another individual when passing it, or leaving as soon as it comes along
15. Flee: quickly running away after an aggressive approach or attack

Others

16. Come close: clearly approaching a specific individual
17. Go away: leaving another individual which was near or in contact until then
18. Watch animal: clearly observing a specific individual
19. Follow: walking after a conspecific

An additional set of 11 solitary behaviours was taken into account, which was included when calculating the activity budget (chapter 3.3).

Solitary behaviours

1. Monitoring: observing conspecifics and the environment without a recognizable main objective
2. Eating: staying at one place and consuming food items

3. Out of sight: being or moving outside the human observer's eyes
4. Moving: locomotion on or off the ground (bipedal, quadruped or climbing)
5. Resting: lying for at least 30 seconds without any signs of monitoring or watching something, often connected with closed eyes (includes sleeping)
6. Self manipulation: includes masturbating, autogrooming and scratching
7. Object manipulation: includes holding, carrying, moving and otherwise manipulating objects
8. Observing: watching an individual, which is not a conspecific or attending a scene beyond the enclosure
9. Foraging: moving around and collecting food items, often eating simultaneously
10. Begging: reaching an arm, clapping hands or otherwise trying to get food items from zoo visitors and keepers
11. Play: play behaviour without the involvement of a conspecific, e.g. wildly climbing, jumping around or doing somersaults

2.4 Data analysis

For all data analysis the software "Monkey Business" (©Weißhaar, 2004) and Excel 2003 (Microsoft® Corporation) were used. Monkey Business is a program for the structured storage of behavioural datasets, with the ability to do queries on them, which can then be handled with calculation programs like Excel.

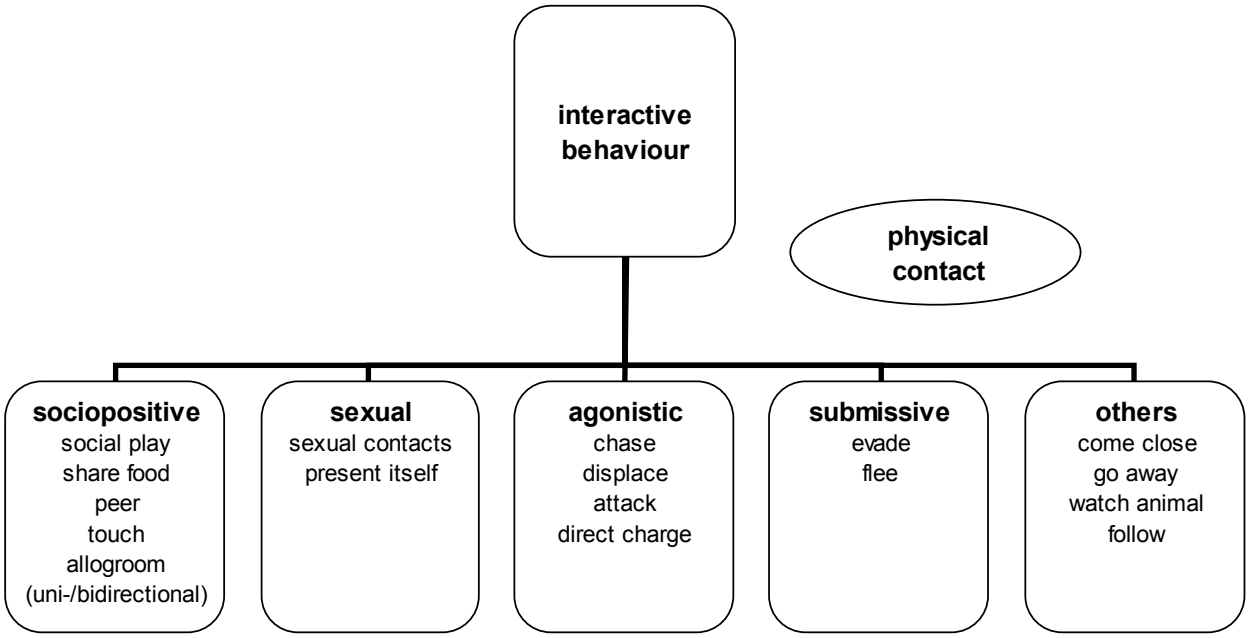


Fig. 2.1: Behaviours taken into account for the overall interactive behaviour.

Nineteen elements of interactive behaviour were analysed, which are listed in figure 2.1. They were subdivided in six categories (physical contact, sociopositive, sexual, agonistic, submissive and others). To be in physical contact to each other was analysed separately because it could happen simultaneously to some of the other behaviours (e.g. peer or touch). Frequencies and durations per time units were calculated.

To portray the social relationships on the level of interactive behaviour and on aspects of spatial behaviour, mainly 2 different approaches were used:
1) All possible partner combinations or all individuals of a group, a subgroup, an age-sex class etc. were taken into account as complex units and described using the calculation of "mean dyad"-, "mean animal"- or "mean group"-values.
2) The social units were referred to as networks of interactions. This approach covered more qualitative traits of social relationships by referring e.g. to "active-passive relations" or "attention structures".
Both approaches were used more than once, depending on the appropriate objectives.

The amount of interactive behaviour in a colony was assessed (chapter 3.1). Frankfurt and Planckendael with 8 individuals each had 28 (possible) dyads. The Cologne colony consisted of 5 animals, resulting in 10 dyads. Frequencies and durations for each dyad were calculated, referring to the observed amount of time in which a given pair of individuals had the chance to interact. Observation times, when the animals were not observable (confined in night cages e.g.), were excluded (Martin and Bateson, 1993).
To investigate the distributions of all 6 different behavioural categories, median values and proportions were calculated for them (chapter 3.1.1).
In order to investigate whether age-sex class specific patterns of relationships existed, average values per class and group and per class referring to all groups were calculated (chapter 3.1.2). The following age-sex classes were defined: male-female, male-male, female-female, mother-adult son, mother-infant(juvenile), adult male-infant(juvenile), adult female-infant(juvenile) and infant(juvenile)-infant(juvenile). An additional investigation in this regard was done for the mother-infant class (only 2 dyads, Frankfurt colony): The decline of physical contact between mother and infant was correlated to the infants increasing age.
In order to investigate some basic qualities of social relationships, selected elements of the interactive behaviour were analysed in more detail with reference to active-passive relations and attention structures. This was done within the groups and, independent of group

membership, with reference to all animal's age and gender and with reference to adult age-sex classes (chapter 3.1.3). As a dimension for active-passive relations, equality indices were calculated, based on a formula used by Silk et al. (2006). Therefore, the absolute difference between the proportion of being active and of being passive concerning a given behaviour was calculated. This resulted in values between -1 and 1: If an animal was the receiver of a given behaviour more often than the sender, the value approached -1 and if it was vice versa the value approached +1. Values around 0 indicated that the active-passive relation was balanced. Values above +0.15 or beneath -0.15 were regarded as trends for the corresponding direction (equivalent to 15% difference).

The social relationships were also investigated by analysing the animal's spatial behaviour (chapter 3.2). Spatial datasets were obtained via scan sampling .The spatial position of all group members was recorded every 10 minutes. For the purpose of analyses, 4 categories of spatial constellations were defined: proximity (≤ 1m, around arm reach) and no proximity (≥ 1m), proximity with body contact and proximity without body contact. This simple categorisation was chosen with reference to the animal's limitations to take larger, equidistant spatial positions resulting from the properties of the different enclosures. The option to stay in another animal's arm reach or not was alike for all individuals, whereas e.g. being in the same enclosure without staying in an approximately 3-5 meter radius to a conspecific was not possible in most of the enclosures in Frankfurt.
Spatial datasets were used to calculate proximity indices, following a formula used by Furuichi (1989). In principle, for any two partners, the number of scans in which they were in proximity was divided by the total number of scans for them, thus giving the percentage of all scans (0-100%), a given pair of individuals was found in proximity.
Proximity indices were calculated and used with reference to three different aspects:
-proximity index for a mean dyad of a given group
-mean proximity index per individual
-inter-individual proximity indices in a group as described by hierarchical cluster analyses

Activity budgets for the animals of all 3 colonies were generated (chapter 3.3). Durations for different activities were calculated and analysed as ratios of the time an animal was observed for. This was done to see how the interactive behaviour was embedded into the overall behaviour.

Finally, the influence of the separation management, as practised in Frankfurt, was investigated (chapter 3.4). It was examined if and how interactive and/or spatial behaviour varied in connection with this keeping condition and if fission tendencies were detectable after a subgroup was kept unchanged for a while. Therefore some time periods under subgroup conditions and some days in which all animals were kept together (subgroup encounter days after a while of subgroup conditions) were analysed in greater detail.

2.5 Statistics

For all statistical analyses the software SigmaStat 3.11 (©Systat, 2004) or the software SsS 1.1m (©Rubisoft, 1998-2005) were used.

To compare the datasets of the 4 different observation periods in Frankfurt, One Way Repeated Measures ANOVA was performed for normally distributed datasets and Friedman Repeated Measures ANOVA on Ranks was used for datasets which were not normally distributed. If significant differences occurred, All Pairwise Comparisons were done with the Holm–Sidak method and the Tukey test respectively.

To test for significant differences between units (groups, age-sex classes, animals), One Way ANOVA (normal distribution) or Kruskal-Wallis One Way ANOVA on Ranks were used with the corresponding All Pairwise Multiple Comparison Procedures (Holm-Sidak or Dunn`s Method, respectively). In cases, were only two units were tested against each other a t-test respectively a Mann-Whitney Rank Sum test was used.

Linear regression was applied to show changes in the infant-mother ties with growing infant age. To test for correlation, Pearson's correlation was used.

To compare the datasets of the Frankfurt group after a change in subgroup composition and before the next change, a Paired t-test respectively a Wilcoxon Signed Rank test was used depending whether the datasets turned out to be normally distributed or not.

The level of significance was set to be $p<0.05$ in all cases. If this level was slightly exceeded, a trend was reported. Datasets were regarded as being normally distributed if $p>0.05$.
All statistical tests used are also mentioned with the corresponding results.

3. Results

The social relationships of the individuals in all three observed groups are described. They are portrayed on the level of interactive behaviour and on aspects of spatial behaviour. Results of the groups are analysed comparatively. Similarities regarding some basic qualitative patterns of the animal's social relationships are exposed. Mainly quantitative variances between the separation management condition and the stable group conditions are shown. Additionally, some effects of the separation management condition, assumedly causing the distinctness in vitality, are identified.

3.1 Interactive behaviour

The overall interactive behaviour for an average animal dyad of each group was evaluated including nineteen interactive behavioural elements (fig. 2.1).

For the Frankfurt colony, average dyad values resulting from all 4 observation blocks were calculated. The results for the interactive behaviour of the separate blocks showed a big similarity, implying that the interactive behaviour of an average animal dyad remained quite stable for the whole observation period stretching from April 2003 to March 2004. Figure 3.1 shows the median values of frequency and duration from all 4 observation blocks in Frankfurt. Frequency and duration medians did not vary significantly ($p>0.8$; Friedman Repeated Measures ANOVA on Ranks). To make the long-term datasets comparable to the datasets of the other observed colonies, average values were calculated for each animal dyad of the Frankfurt group, which are referred to henceforth.

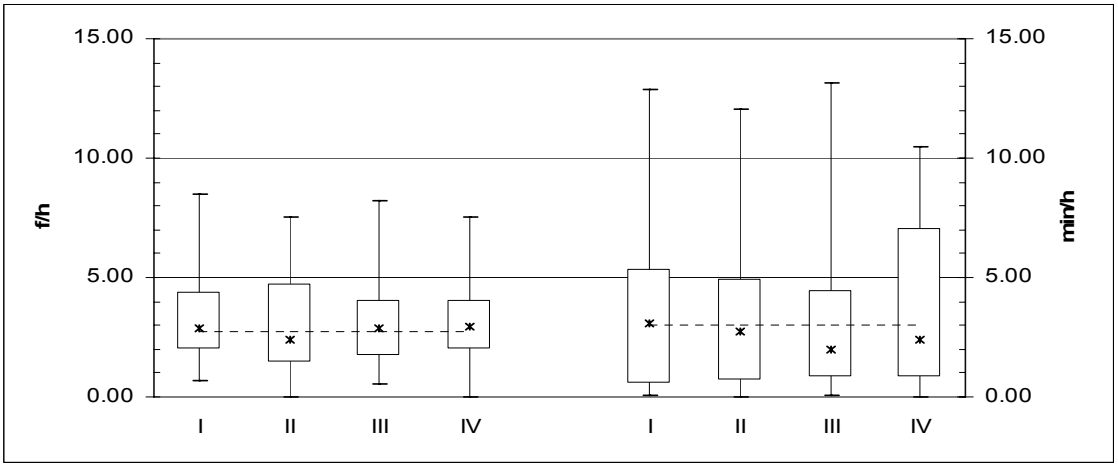


Fig. 3.1: Frankfurt colony: Interactive behaviour per animal dyad (n=28) in all 4 different observation blocks (I-IV). left side=frequency medians (f/h); right side=duration medians (min/h); ranges=minimum, maximum, quartile 1+3; dashed line=overall median values

Median dyad values for the summed interactive behaviour were calculated for all 3 colonies and tested for significant differences (table 3.1, fig. 3.2).

	Frankfurt (n=28)		Planckendael (n=28)		Cologne (n=10)		sign. differences	
	f/h	min/h	f/h	min/h	f/h	min/h	f/h	min/h
interactive behaviour	2.76	3.00	1.73	1.16	2.40	2.46	**F>P**	**F>P**

Table 3.1: Interactive behaviour in all 3 colonies: Frequency (f/h) and duration (min/h) medians for a given animal dyad. significant differences ($p<0.05$) found with Kruskal-Wallis One Way ANOVA on Ranks and All Pairwise Comparisons (Dunn`s method); n=number of dyads in each group

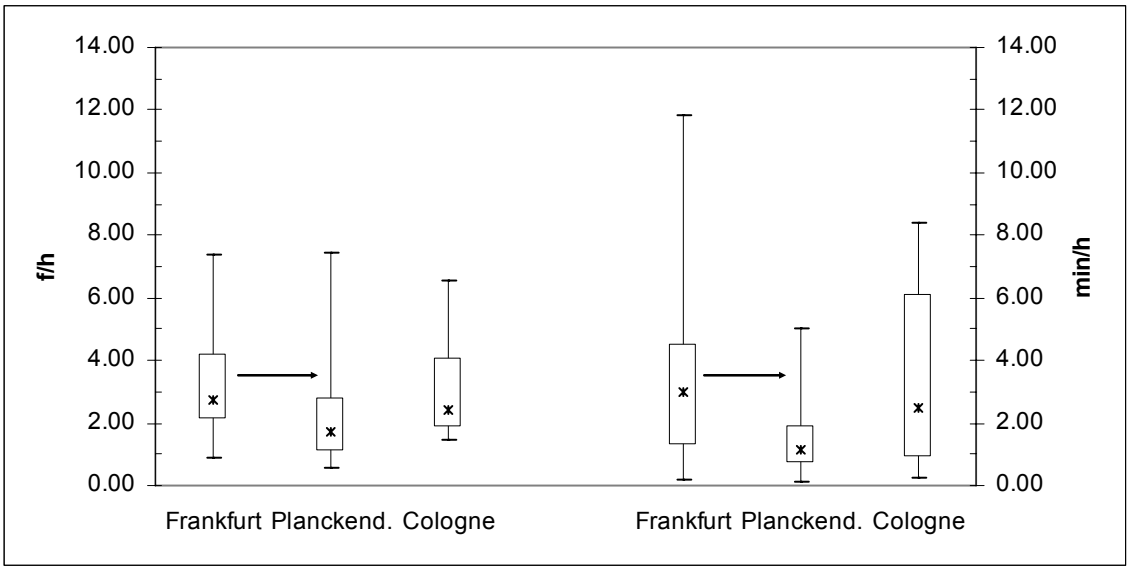


Fig. 3.2: Interactive behaviour in all 3 observed groups: Median dyad values and ranges (minimum, maximum, quartile 1+3). left side=frequency (f/h); right side=duration (min/h); arrows=significant differences ($p<0.05$) found with Kruskal-Wallis One Way ANOVA on Ranks and All Pairwise Comparisons (Dunn`s method)

Individuals were interacting most frequently and longest (2.76 times and 3.00 min/hour) in the Frankfurt group and least frequently and shortest in the Planckendael group (1.73 times and 1.16 min/h). The difference between these two was found to be significant concerning both, frequency and duration.

Datasets of two animals being in physical contact were analysed the same way. For the long-term studied Frankfurt colony, median values and ranges for frequency and duration from all 4 observation blocks are shown (fig. 3.3).

No large variations for the frequency of two animals being in physical contact occurred between the different observation blocks although some larger variations were found concerning duration. No articulate explanation could be found for the decreased duration rates of physical contact in observation periods III and IV. But as the last 2 observation blocks took place in autumn 2003 and spring 2004 respectively, when the animals were kept inside mainly, the generally more crowded situation possibly resulted in the individual's decreased

requirement of being in physical contact to their conspecifics for longer periods of time (chapter 4.1).

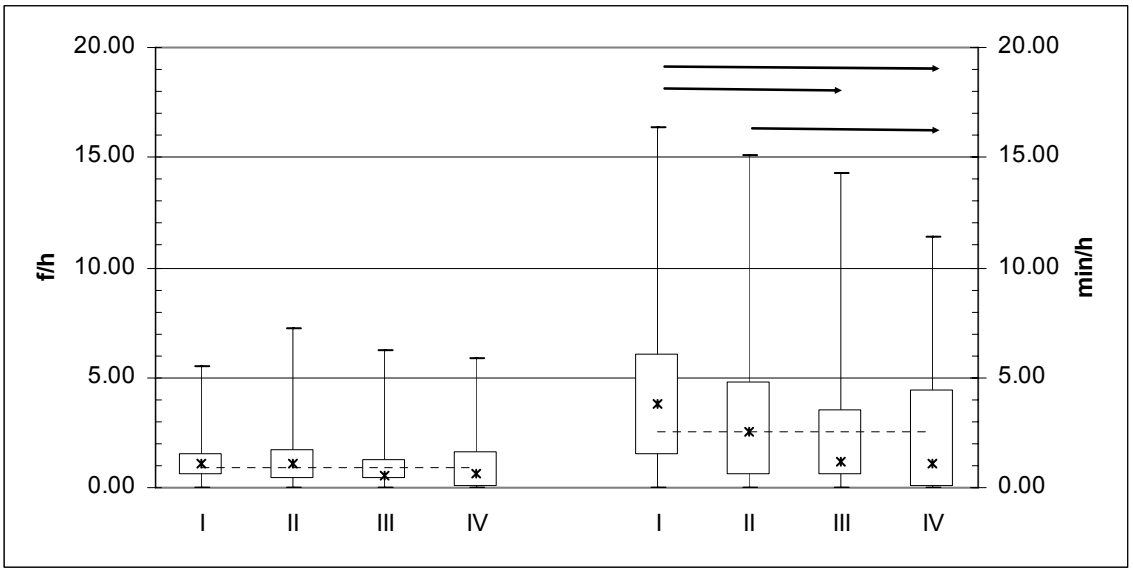


Fig. 3.3: Frankfurt colony: Physical contact within a given animal dyad (n=28) in all 4 different observation blocks (I-IV). left side=frequency medians (f/h); right side=duration medians (min/h); ranges=minimum, maximum, quartile 1+3; arrows=significant differences ($p<0.05$) found with Friedmann Repeated Measures ANOVA on Ranks and All Pairwise Comparisons (Tukey test); dashed line=overall median values

Again average values were calculated for each animal dyad of the Frankfurt group as a base for the comparison with Planckendael and Cologne and are referred to henceforth.

	Frankfurt (n=28)		Planckendael (n=28)		Cologne (n=10)		sign. differences	
	f/h	min/h	f/h	min/h	f/h	min/h	f/h	min/h
physical contact	0.88	2.56	0.27	0.30	0.13	0.09	**F>P, F>C**	**F>P, F>C**

Table 3.2: Physical contact: Frequency (f/h) and duration (min/h) medians for a given animal dyad from all 3 observed groups. significant differences ($p<0.05$) found with Kruskal-Wallis One Way ANOVA on Ranks and All Pairwise Comparisons (Dunn`s method); n=number of possible dyads in each group

The comparison between the different colonies revealed that two animals in physical contact were clearly most often found in the Frankfurt colony, and staying in contact also lasted longer between the bonobos in Frankfurt (table 3.2, fig. 3.4). The Cologne group was found to have the lowest values and only in Cologne the median value for time spent in physical contact was lower than the median value for frequency. An average animal dyad of this group only spent around 5 seconds per hour in physical contact compared to 18 seconds in Planckendael and 154 seconds in Frankfurt.

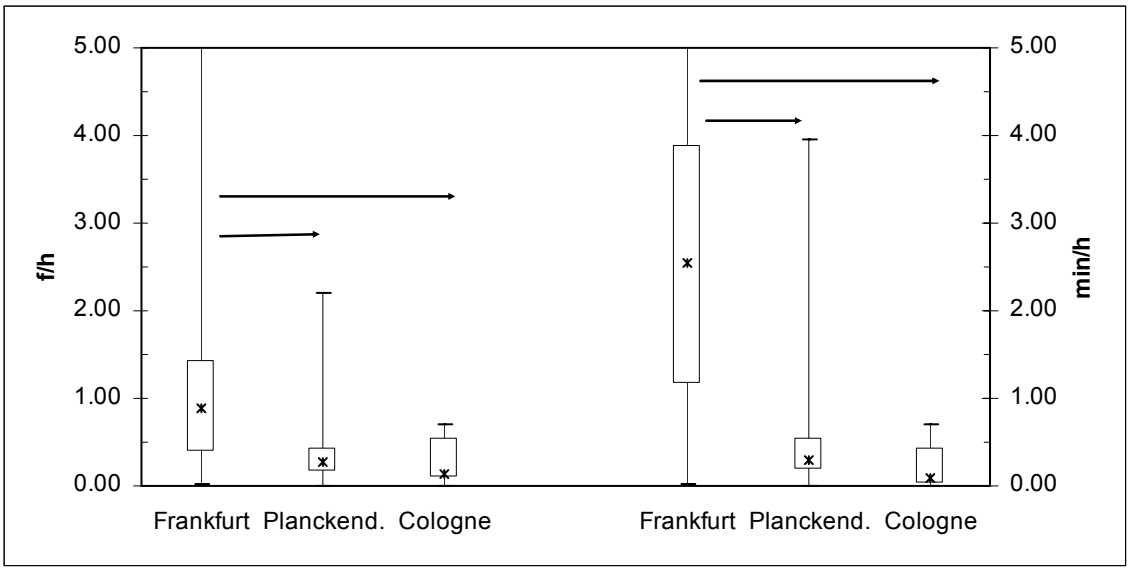


Fig. 3.4: Being in physical contact: Median dyad values and ranges (minimum, maximum, quartile 1+3) found in the differnt colonies. left side=frequency (f/h); right side=duration (min/h); arrows=significant differences ($p<0.05$) found with Kruskal-Wallis One Way ANOVA on Ranks and All Pairwise Comparisons (Dunn`s method)

Significant differences were found between Frankfurt and Cologne and between Frankfurt and Planckendael regarding both, frequency and duration of being in physical contact. The Frankfurt group was also the only one, without a minimum of zero, which means all animals were in physical contact to each other at least once (note that being in contact to each other while grooming is not included). The minimum of zero in Planckendael emerged from a female-female dyad (He+Dj) which also had low values of interacting. The minimum of zero in Cologne was found between the oldest male and the oldest female (Bo+Cl). This dyad, on the other hand, reached values of interacting above the median with the major part coming from allogrooming behaviour but seemed to dislike just being in physical contact to each other without additional interacting.

3.1.1 Categories of interactive behaviour

Analysing the datasets of the 5 different behavioural categories (fig. 2.1) resulted in a more differentiated picture of the interactive behaviour between two animals. Results were tested for significant differences between the observed groups, again considering all single possible dyad values of each colony.

interactive behaviour	Frankfurt (n=28)		Planckendael (n=28)		Cologne (n=10)		sign. differences	
	f/h	s/h	f/h	s/h	f/h	s/h	f/h	s/h
sociopositive	0.99	166.45	0.50	62.45	0.94	123.51	no	F>P
sexual	0.06	0.79	0.02	0.12	0.01	0.06	no	F>P, F>C*
agonistic	0.00	0.00	0.06	0.30	0.03	0.10	P>F	P>F
submissive	0.00	0.00	0.00	0.00	0.00	0.00	no	no
others	1.61	8.98	1.13	8.39	1.48	16.44	F>P, C>P*	no

Table 3.3: Different interactive behavioural categories: Median dyad values from all 3 colonies for frequency (f/h) and duration (s/h). statistical testing (significance level $p<0.05$): Kruskal-Wallis One Way ANOVA on Ranks and All Pairwise Comparisons (Dunn`s method); *significant differences found with ANOVA on Ranks but All Pairwise Comparison failed, so post hoc Mann-Whitney Rank Sum tests were used; n=number of dyads in each group

For the frequency of sociopositive behaviours, no significant differences between the groups could be found, but regarding duration, the dyads of the Frankfurt colony reached significantly higher values than the Planckendael ones.

Sexual behaviours were seen most often in the Frankfurt colony and sexual contacts also lasted longest between two animals of the Frankfurt group. A trend of being engaged in sexual contacts for significantly longer times was found for the Frankfurt individuals, compared to the other 2 groups (as ANOVA on Ranks revealed a significant difference but All Pairwise Comparisons failed, Mann-Whitney Rank Sum tests were used and therefore results must be assessed cautiously).

Regarding agonistic behaviours, the Planckendael colony had significantly higher values than the Frankfurt group (frequency and duration), with the Cologne group being in between. Submissive behaviours were extremely rare in all colonies and led to median values of zero.

To investigate the ratios of each behavioural category within the interactive behaviour, rates were calculated for each one, referring to the values listed in table 3.3.

Although behaviours between two animals summed as others were seen most frequently of all categories, sociopositive behaviours were clearly dominant regarding the time budget. These patterns were found in all 3 studied groups and therefore seem to be independent of different keeping conditions and settings (fig. 3.5).

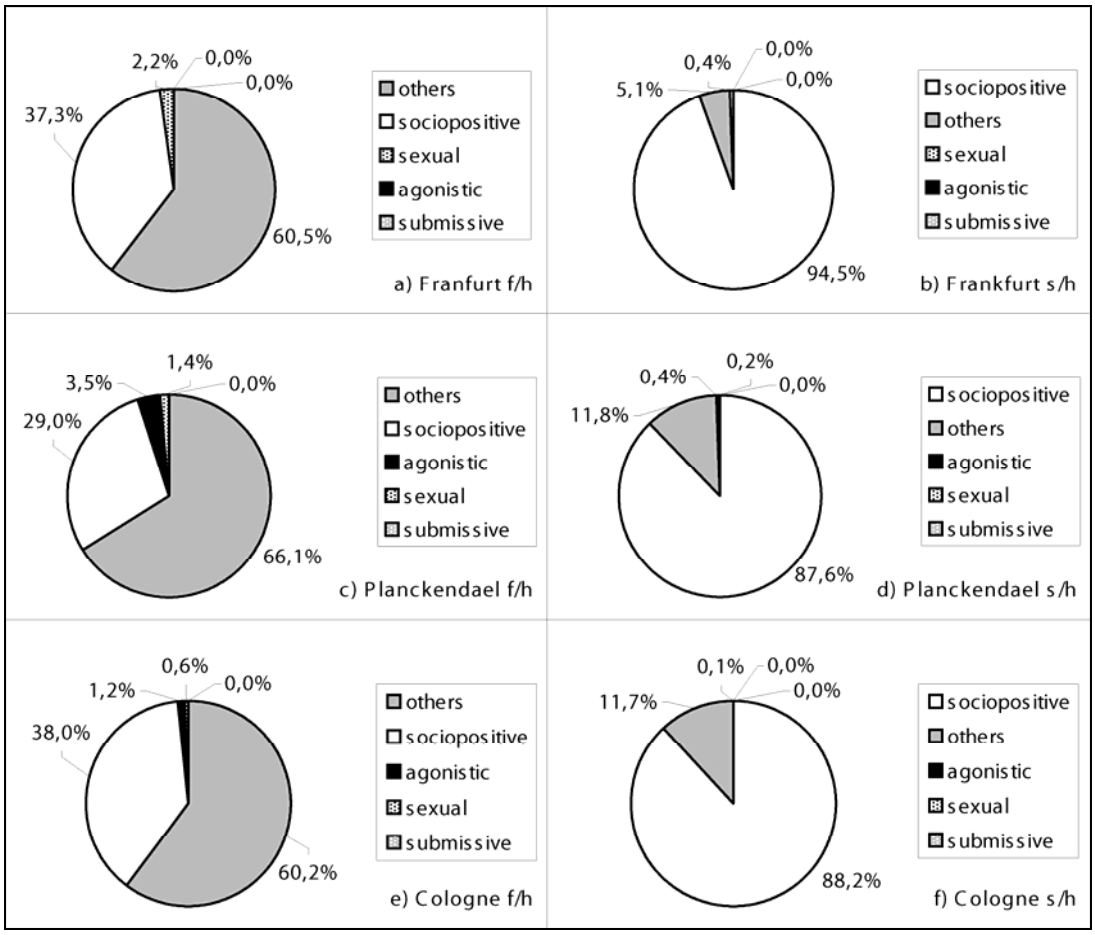


Fig. 3.5a)-f): Proportions of different interactive behavioural categories per animal dyad in all 3 colonies. a, c, e: frequency (f/h), b, d, f: duration (s/h)

3.1.2 Age-sex class specific patterns

To investigate age-sex class specific differences as often discussed in literature (chapter 1.4), datasets were also analysed regarding different age and/or sex combinations which existed in each group of the observed zoo-living animals. It was expected that female-female and mixed sex pairs would interact more often than males would do among each other. For the case of existing mother-adult son relationships it was assumed that this dyad would also show a high amount of interacting. Comparisons were made within all three groups. Finally an overall picture was drawn which gives an idea about age-sex class differences on a more general level. Statistical testing was only done for age-sex classes involving adult animals and existing of more than two dyads.

Interactive behaviour

a) Frankfurt

The 28 dyads in Frankfurt were sorted into six age-sex classes (table 3.4). For the different age-sex classes, the median values for frequency and duration regarding the total interactive behaviour did not differ significantly between the 4 observation periods ($p>0.05$; Friedmann Repeated Measures ANOVA on Ranks).

age-sex classes frequency (f/h)	block I	block II	block III	block IV	total	
male-female (n=5)	2.04	1.52	2.42	1.88	**2.54**	
female-female (n=10)	3.57	3.00	3.19	4.10	**3.20**	
mother-infant (n=2)	4.13	4.81	5.15	3.38	**4.37**	*
adult male-infant (n=2)	4.07	3.11	4.28	3.33	**3.70**	
adult female-infant (n=8)	1.21	1.40	1.54	2.11	**1.34**	
infant-infant (n=1)	6.23	7.52	8.22	7.53	**7.38**	
duration (min/h)	**I**	**II**	**III**	**IV**	**total**	
male-female (n=5)	2.99	2.46	0.88	0.82	**1.80**	*
female-female (n=10)	5.02	3.81	4.66	7.88	**5.08**	
mother-infant (n=2)	3.98	3.31	4.10	1.48	**3.22**	*
adult male-infant (n=2)	1.63	3.28	3.07	5.82	**3.45**	
adult female-infant (n=8)	0.50	0.50	0.70	0.47	**0.50**	
infant-infant (n=1)	12.87	12.07	13.14	9.34	**11.86**	

Table 3.4: Frankfurt colony: Interactive behaviour per dyad (medians) in different age-sex classes and different observation periods. n=number of dyads per age-sex class; total=medians of average single dyad values (block I-IV); bold type=classes involving more than 2 dyads; *=significant difference ($p<0.05$) found with One Way ANOVA and All Pairwise Comparisons (Holm-Sidak method)

Based on the average values of all dyads per class (block I-IV), total medians were calculated for each one (table 3.4, last column). Concentrating on these total values and regarding the age-sex classes involving more than 2 dyads, revealed a significant difference between the female-female and the adult female-infant class, with dyads of the first one interacting more often and for longer times. Female-female dyads were also interacting for significantly longer time periods than the male-female ones.

b) Planckendael

Animal dyads observed in Planckendael were sorted into eight age-sex classes (table 3.5). There were two classes, not present in the Frankfurt colony (male-male and mother-adult son).

age-sex classes	frequency f/h	duration min/h
male-female (n=7)	1.77	1.03
mother-adult son (n=2)	1.47	1.81
female-female (n=3)	0.86	1.39
male-male (n=3)	0.67	0.77
mother-juvenile (n=2)	3.19	2.60
adult male-juvenile (n=6)	2.24	1.24
adult female-juvenile (n=4)	2.54	1.54
juvenile-juvenile (n=1)	7.42	5.05

Table 3.5: Planckendael colony: Interactive behaviour per dyad (medians) in different age-sex classes. n=number of dyads per age-sex class; bold type=classes involving more than 2 dyads

Comparing the age-sex classes which involved adult animals only (first 4 in table 3.5) showed that the male-male dyads interacted the least frequent and shortest. The most frequent interactions were found in the male-female class, but concerning duration the mother-adult son class reached the highest median value. Although females interacted with each other less frequently than they did with males they did on average spend more time on it than on interacting with the other gender. Nevertheless statistical testing revealed no significant differences between the classes involving more than 2 dyads, neither for frequency nor for duration ($p>0.05$; One Way ANOVA).

c) Cologne

Animal dyads observed in Cologne were sorted into four age-sex classes (table 3.6).

age-sex classes	frequency f/h	duration min/h
male-female (n=5)	2.47	1.12
mother-adult son (n=1)	2.03	5.66
female-female (n=1)	6.53	6.26
male-male (n=3)	1.75	0.36

Table 3.6: Cologne colony: Interactive behaviour per dyad (medians) in different age-sex classes. n=number of dyads per age-sex class; bold type=classes involving more than 2 dyads

The Cologne colony only consisted of adult animals. The highest frequency and duration values in Cologne were reached by the only female-female dyad and lowest values regarding both were reached by the three male-male dyads (table 3.6). Statistical testing revealed no significant differences between the adult age-sex classes involving more than 2 dyads (male-female and male-male), neither for frequency nor for duration ($p>0.05$; One Way ANOVA).

Physical contact

a) Frankfurt

No bigger fluctuations between the 4 different observation periods could be found in the different age-sex classes regarding the physical contact datasets. For 2 age-sex classes, the medians differed significantly between the blocks ($p<0.05$; Friedman Repeated Measures ANOVA on Ranks): frequency medians differed in the female-female class; duration values did so for the female-female class and for the adult female-infant class. No articulate explanation could be found for these fluctuating rates of physical contact but possible reasons are discussed in chapter 4.1.

As expected for groups involving infants and juveniles, the 2 mothers and their infants were found in physical contact very frequently and for long durations.

age-sex classes frequency (f/h)	block I	block II	block III	block IV	total	
male-female (n=5)	0.05	0.07	0.11	0.18	**0.09**	
female-female (n=10) **	0.96	0.73	0.49	0.12	**0.62**	
mother-infant (n=2)	4.43	6.34	5.20	4.31	**5.07**	* *
adult male-infant (n=2)	0.94	1.35	0.86	1.30	**1.11**	
adult female-infant (n=8)	1.47	1.74	1.25	1.62	**1.53**	
infant-infant (n=1)	1.09	2.27	1.36	1.66	**1.60**	
duration (min/h)	**I**	**II**	**III**	**IV**	**total**	
male-female (n=5)	0.22	0.11	0.07	0.05	**0.10**	
female-female (n=10) **	3.51	1.58	1.01	0.12	**1.91**	
mother-infant (n=2)	13.55	14.04	11.88	10.20	**12.42**	* *
adult male-infant (n=2)	1.80	2.11	1.39	0.66	**1.49**	
adult female-infant (n=8) **	6.43	5.54	3.62	4.28	**4.60**	
infant-infant (n=1)	3.83	4.54	2.41	3.03	**3.45**	

Table 3.7: Frankfurt colony: Physical contact per dyad (medians) in different age-sex classes and different observation periods. n=number of dyads per age-sex class; **=significant differences ($p<0.05$) between the blocks found with Friedman Repeated Measures ANOVA on Ranks; total=medians of average single dyad values (block I-IV); bold type=classes involving more than 2 dyads; *=significant difference ($p<0.05$) found with Kruskal-Wallis One Way ANOVA on Ranks and All Pairwise Comparisons (Dunn's method, frequency) and One Way ANOVA and All Pairwise Comparison (Holm-Sidak method, duration)

Based on the average values of all dyads per class, total medians were calculated (table 3.7, last column) for each one. Statistical testing between the 3 classes involving more than 2 dyads revealed the values for the adult female-infant class to be significantly higher compared to the other two classes (frequency and duration).

Infants disengagement

Because observations in Frankfurt lasted for nearly 1 year and there were two mothers with dependent offspring in the group it was also tested whether the time the infants spent in physical contact to their mothers decreased when they grew older. Duration values (min/h) from all 4 single observation periods (block I-IV) were correlated to the infant's age, considering both mother-infant pairs (fig. 3.6).

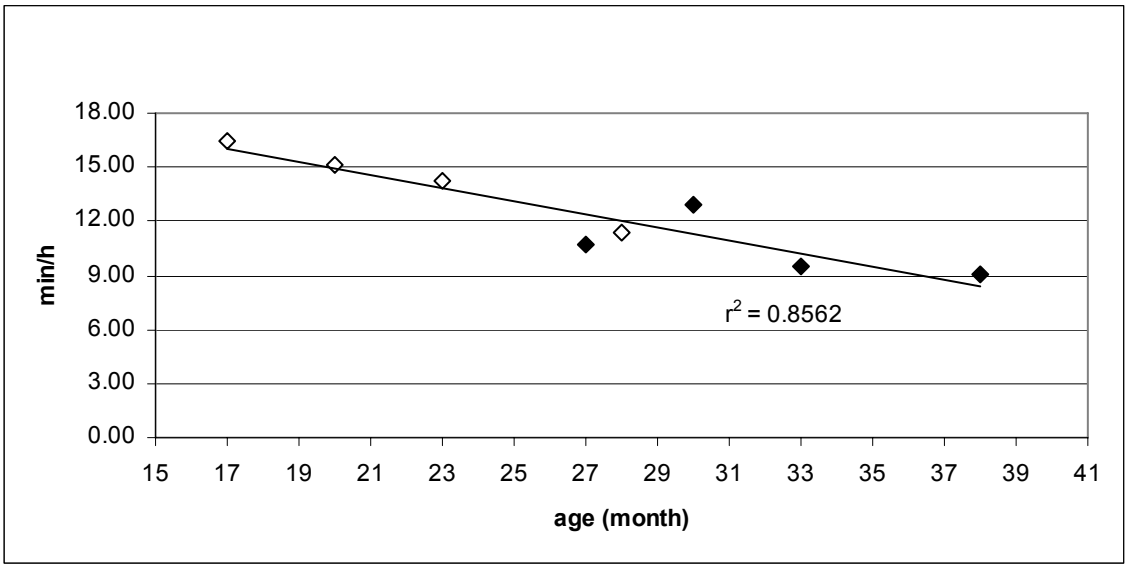


Fig. 3.6: Frankfurt colony, infants disengagement: Relationship of time a mother-infant dyad spent in physical contact (min/h) and an infant's age (month). white symbols=Uk+Ha: dyad with younger infant (17month in block I/ 28 month in block IV); black symbols=Na+He: dyad with older infant (27 month in block I/ 38 month in Block IV). Pearson`s correlation coefficient: r=-0.925, p<0.001; n=8; r^2=stability index

The youngest infant (Ha, female) was 17 months old when data collection started (block I) and 28 months of age when it ended (block IV). The male infant (He) was a bit older: he was 27 months old in the beginning and 38 month of age in observation block IV. A significant negative correlation was found between the age of the infants and the time that mothers and infants spent in physical contact to each other (Pearson`s correlation coefficient: r=-0.925, p<0.001; n=8). Thereby the value of Na+He from the first observation period was similar to the value of Uk+Ha from the last observation period: both mother-infant pairs spent around 11 minutes per hour in physical contact when the infants were roughly 2 years and 1 quarter of age.

b) Planckendael

As expected, an average mother-juvenile pair was in contact most frequently and for longest times in Planckendael as well as in Frankfurt (table 3.8).

An average mother-adult son dyad was in physical contact more often and for longer time periods than an average dyad of all other adult age-sex classes was (first 4 in table 3.8). A male-female dyad was in physical contact more often and spent more time there than a female-female dyad did. The lowest values of all classes were found between males. Statistical testing was performed for all age sex-classes involving more than two dyads. It revealed a significant difference between the adult female-juvenile and the male-male class, with the animals of the latter one being significantly less often in physical contact ($p<0.05$; One Way ANOVA and Holm-Sidak method).

age-sex classes		frequency f/h	duration min/h
male-female (n=7)		0.19	0.22
mother-adult son (n=2)		0.23	0.33
female-female (n=3)		0.14	0.18
male-male (n=3)		0.02	0.01
mother-juvenile (n=2)	*	1.55	3.35
adult male-juvenile (n=6)		0.42	0.45
adult female-juvenile (n=4)		0.48	0.50
juvenile-juvenile (n=1)		0.48	0.44

Table 3.8: Planckendael colony: Physical contact per dyad (medians) in different age-sex classes. n=number of dyads per age-sex class; bold type=classes involving more than 2 dyads; *=significant difference ($p<0.05$) found with One Way ANOVA and All Pairwise Comparisons (Holm-Sidak method)

c) Cologne

The Cologne colony just involved adult animals. The only two females were found in physical contact most frequently and for longest time periods whereas this was the opposite for the only mother-adult son pair (table 3.9).

Regarding classes, involving more than one dyad (male-female and male-male), the male-female class reached higher values than the male-male class did, although statistical testing revealed no significant difference ($p>0.05$; One Way ANOVA).

age-sex classes	frequency f/h	duration min/h
male-female (n=5)	0.15	0.11
mother-adult son (n=1)	0.03	0.02
female-female (n=1)	0.65	0.50
male-male (n=3)	0.12	0.07

Table 3.9: Cologne colony: Physical contact per dyad (medians) in different age-sex classes. n=number of dyads per age-sex class; bold type=classes involving more than 2 dyads

Overall picture

Although there were some differences between the age-sex classes of the different colonies, summarizing all single age-sex class dyad values from all three groups can give a rough picture of differences between age-sex class dyads of adult zoo-living bonobos in general. Table 3.10 summarizes the datasets from all 3 observed colonies just considering age-sex classes, consisting of adult animals.

interactive behaviour			physical contact		
age-sex c.	**f/h**	**min/h**	**age-sex c.**	**f/h**	**min/h**
1. m-f (n=17)	2.14	1.12	1. m-f (n=17)	0.15	0.13
2. f-f (n=14)	2.94	4.41	2. f-f (n=14)	0.47	0.80
3. m-m (n=6)	1.61	0.56	3. m-m (n=6)	0.10	0.04
4. mo-ad.son (n=3)	1.70	2.60	4. mo-ad.son (n=3)	0.17	0.29
signi. diff.	**no**	**2.>3.**	**signi. diff.**	**2.>1.**	**2.>3.**

Table 3.10: Interactive behaviour and physical contact in different age-sex classes: Median dyad values of frequency (f/h) and duration (min/h) including adult animal dyads of all 3 colonies. n=number of dyads, statistical testing (significance level $p<0.05$): Kruskal-Wallis ANOVA on Ranks and All Pairwise Comparisons (Dunn`s method), age-sex classes: m-f=male-female, f-f=female-female, m-m=male-male, mo-ad.son=mother-adult son

Females interacted with each other most often and longest and also stayed in contact most frequently and longest. Second highest median values for both, interacting and being in physical contact were reached either by the male-female or the mother-adult son classes. The lowest values were always found for the male-male age-sex class. Significant differences were found for the time spent on interactive behaviour and the time being in physical contact between female-female dyads and male-male dyads. Females were also found in physical contact to each other significantly more often than to males (fig. 3.7 and 3.8).

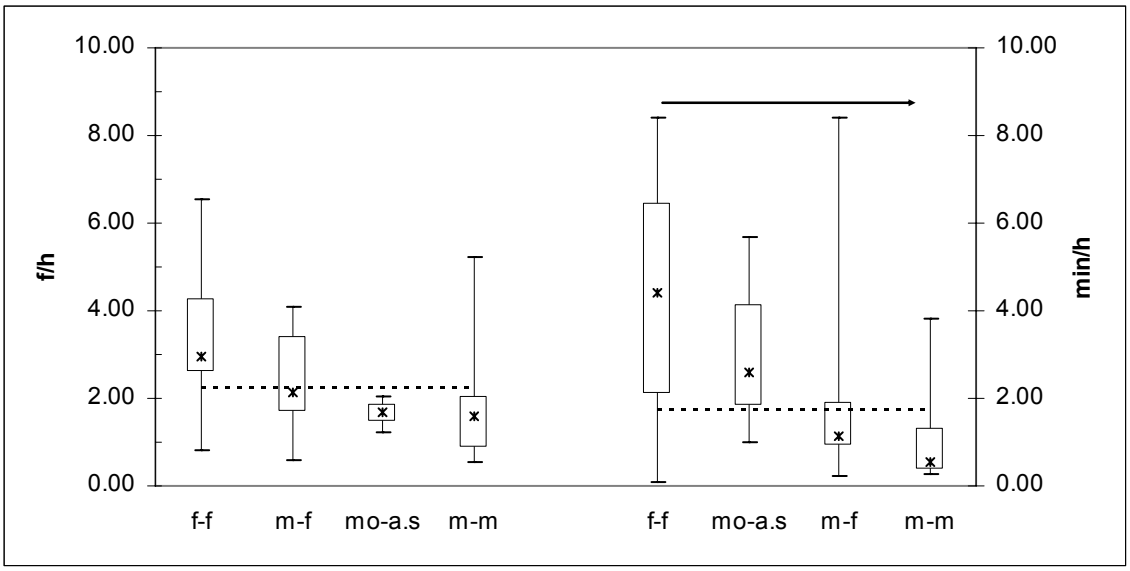


Fig. 3.7: Interactive behaviour in age-sex classes (median dyad values and ranges; minimum, maximum, quartile 1+3). left side=frequency (f/h); right side=duration (min/h); arrow=significant difference ($p<0.05$) found with Kruskal-Wallis ANOVA on Ranks and All Pairwise Comparisons (Dunn`s method); dashed line=overall median values including all adult animal dyads (n=40)
age-sex classes: f-f=female-female, m-f=male-female, mo-ad.son=mother-adult son , m-m=male-male

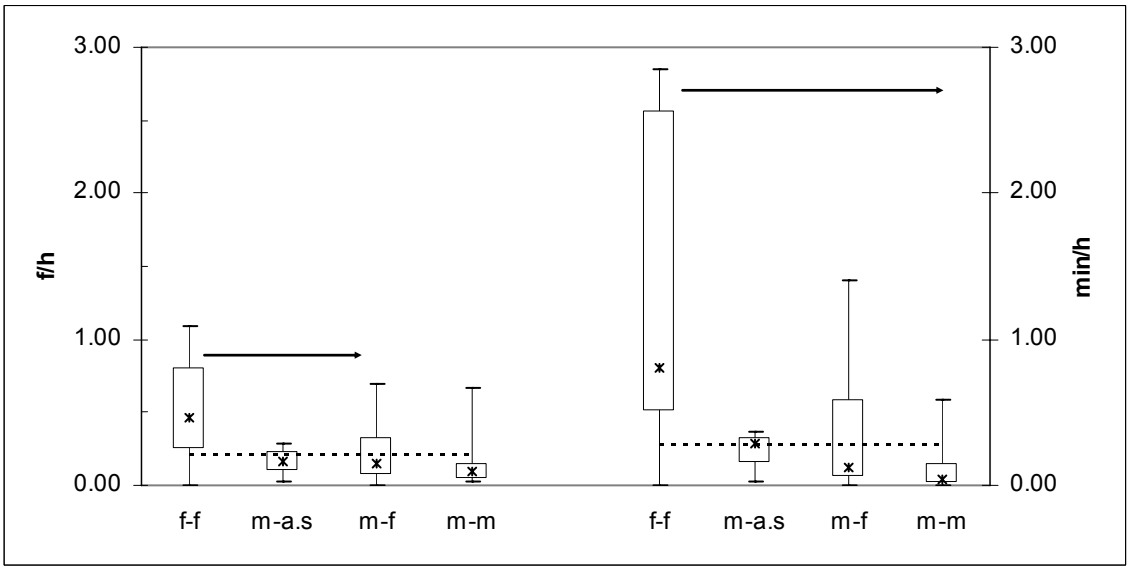


Fig. 3.8: Physical contact in age-sex classes (median dyad values and ranges; minimum, maximum, quartile 1+3). left side=frequency (f/h); right side=duration (min/h); arrows=significant differences ($p<0.05$) found with One Way ANOVA (frequency) and Kruskal-Wallis ANOVA on Ranks (duration) and All Pairwise Comparisons (Holm-Sidak method for frequency and Dunn`s method for duration values); dashed line=overall median values including all adult animal dyads (n=40)
age-sex classes: f-f=female-female, m-f=male-female, mo-ad.son=mother-adult son , m-m=male-male

3.1.3 Specific aspects of the social network

Until now, a more compact picture was presented of the different groups by investigating "average dyads", calculated from all possible partner combinations. In the following section some aspects of the network of social relationships within each group will be presented in more detail, with regard to active-passive relations and attention structures. For this purpose some pivotal behaviours from 3 behavioural categories were chosen: all agonistic behaviours, allogrooming (uni- and bidirectional) from the category of sociopositive behaviours and sexual contacts from the category of sexual behaviours (fig. 2.1).
The behaviours were analysed regarding their total number of occurrences. Sociograms were generated by means of the rates obtained for all individuals in each colony. It was looked for significant differences between the animals of a colony and additionally active-passive relations were investigated for each individual by means of equality indices (chapter 2.4).
To make the total number results of the Frankfurt colony (502 hours) comparable to the values of the much shorter studied groups from Planckendael (168 hours) and Cologne (86 hours), only the results of one observation period (block II, 157 hours) were taken into account. No significant differences could be found regarding the interactive behaviour in Frankfurt between the 4 different observation periods (fig. 3.1). The second observation period was chosen because it took place in the summer of 2003, when the animals had access to the outdoor enclosures for nearly the whole time and therefore the most "spacious conditions" within their, otherwise fairly limited, spatial situation compared to the other 2 settings.
Finally an overall picture was generated, referring to all observed individuals from all 3 colonies to highlight similarities and to get an impression about aspects of the social network in zoo-living bonobos in general.

Agonistic behaviours

a) Frankfurt

Agonistic behaviours were rare in the Frankfurt colony and just occurred between a few animals (table 3.11). Therefore, no statistical analyses were performed and no equality indices were calculated. The highest amount of agonistic behaviours was received by the only adult male (Lu, 5 times), performed by 5 different conspecifics. Lu never showed agonistic

behaviours. For the Frankfurt colony, agonistic interactions were clearly focused on the only adult male (fig. 3.9).

	Lu	Ma	Na	Sa	Uk	Ka	He	Ha	act.
Lu		0	0	0	0	0	0	0	**0**
Ma	1		0	1	0	0	0	0	**2**
Na	0	0		0	0	0	0	0	**0**
Sa	1	0	0		0	0	0	0	**1**
Uk	1	0	0	0		0	0	0	**1**
Ka	1	0	0	0	0		0	0	**1**
He	1	0	0	0	0	0		1	**2**
Ha	0	0	0	0	0	0	0		**0**
pas.	**5**	**0**	**0**	**1**	**0**	**0**	**0**	**1**	**Σ 7**

Table 3.11: Frankfurt colony, block II: Numbers of agonistic interactions within all dyads (n=28) with resulting sum for each animal. pas.=passive, act.=active; left→right=animal listed left was the active animal; top→down=animal listed above was the passive animal; Σ=total sum of agonistic interactions
animals: Lu=Ludwig (♂), Ma=Margrit (♀), Na=Natalie (♀), Sa=Salonga (♀), Uk=Ukela (♀), Ka=Kamiti (♀), He=Heri (♂, infant), Ha=Haiba (♀, infant)

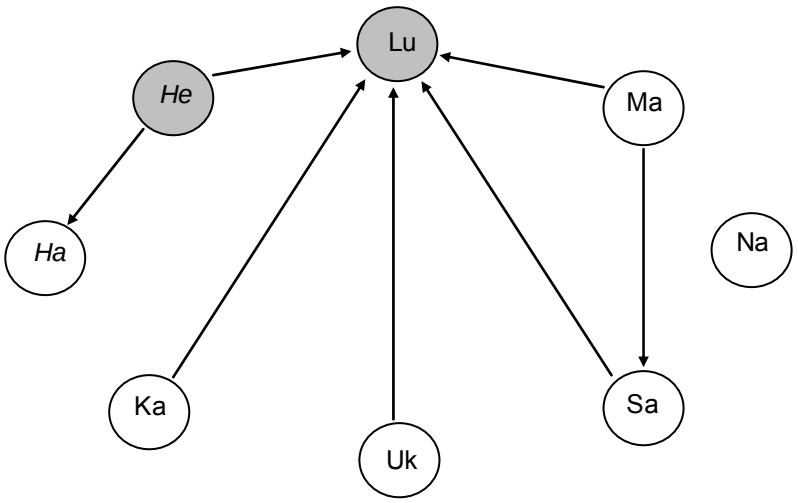


Fig. 3.9: Frankfurt colony, block II: Sociogram of agonistic interactions. arrows=direction of interaction (sender→recipient), arrow thickness=level of intensity
animals: Lu=Ludwig (♂), Ma=Margrit (♀), Na=Natalie (♀), Sa=Salonga (♀), Uk=Ukela (♀), Ka=Kamiti (♀), He=Heri (♂, infant), Ha=Haiba (♀, infant); grey=male, cursive letters=infants

b) Planckendael

Compared to the other two groups, agonistic interactions were observed rather frequently between the animals of the Planckendael colony (table 3.12). No significant differences were found between the animals regarding acting agonistically. Although the total variance of being the receiver of agonistic interactions was high (ANOVA on Ranks revealed a significant difference), no animal stuck out (All Pairwise Multiple Comparison Procedures failed to find significant differences).

The only animal, not acting agonistically against a conspecific at all was the oldest male (Ki) although he received agonistic behaviours from 4 out of his 7 conspecifics, most of them from one of the elderly females (He). The only animal never receiving agonistic interactions was the male Re (eldest son of Ho) although he was a multiple sender. Animals receiving agonistic interactions most often were the young female Dj (31 times) and the two juveniles (female Zo, 35 times and male Za, 27 times). The main senders of agonistic interactions were 2 males (Re and Vi, 24 times each) and the young female Dj (25 times). Unlike the main target of the Frankfurt group, the main targets in Planckendael also acted agonistically themselves (fig. 3.10).

	Ho	He	Dj	Ki	Re	Vi	Zo	Za	act.
Ho		0	2	0	0	0	0	2	**4**
He	0		10	4	0	5	0	3	**22**
Dj	0	0		1	0	2	11	11	**25**
Ki	0	0	0		0	0	0	0	**0**
Re	0	2	8	3		5	5	1	**24**
Vi	0	5	6	0	0		8	5	**24**
Zo	1	0	3	1	0	0		5	**10**
Za	0	1	2	0	0	1	11		**15**
pas.	**1**	**8**	**31**	**9**	**0**	**13**	**35**	**27**	**Σ 124**

Table 3.12: Planckendael colony: Numbers of agonistic interactions within all dyads (n=28) with resulting sum for each animal. left→right=animal listed left was the active part; top→down=animal listed above was the passive part; Σ=total sum of agonistic interactions
animals: Ho=Hortense (♀), He=Hermien (♀), Dj=Djanoa (♀), Zo=Zomi (♀, juvenile), Ki=Kidogo (♂), Re=Redy (♂), Vi=Vifijo (♂), Za=Zamba (♂, juvenile)

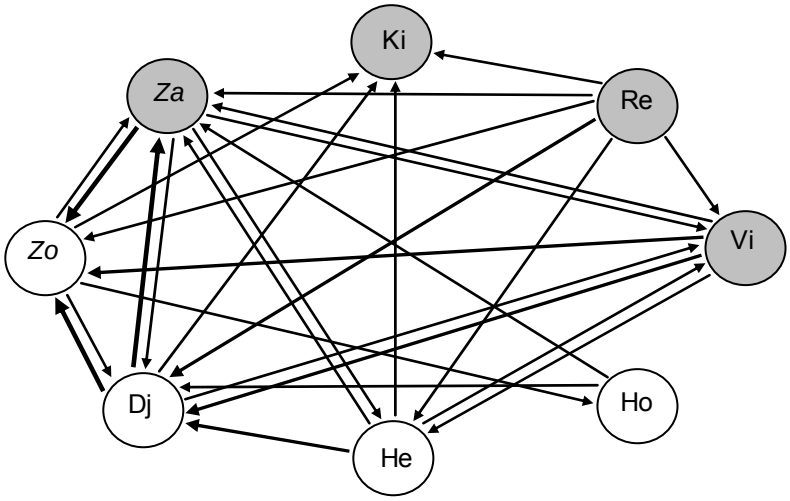


Fig. 3.10: Planckendael colony: Sociogram of agonistic interactions. arrows=direction of interaction (sender→recipient), arrow thickness=level of intensity
animals: Ho=Hortense (♀), He=Hermien (♀), Dj=Djanoa (♀), Zo=Zomi (♀, juvenile), Ki=Kidogo (♂), Re=Redy (♂), Vi=Vifijo (♂), Za=Zamba (♂, juvenile); grey=males, cursive letters=juveniles

Calculating equality indices for each animal showed that the 2 oldest females (He and Ho) and the 2 adult sons of Ho were more often acting agonistically against others than receiving agonistic behaviours (fig. 3.11). For the oldest adult son of Ho, who never received agonistic behaviours (equality index=1) the difference between the datasets was significant (Mann-Whitney Rank Sum Test, p=0.004). The 2 juveniles and the oldest male clearly received more agonistic behaviours than sending them. For the oldest male (Ki), who never acted agonistically himself (equality index=-1) the difference between the datasets was almost significant (Mann-Whitney Rank Sum Test, p=0.073). For the youngest adult female (Dj), the active/passive relation was equitable (equality index=-0.11, difference ≤15% respectively).

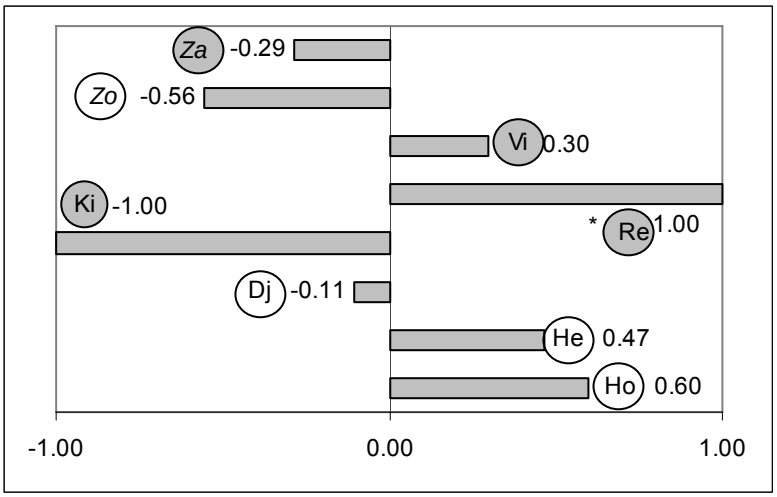


Fig. 3.11: Planckendael colony: Equality indices for each animal. negative prefix=receiving>sending, positive prefix=sending>receiving, values between -0.15 & 0.15=equitable relation, *=significant difference between the datasets of sending and receiving (Mann-Whitney Rank Sum Test, $p<0.05$)
animals: Ho=Hortense (♀), He=Hermien (♀), Dj=Djanoa (♀), Zo=Zomi (♀, juvenile), Ki=Kidogo (♂), Re=Redy (♂), Vi=Vifijo (♂), Za=Zamba (♂, juvenile); grey=males, cursive letters=juveniles

c) Cologne

Like in Frankfurt, agonistic behaviours occurred infrequently in the Cologne colony and just between a few animals (table 3.13). The young female (Bi) acted agonistically most often of all animals (22 times) and against all her possible dyad partners. Statistical analyses were only done with the active-passive datasets of Bi. The difference between agonistic behaviours given and the lack of agonistic behaviours received by Bi was clearly significant (Mann-Whitney Rank Sum Test, p=0.029). She mainly acted agonistically against the youngest male Bol (17 times), which made him being the most frequent target of agonistic behaviours of all animals. In contrast, the young female did not receive agonistic behaviours from any of her dyad partners.

Two individuals of the Cologne colony were not acting agonistically at all but received agonistic behaviours from two conspecifics each. Like in Frankfurt and Planckendael, these animals were males (fig. 3.12).

	Cl	Ki	Bol	Bo	Bi	act.
Cl		0	0	0	0	**0**
Ki	5		0	0	0	**5**
Bol	0	0		0	0	**0**
Bo	0	0	1		0	**1**
Bi	1	2	17	2		**22**
pas.	**6**	**2**	**18**	**2**	**0**	**Σ 28**

Table 3.13: Cologne colony: Numbers of agonistic interactions within all dyads (n=10) with resulting sum for each animal. left→right=animal listed left was the active part, top→down=animal listed above was the passive part; Σ=total sum of agonistic interactions
animals: Cl=Clyde (♂), Ki=Kindu (♂), Bol=Bolombo (♂), Bo=Bonnie (♀), Bi=Binti (♀)

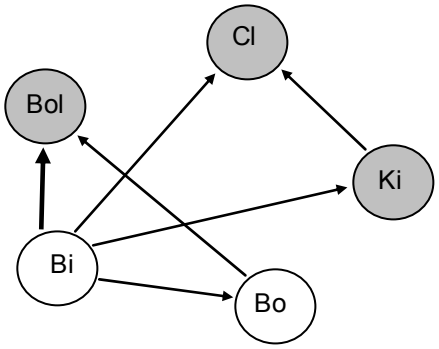


Fig. 3.12: Cologne colony: Sociogram of agonistic interactions. arrows=direction of interaction (sender→recipient), arrow thickness=level of intensity
animals: Cl=Clyde (♂), Ki=Kindu (♂), Bol=Bolombo (♂), Bo=Bonnie (♀), Bi=Binti (♀); grey=males

Allogrooming behaviour

Two different kinds of allogrooming bouts were recorded and analysed:
-individual X grooming individual Y (unidirectional allogrooming: 1 active sender & 1 passive receiver)
-individual X and individual Y grooming each other simultaneously (bidirectional allogrooming)

a) Frankfurt

As can be seen in table 3.14, active unidirectional allogrooming occurred most frequently with an adult female (Uk, 111 times) and least frequently with the two infants (He, 9 times and Ha, 4 times) and the oldest adult female (Ma, 15 times). Only the difference between the

datasets of Uk and Ha was found to be significant (Kruskal-Wallis One Way ANOVA on Ranks and Tukey Test, $p<0.05$). Unidirectional allogrooming was received most frequently by an adult female (Na, 84 times) and least frequently by the female infant (Ha, 24 times). No significant differences between the animals were found regarding the datasets of unidirectional grooming bouts received. Bidirectional allogrooming was observed considerably less often than unidirectional allogrooming. It was absent with the 2 infants and rare with the oldest female (Ma, 1 time).

a) unidirectional allogrooming

	Lu	Ma	Na	Sa	Uk	Ka	He	Ha	act.
Lu		2	3	13	4	0	4	2	**28**
Ma	0		6	1	1	7	0	0	**15**
Na	5	9		1	35	16	14	0	**80**
Sa	31	4	2		4	8	0	0	**49**
Uk	9	4	41	21		14	2	20	**111**
Ka	0	11	27	8	10		19	2	**77**
He	2	1	4	0	0	2		0	**9**
Ha	0	0	1	0	1	0	2		**4**
pas.	**47**	**31**	**84**	**44**	**55**	**47**	**41**	**24**	**Σ 373**

*

b) bidirectional allogrooming

	Lu	Ma	Na	Sa	Uk	Ka	He	Ha	
Lu		0	0	13	1	0	0	0	**14**
Ma	*0*		0	0	0	1	0	0	**1**
Na	*0*	*0*		1	6	9	0	0	**16**
Sa	*13*	*0*	*1*		2	0	0	0	**16**
Uk	*1*	*0*	*6*	*2*		3	0	0	**12**
Ka	*0*	*1*	*9*	*0*	*3*		0	0	**13**
He	*0*	*0*	*0*	*0*	*0*	*0*		0	**0**
Ha	*0*	*0*	*0*	*0*	*0*	*0*	*0*		**0**
									Σ 36

Table 3.14: Frankfurt colony, block II: Numbers of a) unidirectional and b) bidirectional (cursive numerals reflect normal ones) allogrooming bouts in all dyads (n=28) with resulting sums for each animal. left→right=animal listed left was the active part; top→down=animal listed above was the passive part; Σ=total sum of allogrooming bouts, *=significant difference ($p<0.05$) between the datasets found with Kruskal-Wallis One Way ANOVA on Ranks and All Pairwise Multiple Comparison Procedures (Tukey Test)
animals: Lu=Ludwig (♂), Ma=Margrit (♀), Na=Natalie (♀), Sa=Salonga (♀), Uk=Ukela (♀), Ka=Kamiti (♀), He=Heri (♂, infant), Ha=Haiba (♀, infant)

Generally, adult females had more intense grooming relationships between each other than to the rest of the group, as can be seen in the beneath sociogram (fig. 3.13).

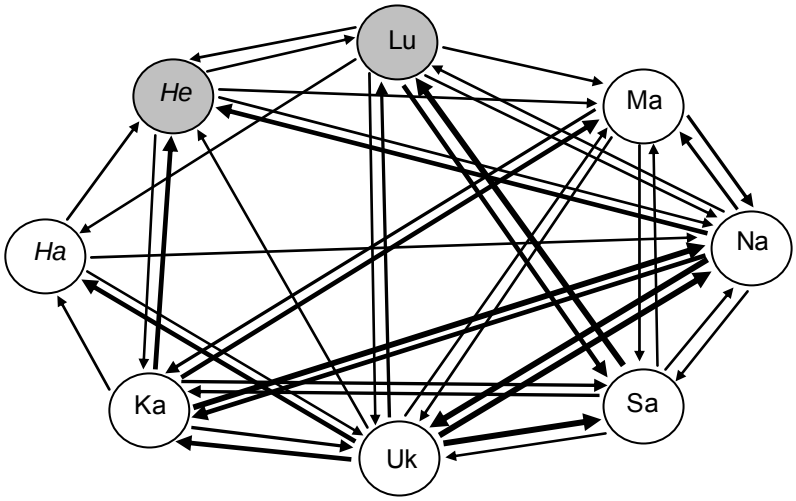


Fig. 3.13: Frankfurt colony, block II: Sociogram of unidirectional allogrooming. arrows=direction of interaction (sender→recipient), arrow thickness=level of intensity
animals: Lu=Ludwig (♂), Ma=Margrit (♀), Na=Natalie (♀), Sa=Salonga (♀), Uk=Ukela (♀), Ka=Kamiti (♀), He=Heri (♂, infant), Ha=Haiba (♀, infant); grey=male, cursive letters=infants

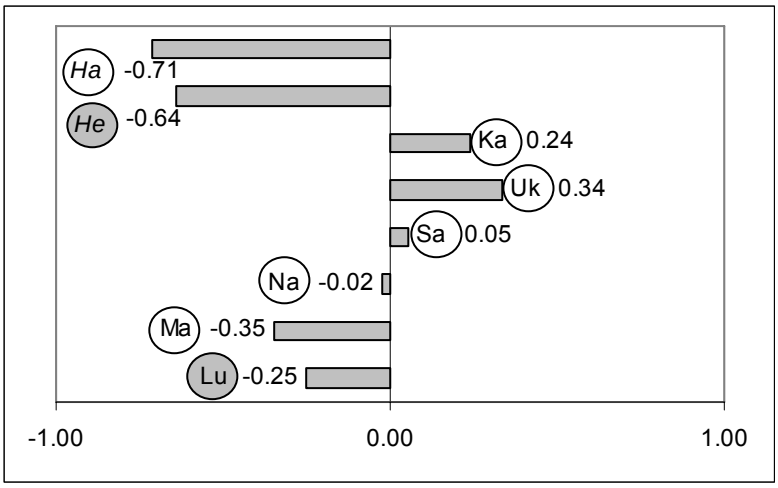


Fig. 3.14: Frankfurt colony, block II: Equality indices for each animal. negative prefix=receiving>sending, positive prefix=sending>receiving, values between -0.15 & 0.15=equitable relation
animals: Lu=Ludwig (♂), Ma=Margrit (♀), Na=Natalie (♀), Sa=Salonga (♀), Uk=Ukela (♀), Ka=Kamiti (♀), He=Heri (♂, infant), Ha=Haiba (♀, infant); grey=male, cursive letters=infants

No significant differences were found between the datasets of grooming given and grooming received for any of the individuals (t-test and Mann-Whitney Rank Sum Test respectively, $p>0.05$). The active/passive equality indices per individual (fig. 3.14) showed that especially the two infants (He and Ha) clearly received grooming more often than they did groom which was expected for young, mother-dependent infants. But also the only adult male (Lu) and the oldest female (Ma) were more often the receiver than the sender of unidirectional allogrooming. For the other two elderly females above 20 years of age (Na and Sa) the grooming relation was quite balanced. The two females between 10-20 years of age (Uk and Ka) did groom more than they were groomed.

b) Planckendael

a) unidirectional allogrooming

	Ho	He	Dj	Ki	Re	Vi	Zo	Za	act.
Ho		6	7	4	4	16	0	11	**48**
He	9		0	0	0	1	28	0	**38**
Dj	10	0		3	5	0	1	4	**23**
Ki	7	3	0		2	1	0	5	**18**
Re	7	5	0	9		4	1	5	**31**
Vi	21	17	0	3	6		0	0	**47**
Zo	1	13	2	7	0	1		1	**25**
Za	7	3	5	4	4	0	1		**24**
pas.	**62**	**47**	**14**	**30**	**21**	**23**	**31**	**26**	**Σ 254**

b) bidirectional allogrooming

	Ho	He	Dj	Ki	Re	Vi	Zo	Za	
Ho		1	0	0	0	2	0	1	**4**
He	*1*		0	0	0	0	0	0	**1**
Dj	*0*	*0*		0	0	0	0	0	**0**
Ki	*0*	*0*	*0*		0	0	0	0	**0**
Re	*0*	*0*	*0*	*0*		1	0	2	**3**
Vi	*2*	*0*	*0*	*0*	*1*		0	0	**3**
Zo	*0*	*0*	*0*	*0*	*0*	*0*		0	**0**
Za	*1*	*0*	*0*	*0*	*2*	*0*	*0*		**3**
									Σ 7

Table 3.15: Planckendael colony: Numbers of a) unidirectional and b) bidirectional (cursive numerals reflect normal ones) allogrooming bouts in all dyads (n=28) with resulting sums for each animal. left→right=animal listed left was the active part; top→down=animal listed above was the passive part; Σ=total sum of allogrooming bouts
animals: Ho=Hortense (♀), He=Hermien (♀), Dj=Djanoa (♀), Zo=Zomi (♀, juvenile), Ki=Kidogo (♂), Re=Redy (♂), Vi=Vifijo (♂), Za=Zamba (♂, juvenile)

Active unidirectional allogrooming in Planckendael occurred most frequently with one of the two oldest females (Ho, 48 times) and with an adult male (Vi, 47 times). It was observed least frequently with the oldest male (Ki, 18 times). No significant differences were found between the animals regarding the datasets of active unidirectional allogrooming (Kruskal-Wallis One Way ANOVA on Ranks, $p>0.05$). The elderly female (Ho), who groomed most often, also received grooming most frequently of all animals (62 times). Second highest values were found with the other elderly female (He, 47 times). The animal, receiving grooming least frequently was the youngest adult female (Dj, 14 times). But, no significant differences could be found between the datasets of the animals (Kruskal-Wallis One Way ANOVA on Ranks, $p>0.05$). Bidirectional allogrooming was even less common in the Planckendael colony compared to the Frankfurt group. It was only observed on 7 occasions and just the two oldest females (Ho and He) and the 3 sons of Ho were involved in bidirectional grooming sessions at all.

The sociogram (fig. 3.15) shows that the amount and intensity of grooming relationships was more evenly distributed in the Planckendael than in the Frankfurt colony but like in Frankfurt, an elderly female (Ho) played a central role.

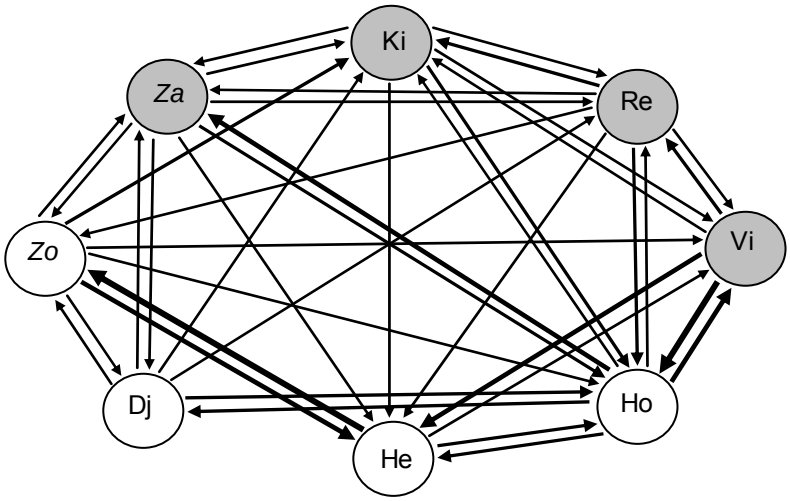


Fig. 3.15: Planckendael colony: Sociogram of unidirectional allogrooming. arrow=direction of interaction (sender→recipient), arrow thickness=level of intensity
animals: Ho=Hortense (♀), He=Hermien (♀), Dj=Djanoa (♀), Zo=Zomi (♀, juvenile), Ki=Kidogo (♂), Re=Redy (♂), Vi=Vifijo (♂), Za=Zamba (♂, juvenile); grey=males, cursive letters=juveniles

No significant differences were found between the datasets of grooming given and grooming received for any of the individuals (t-test and Mann-Whitney Rank Sum Test respectively, $p>0.05$). The active-passive equality indices per individual (fig. 3.16) showed that only the oldest male (Ki) clearly received grooming more often than he did groom others (difference >15%). For the other two adult males (Re and Vi) and for the young adult female (Dj) it was

vice versa, meaning that they groomed others more often than they were groomed. For the two juveniles and the two oldest females above 20 years of age the active/passive grooming relation was balanced.

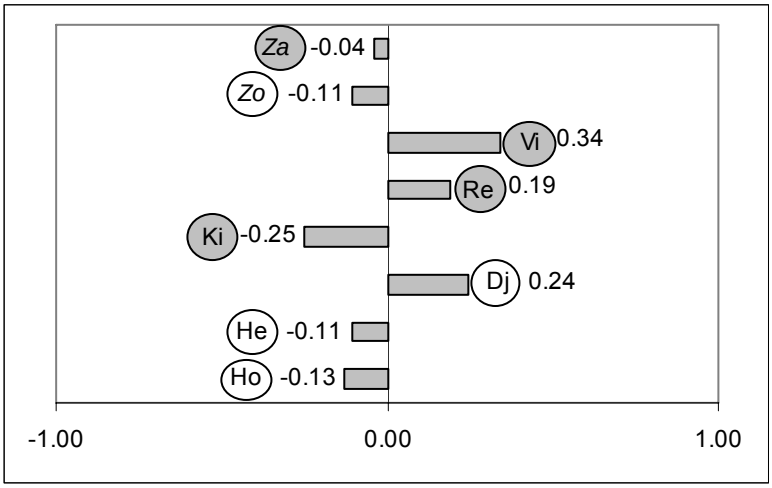


Fig. 3.16: Planckendael colony: Equality indices for each animal. negative prefix=receiving>sending, positive prefix=sending>receiving, values between -0.15&0.15=equitable relation
animals: Ho=Hortense (♀), He=Hermien (♀), Dj=Djanoa (♀), Zo=Zomi (♀, juvenile), Ki=Kidogo (♂), Re=Redy (♂), Vi=Vifijo (♂), Za=Zamba (♂, juvenile); grey=males, cursive letters=juveniles

c) Cologne

a) unidirectional allogrooming

	Cl	Ki	Bol	Bo	Bi	act.
Cl		0	0	28	0	**28**
Ki	0		8	11	48	**67**
Bol	0	7		7	1	**15**
Bo	28	25	0		36	**89**
Bi	3	7	0	9		**19**
pas.	**31**	**39**	**8**	**55**	**85**	**Σ 218**

b) bidirectional allogrooming

	Cl	Ki	Bol	Bo	Bi	
Cl		0	0	0	0	**0**
Ki	*0*		0	6	3	**9**
Bol	*0*	*0*		0	0	**0**
Bo	*0*	*6*	*0*		11	**17**
Bi	*0*	*3*	*0*	*11*		**14**
						Σ 20

Table 3.16: Cologne colony: Numbers of a) unidirectional and b) bidirectional (cursive numerals reflect normal ones) allogrooming bouts in all dyads (n=10) with resulting sums for each animal. left→right=animal listed left was the active part; top→down=animal listed above was the passive part; Σ=total sum of allogrooming bouts
animals: Cl=Clyde (♂), Ki=Kindu (♂), Bol=Bolombo (♂), Bo=Bonnie (♀), Bi=Binti (♀)

Like in Frankfurt and Planckendael active unidirectional allogrooming in Cologne occurred most frequently with a female (Bo, 89 times). It was observed least frequently with the youngest male (Bol, 15 times). No significant differences were found between the animals regarding the datasets of allogrooming given (One Way ANOVA, $p>0.05$). Unidirectional allogrooming was also mainly received by a female (Bi, 85 times). The youngest male (Bol) was groomed least frequently and received allogrooming only from the second oldest male (Ki>Bol, 8 times). No significant difference could be found regarding the datasets of allogrooming received (Kruskal-Wallis One Way ANOVA on Ranks, $p>0.05$). Bidirectional

allogrooming was observed 20 times, so it was less frequent than in Frankfurt but occurred more often than in Planckendael. The oldest male (Cl) and the youngest one (Bol) were not involved at all.

Like with the other two groups, an elderly female (Bo) played a major role in terms of allogrooming behaviour (fig. 3.17).

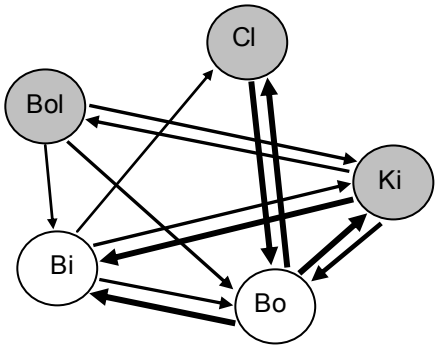


Fig. 3.17: Cologne colony: Sociogram of unidirectional allogrooming. arrow=direction of interaction (sender→recipient), arrow thickness=level of intensity
animals: Cl=Clyde (♂), Ki=Kindu (♂), Bol=Bolombo (♂), Bo=Bonnie (♀), Bi=Binti (♀); grey=males

When total numbers per animal were tested for their active-passive relation no significant differences were found between the datasets of grooming given and grooming received for any of the individuals (t-test and Mann-Whitney Rank Sum Test respectively, $p>0.05$). The active-passive equality indices per individual (fig. 3.18) showed that only the young female (Bi) clearly received grooming more often than she did groom others (difference >15%). The old female (Bo) and 2 males (Ki and Bol) groomed others more often than they were groomed. For the oldest males the active-passive grooming relation was balanced.

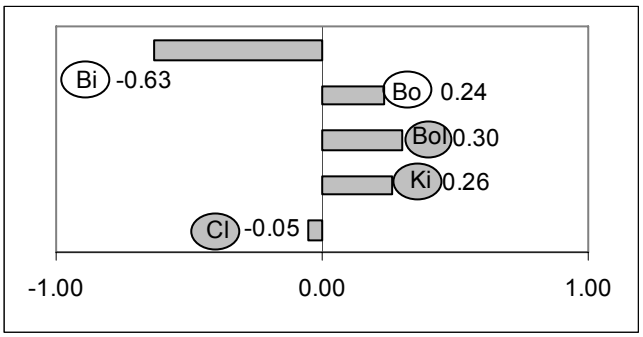


Fig. 3.18: Cologne colony: Equality indices for each animal. negative prefix=receiving>sending, positive prefix=sending>receiving, values between -0.15&0.15=equitable relation
animals: Cl=Clyde (♂), Ki=Kindu (♂), Bol=Bolombo (♂), Bo=Bonnie (♀), Bi=Binti (♀); grey=males

Sexual contacts

a) Frankfurt

	Lu	Ma	Na	Sa	Uk	Ka	He	Ha	
Lu		0	0	2	0	0	5	4	**11**
Ma	*0*		1	0	0	7	1	3	**12**
Na	*0*	*1*		0	0	7	0	0	**8**
Sa	*2*	*0*	*0*		0	5	0	0	**7**
Uk	*0*	*0*	*0*	*0*		10	0	1	**11**
Ka	*0*	*7*	*7*	*5*	*10*		6	8	**43**
He	*5*	*1*	*0*	*0*	*0*	*6*		10	**22**
Ha	*4*	*3*	*0*	*0*	*1*	*8*	*10*		**26**
									Σ 70

Table 3.17: Frankfurt colony, block II: Numbers of sexual contacts (cursive numerals reflect normal ones) in all dyads (n=28) with resulting sums for each animal. Σ=total amount of sexual contacts
animals: Lu=Ludwig (♂), Ma=Margrit (♀), Na=Natalie (♀), Sa=Salonga (♀), Uk=Ukela (♀), Ka=Kamiti (♀), He=Heri (♂, infant), Ha=Haiba (♀, infant)

Each animal of the Frankfurt colony had sexual contacts with at least 2 conspecifics. No significant differences were found regarding the datasets of sexual contacts between the animals. As can be seen in table 3.17, the highest total amount was reached by a young female (Ka, 43 times) and the lowest value was found for an elderly female (Sa, 7 times). The dyads having sexual contacts most frequently were a female-female dyad (Uk+Ka, 10 times) and the only infant-infant one (He+Ha, 10 times). Some dyads had no sexual contacts at all.

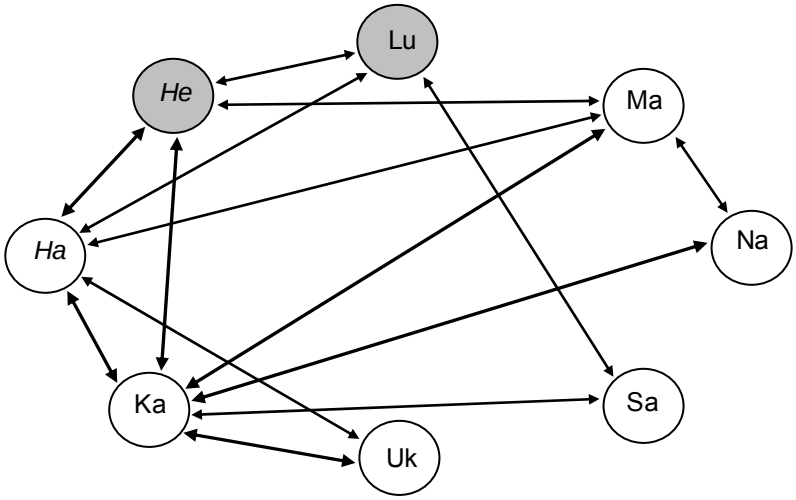


Fig. 3.19: Frankfurt colony, block II: Sociogram of sexual contacts (arrow thickness=level of intensity).
animals: Lu=Ludwig (♂), Ma=Margrit (♀), Na=Natalie (♀), Sa=Salonga (♀), Uk=Ukela (♀), Ka=Kamiti (♀), He=Heri (♂, infant), Ha=Haiba (♀, infant); grey=male, cursive letters=infants

Figure 3.19 illustrates the major role of the youngest adult female (Ka) in terms of sexual contacts. This immigrant female was introduced into the Frankfurt colony 1 year before. The sociogram also pictures the high involvement of the two infants (He+Ha) in sexual contacts.

b) Planckendael

	Ho	He	Dj	Ki	Re	Vi	Zo	Za	
Ho		0	0	1	0	0	0	0	**1**
He	*0*		0	0	2	0	1	9	**12**
Dj	*0*	*0*		0	11	11	20	10	**52**
Ki	*1*	*0*	*0*		0	0	0	1	**2**
Re	*0*	*2*	*11*	*0*		0	4	0	**17**
Vi	*0*	*0*	*11*	*0*	*0*		1	1	**13**
Zo	*0*	*1*	*20*	*0*	*4*	*1*		7	**33**
Za	*0*	*9*	*10*	*1*	*0*	*1*	*7*		**28**
									Σ 79

Table 3.18: Planckendael colony: Numbers of sexual contacts (cursive numerals reflect normal ones) in all dyads (n=28) with resulting sums for each animal. Σ=total amount of sexual contacts
animals: Ho=Hortense (♀), He=Hermien (♀), Dj=Djanoa (♀), Zo=Zomi (♀, juvenile), Ki=Kidogo (♂), Re=Redy (♂), Vi=Vifijo (♂), Za=Zamba (♂, juvenile)

No significant differences were found between the animals regarding the datasets of sexual contacts in general. Sexual contacts were observed with each individual, but one female (Ho) was involved just once (it should be noted that she was highly pregnant which presumably influenced her sexual activities). Like in Frankfurt, the two youngest animals (Zo+Za in this case) and the young immigrant female (Dj) had highest total amounts of sexual contacts. Only these 3 animals had more than 3 different partners. The dyad having sexual contacts most frequently was a female-juvenile one (Dj+Zo, 20 times).

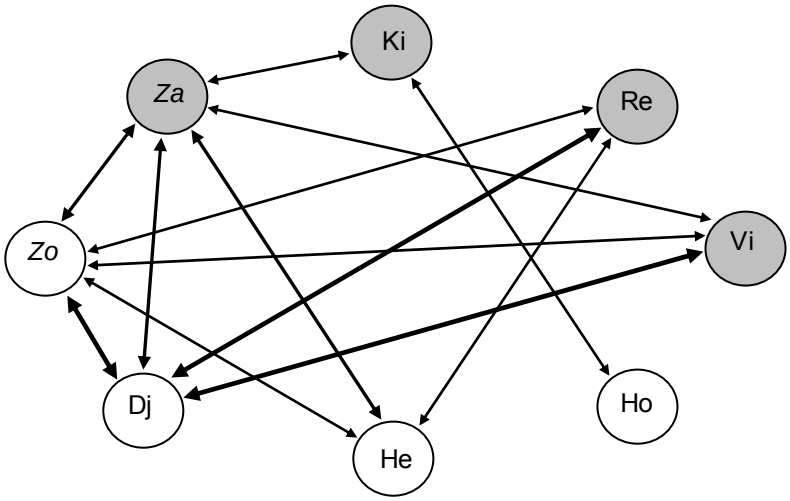


Fig. 3.20: Planckendael colony: Sociogram of sexual contacts (arrow thickness=level of intensity).
animals: Ho=Hortense (♀), He=Hermien (♀), Dj=Djanoa (♀), Zo=Zomi (♀, juvenile), Ki=Kidogo (♂), Re=Redy (♂), Vi=Vifijo (♂), Za=Zamba (♂, juvenile); grey=males, cursive letters=juveniles

c) Cologne

Sexual contacts were found with each animal but occurred rarely in Cologne (table 3.19) and therefore no statistical testing was performed. Like in Frankfurt and Planckendael, the youngest animals had the highest total amounts of sexual contacts. Sexual contacts were observed most frequently with the young female (Bi, 12 times) and the second highest amount was with the young male (Bol, 10 times). These 2 animals also reached the highest dyad value (Bi+Bol, 7 times).

	Cl	**Ki**	**Bol**	**Bo**	**Bi**	
Cl		2	0	0	0	**2**
Ki	*2*		0	0	1	**3**
Bol	*0*	*0*		3	7	**10**
Bo	*0*	*0*	*3*		4	**7**
Bi	*0*	*1*	*7*	*4*		**12**
						Σ 17

Table 3.19: Cologne colony: Numbers of sexual contacts (cursive numerals reflect normal ones) in all dyads (n=10) with resulting sums for each animal. Σ=total amount of sexual contacts
animals: Cl=Clyde (♂), Ki=Kindu (♂), Bol=Bolombo (♂), Bo=Bonnie (♀), Bi=Binti (♀)

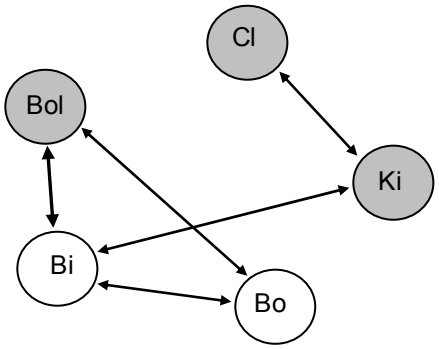


Fig. 3.21: Cologne colony: Sociogram of sexual contacts (arrow thickness=level of intensity).
animals: Cl=Clyde (♂), Ki=Kindu (♂), Bol=Bolombo (♂), Bo=Bonnie (♀), Bi=Binti (♀); grey=males

Overall picture

With regard to the total frequency of agonistic interactions, clearly the highest amount was found in Planckendael, followed by Cologne and Frankfurt (table 3.20). The total amount of allogrooming bouts was found to be highest in the Frankfurt group, followed by Planckendael and Cologne. The total amount of sexual contacts was quite similar in Planckendael and Frankfurt (note that results from "subgroup consolidations" in Frankfurt are not included), and comparatively low in Cologne. By considering the different observation times, the

Frankfurt colony occupied the lowest rank for agonistic interactions but lay in the upper range regarding both, unidirectional allogrooming and sexual contacts.

	total amount			f/h					means from
behavioural elements	**F. II**	**P.**	**C.**	**F. II**	**P.**	**C.**	**Ø**	**SD**	**literature**
agonistic behaviours	7	124	28	0.04	0.74	0.33	0.37	0.35	0.15[1], 0.26[2]
allogrooming (unidirectional)	373	254	218	2.37	1.51	2.54	2.14	0.55	0.68[3], 2.40[4]
sexual contacts	70	79	17	0.45	0.47	0.20	0.37	0.15	0.31[5]; 1.22[6]

Table 3.20: Total amount of frequencies for 3 behavioural elements, found in the 3 different groups, together with the mean values according to the different observation times (f/h). F.II=Frankfurt, observation period II (157h); P.=Planckendael (168h); C=Cologne (86h); Ø=average of all 3 groups; SD=standard deviation
mean rates obtained from literature (f/h): [1]calculated from datasets by Idani (1991, wild animals), [2]calculated from datasets by Palagi et al. (2004, captive animals), [3]calculated from datasets by Kuroda (1980, w. a.), [4]calculated from datasets by Vervaecke et al. (2000c), [5]calculated from datasets by Kano (1992, w. a., copulations under natural conditions=without provisioning), [6]calculated from datasets by de Waal (1990, c. a.)

The Planckendael group occupied the last rank regarding allogrooming bouts, whereas the Cologne colony occupied the last rank regarding sexual contacts. Statistical testing (One Way ANOVA on Ranks & Dunn`s all Pairwise Comparison) revealed a significant difference regarding agonistic interactions between the Frankfurt and the Planckendael individuals ($p<0.05$) which is compatible with the results of chapter 3.1.1 (table 3.3). The mean values, resulting from these 3 observed captive groups are quite compatible with the values, calculated from datasets obtained from literature (table 3.20, last column): The amounts of agonistic behaviours and allogrooming lay a bit closer to the results from studies of other zoo-living animals, whereas the average frequency of sexual behaviours more closely followed the results of a study conducted under natural conditions in the wild.

Some similar patterns within the different colonies were found concerning the attention structure of the investigated behavioural elements: In Frankfurt and Cologne, the main receiver of agonistic interactions were males (without acting agonistically themselves). Elderly females played a central role in terms of allogrooming behaviour and young immigrant females stuck out in terms of sexual contacts in all 3 colonies.

For an overall view, individuals from all 3 groups (n=21) were combined and grouped according to their age and gender. Mean values per animal of a given age and gender class were calculated. Additionally, all adult animal dyads were separated into 4 age-sex classes and observed versus expected values were calculated for each class (table 3.21). Because of the low number of animals in each age and gender class, results must be stated cautiously but some tendencies are mentionable:

Agonistic behaviours occurred most often with animals between 5 and 10 years of age. A male of this age class was more often the recipient of agonistic behaviours than the sender

(equality index revealed a difference >15%), whereas for a female the ratio was rather balanced.

Older females (>11 years) generally groomed more frequently than older males and also received allogrooming more often. For a male above 11 years of age the active-passive allogrooming ratio was rather balanced whereas a female was more often the groomer than the groomee between 11-20 years and had a balanced ratio only above 20 years of age. An infant was clearly groomed more often than it did groom, regardless of gender.

Sexual contacts occurred in females more often than in males and were found with females between 5-10 years of age most frequently. They were observed more rarely with animals above 20 years of age.

Summing up the total frequency values of the above mentioned behaviours and analysing them with regard to age-sex classes of adult animal dyads resulted in the following: Neither of the analysed behavioural elements was distributed according to the number of dyads present ("Chi square Goodness-of-Fit test", $p<0.001$). Agonistic behaviours were found more often than expected in male-female dyads, less often than expected between females, as often as expected only between males and were absent between mothers and their adult sons. Allogrooming occurred less often as expected between males and females and between the males. It was observed clearly more often than expected between the females and between mothers and their adult sons. Sexual contacts were observed more often than expected between males and females and between females, less often between males and they were absent again within the mother-adult son pairs.

a)	**age (years)**	**0-4**		**5-10**		**11-20**		**>20**	
behavioural elements	**gender**	**♂ (1)**	**♀ (1)**	**♂ (3)**	**♀ (3)**	**♂ (3)**	**♀ (2)**	**♂ (2)**	**♀ (6)**
agonistic behaviours	active	2.0	0.0	13.0	19.0	9.7	1.0	0.0	5.0
	passive	0.0	1.0	19.3	22.0	2.3	0.0	7.5	2.0
allogrooming (unidirectional)	active	9.0	4.0	28.7	22.3	42.0	94.0	23.0	53.2
	passive	41.0	24.0	19.0	43.3	35.7	51.0	30.5	53.8
sexual contacts		22.0	26.0	17.0	32.3	10.3	27.0	2.0	7.8
b)		**m-f (17)**		**f-f (14)**		**m-m (6)**		**mo-ad.son (3)**	
behavioural elements	**X^2**	**obs.**	**exp.**	**obs.**	**exp.**	**obs.**	**exp.**	**obs.**	**exp.**
agonistic behaviours	26.61	58	36.6	15	30.1	13	12.9	0	6.5
allogrooming (unidirectional)	91.16	234	282.6	307	232.8	40	99.8	84	49.9
sexual contacts	16.91	38	31.5	34	25.9	2	11.1	0	5.6

Table 3.21: Frequency distribution of 3 pivotal behavioural elements in captive bonobo groups (n=3) with regard to: a) mean values per individual (active & passive) and corresponding age and gender and b) observed and expected frequencies per age-sex class, only including adult animal dyads. parantheses=number of animals in each age and gender combination and number of age-sex class dyads respectively; ♂=male, ♀=female; age-sex classes: m-f=male-female, f-f=female-female, m-m=male-male, mo-ad.son=mother-adult son; X^2=Chi square Goodness-of-Fit Test ($p<0.001$)

Additionally, mean values per dyad of a given adult age-sex class were calculated and correlated to each other (fig. 3.22). An average male-female dyad reached the highest rate of agonistic behaviours (51%). Allogrooming rates were the highest for an average mother-adult son dyad (40%). The average rate of sexual contacts was quite similar between a female-female (48%) and a male-female (45%) dyad. Agonistic and sexual behaviours were absent between mothers and their adult sons. Again, results must be stated carefully because of the high variation in the actual quantity of dyads per class but they confirmed traits, found in each colony.

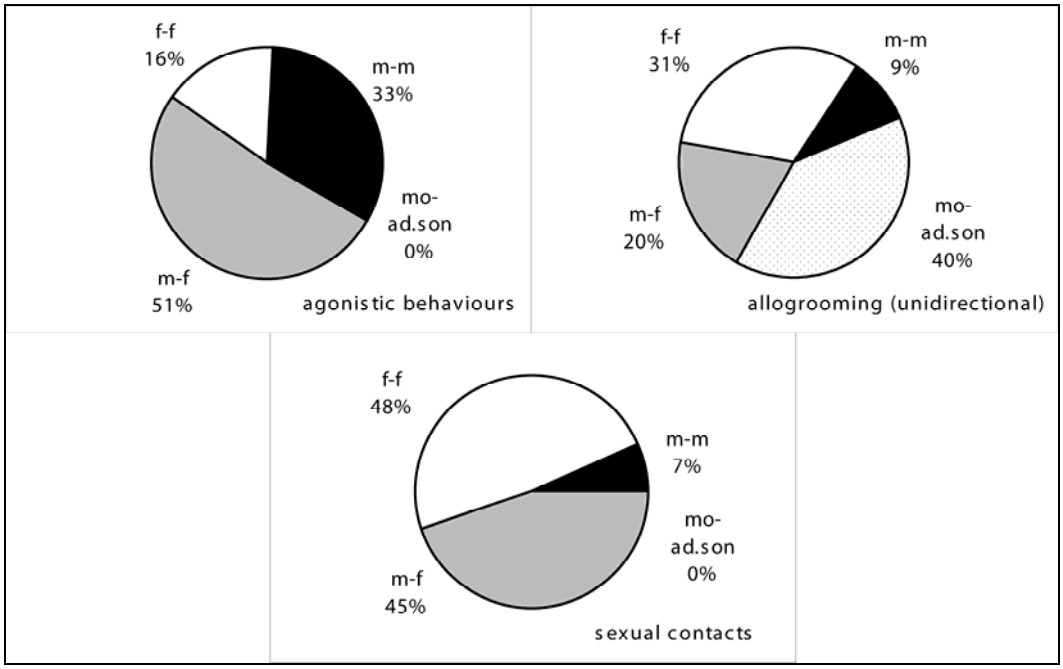


Fig. 3.22: Frequency proportions of 3 pivotal behavioural elements in 4 different age-sex classes of adult bonobos, referring to mean values per dyad of a given class. age-sex classes: m-f=male-female, f-f=female-female, m-m=male-male, mo-ad.son=mother-adult son

3.2 Spatial behaviour

The social relationships were also investigated with regard to the animal's spatial behaviour. The unit, referred to in the following section is the spatial proximity index (chapter 2.4). Generally, two animals were scored as being in spatial proximity to each other if the distance between them was ≤1 meter.

For the Frankfurt colony, average dyad values resulting from all 4 observation blocks (I-IV) were used for the calculations. Figure 3.23 pictures median proximity indices plus ranges (first and third quartile, lowest and highest value), obtained in all single observation blocks. Statistical testing revealed observation block III to be significantly different from blocks I and II ($p<0.05$; ANOVA on Ranks with following Tukey Test). No concrete explanations could be found for the differences between the first two and the third observation period but possible reasons are discussed in chapter 4.1. The overall median value revealed that two animals in Frankfurt were near to each other in 22% of all scans (proximity index: p.i.=0.22).

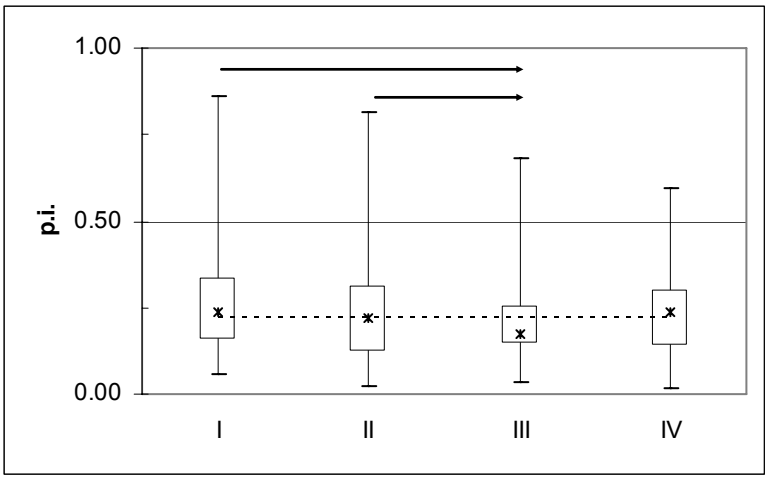


Fig. 3.23: Frankfurt colony: Proximity index (p.i., median value) per animal dyad (n=28) in all 4 different observation blocks (I-IV). ranges=minimum, maximum, quartile 1+3; dashed line=overall median value; arrows=significant differences ($p<0.05$) found with Friedman Repeated Measures ANOVA on Ranks and All Pairwise Comparisons (Tukey Test)

Median proximity index values from all three observed colonies were compared (fig. 3.24), taking into account all average dyad values (observation blocks I-IV) of the Frankfurt individuals.

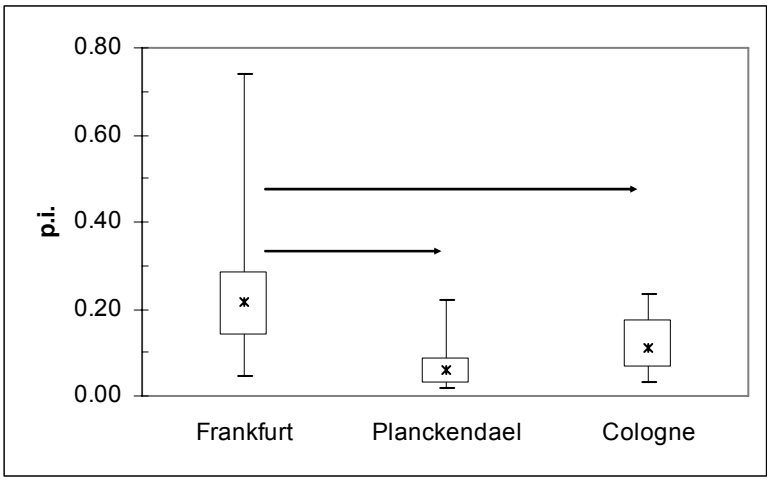


Fig. 3.24: Spatial behaviour in all 3 observed groups: Median proximity indices (p.i.) per dyad and ranges (minimum, maximum, quartile 1+3). arrows=significant differences found with Kruskal-Wallis One Way ANOVA on Ranks and All Pairwise Comparisons (Dunn`s method, $p<0.05$)

Statistical testing revealed significant differences between the Frankfurt colony and the other 2 groups. The median proximity index was significantly higher in Frankfurt (0.22) than in Planckendael (0.06) and in Cologne (0.11). Although the 3 colonies differed in terms of space useable for the animals (chapter 2.1), these significant differences can not be explained with a varying population density for several reasons:

1. It was without any difficulty even for the individuals in Frankfurt (least freedom of space), to avoid the referred to degree of spatial closeness (≤1m in distance) to a conspecific.
2. When population density increased in Frankfurt (nearly no access to the outdoor enclosures during the cold seasons) proximity indices tended to decrease rather than to increase (fig. 3.23).
3. A significant difference was found also between the Frankfurt and the Cologne colony even though their population densities did not differ that much (average amount of space in m^2/individual: Frankfurt=21, Cologne=29) whereas no significant difference was found between the Cologne and the Planckendael colony (Planckendael=385m^2/individual).

3.2.1 Categories of spatial proximity

Median proximity indices were also calculated, referring to the division into proximity with body contact and proximity without body contact in all observed colonies. Additionally the ratio of being rather in body contact or just next to each other (≤ 1m) for a given dyad was also compared between the groups. All results are shown in figure 3.25.

Statistical testing resulted in significantly higher values for the Frankfurt colony compared to Planckendael and Cologne for both subcategories. Two animals of the Frankfurt group were found in body contact to each other in 10% of all scans whereas two animals in the other colonies could only be found in body contact to each other in 4% (Cologne) and 3% (Planckendael) of all scans, respectively. Animals of a mean Frankfurt dyad were found next to each other in 11% of all scan samplings whereas this percentage was only 5% for Cologne and 3% for Planckendael. As can be seen in figure 3.25, the ratio between being in body contact and being next to each other was balanced in all three colonies. Animals of a mean dyad tended to be in proximity with body contact just as often as in proximity without body contact. Only for the Cologne individuals, a slightly preference (57% compared to 43%) was found to be in proximity to each other without body contact.

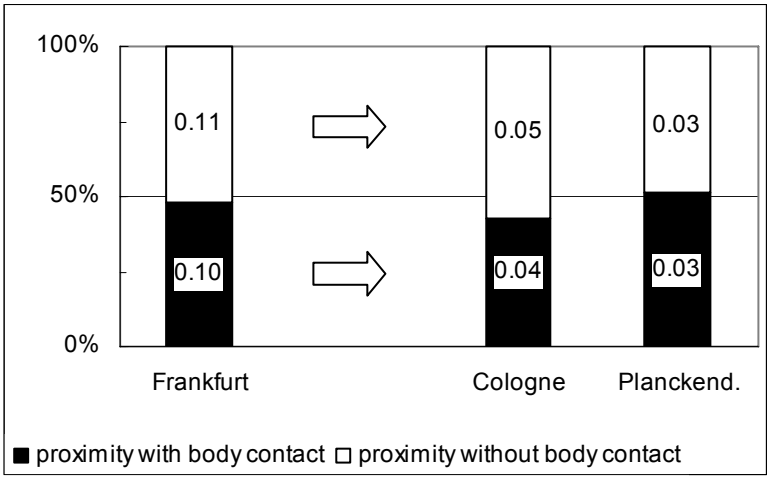


Fig. 3.25: Median values and intra-group ratios of the two p.i.-subcategories: proximity with body contact and proximity without body contact to each other. arrows=significant differences found with Kruskal-Wallis One Way ANOVA on Ranks and All Pairwise Comparisons (Dunn`s method, $p<0.05$)

3.2.2 Individual differences

Proximity indices were also calculated for each animal to see how often a specific individual was near to a conspecific when scan sampling took place. Therefore medians were calculated for each individual, taking into account all dyad values including the given individual.

a) Frankfurt

Each animal of the Frankfurt colony had seven possible partners to be in spatial proximity with. Five animals of the Frankfurt group reached the median dyad proximity index of 0.22

(fig.3.26, dashed line). The highest value was reached by the second oldest adult female (Na) who was near to a partner in 29% of all scans. The only adult male (Lu) clearly had the lowest proximity index and was near to another animal only in 11% of all scans. The difference between these two was found to be significant ($p<0.05$; Kruskal-Wallis One Way ANOVA on Ranks and Tukey test). Dyad values including the only adult male were responsible for the minimum values of all animals except for the male infant's minimum value (He, who obtained the lowest dyad index with an adult female).

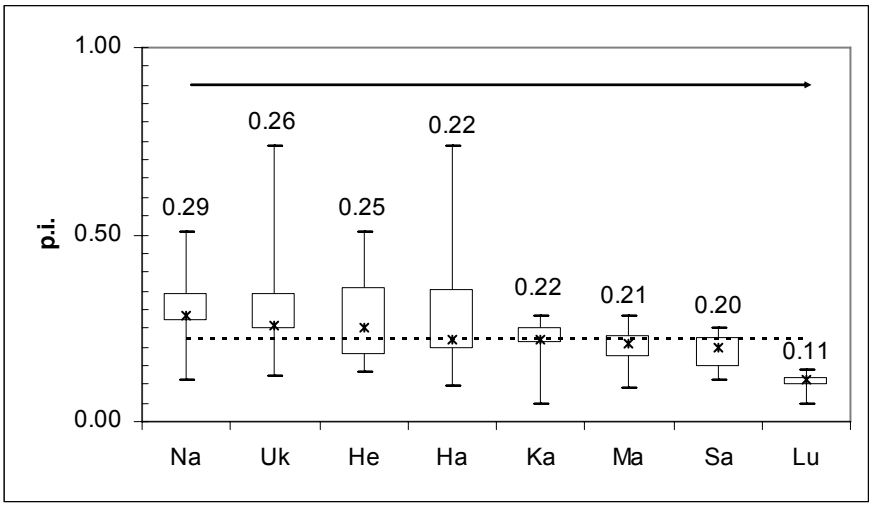


Fig. 3.26: Frankfurt colony: Proximity index (p.i.) per animal (n=8): median values and ranges (minimum. maximum. quartile 1+3). dashed line=overall median value per animal dyad (n=28); arrow=significant difference found with Kruskal-Wallis One Way ANOVA on Ranks and All Pairwise Comparisons (Tukey test, $p<0.05$)
animals: Na=Natalie (♀), Uk=Ukela (♀), He=Heri (♂, infant), Ha=Haiba (♀, infant), Ka=Kamiti (♀); Ma=Margrit (♀), Sa=Salonga (♀), Lu=Ludwig (♂)

b) Planckendael

Like for the Frankfurt group, each animal of the Planckendael colony had seven possible partners. Six animals reached the median proximity index of 0.06 (fig. 3.27, dashed line).
The highest value was reached by the juvenile male (Za). Regarding adult males, the highest value was reached by the oldest son of the females present (Re). The oldest adult male, (Ki) clearly had the lowest median proximity index of all animals with nearly no range. Only his median proximity value was significantly lower compared to the highest one, reached by the juvenile male ($p<0.05$; Kruskal-Wallis One Way ANOVA on Ranks and Tukey test). Dyad values including him were responsible for the minimum values of all animals except for the ones of two females (He and Dj). These two females were in proximity to each other even less often than each of them to the oldest male.

In Planckendael, as well as in Frankfurt, the infants and juveniles respectively seemed to fulfil important role as "liaisons" for the group. Both of them were in the upper half regarding the median proximity indices per animal, indicating that they were in proximity not only to their mothers but to all of their different conspecifics regularly.

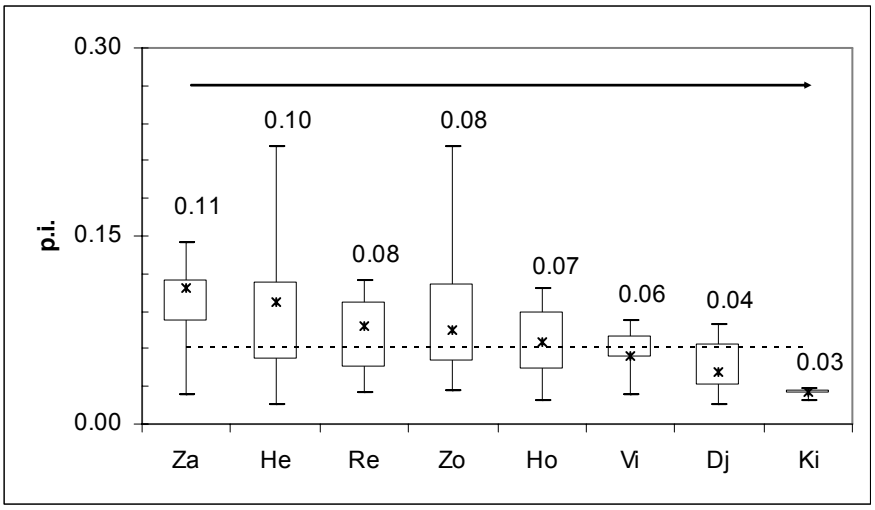


Fig. 3.27: Planckendael colony: Proximity index (p.i.) per animal (n=8): median values and ranges (minimum, maximum, quartile 1+3). dashed line=overall median value per animal dyad (n=28); arrow=significant difference found with Kruskal-Wallis One Way ANOVA on Ranks and All Pairwise Comparisons (Tukey test, $p<0.05$)
animals: Za=Zamba (♂, juvenile), He=Hermien (♀), Re=Redy (♂), Zo=Zomi (♀, juvenile), Ho=Hoertense (♀), Vi=Vifijo (♂), Dj=Djanoa (♀), Ki=Kidogo (♂)

c) Cologne

The animals of the Cologne colony had four possible partners each. No significant differences were found between the median proximity indices of the animals ($p>0.05$; One Way ANOVA).

Two females and one male exceeded the median proximity index of 0.11 (fig. 3.28, dashed line).

The highest value was reached by the oldest female (Bo, 0.17), followed by her adult son (Ki, 0.15) and the young immigrated female (Bi, 0.13). The youngest male had the lowest proximity index of all animals (Bol, 0.06). One of the two females (Bi) was responsible for the highest overall maximum and the lowest overall minimum value: She and the only other female reached the highest p.i. value of all dyads (Bo+Bi, p.i.=0.24) but she and the youngest male also obtained the lowest value of all dyads (Bi+Bol, p.i.=0.03).

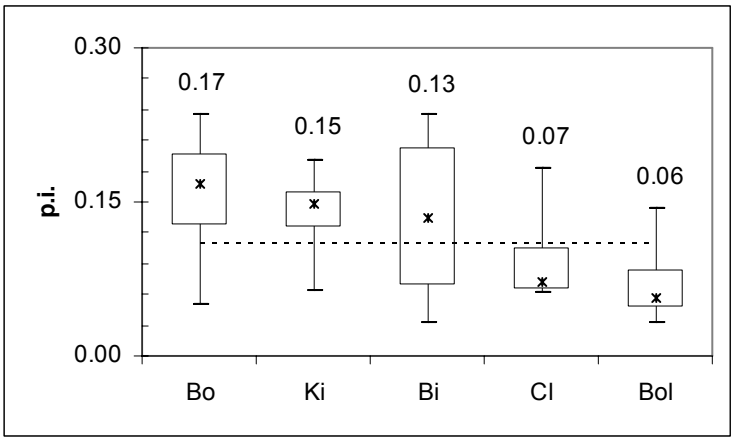


Fig. 3.28: Cologne colony: Proximity index (p.i.) per animal (n=5): median values and ranges (minimum, maximum, quartile 1+3). dashed line=overall median value per animal dyad (n=10)
animals: Bo=Bonnie (♀), Ki=Kindu (♂), Bi=Binti (♀), Cl=Clyde (♂), Bol=Bolombo (♂)

Overall picture

The comparison of the maximum and the minimum values per individual for being in spatial proximity to a conspecific revealed that, as for the overall median dyad values (fig. 3.24), the highest value was found in the Frankfurt colony and the lowest in Planckendael (table 3.22). Similarities regarding the age and the gender of individuals holding the highest and the lowest values were found: In two groups (Frankfurt and Cologne) the highest individual proximity index was reached by a female above twenty years of age. For the Planckendael animals, the highest value was reached by the juvenile male, but the second highest value was also achieved by a female older than twenty years of age. As another similarity minimum values were occupied by males in all three groups.

proximity index		age (years)		
	max	**>20**	**11-20**	**5-10**
Frankfurt	0.29	Na (♀)		
Planckendael	0.11			Za (♂)
Cologne	0.17	Bo (♀)		
	min	**>20**	**11-20**	**5-10**
Frankfurt	0.11		Lu (♂)	
Planckendael	0.03	Ki (♂)		
Cologne	0.06			Bol (♂)

Table 3.22: Proximity index per animal: Comparison of maximum and minimum values reached in each group. Corresponding animals are sorted according to age classes. max=maximum value of each group, min=minimum value of each group; ♀=females, ♂=males

3.2.3 Hierarchical cluster analysis

The spacing of all individuals in the different groups was also analysed using hierarchical cluster analysis, based on the dyadic proximity indices. The group average method was employed for linkage. Cluster-group average values were transformed and larger cluster steps were then defined via a resulting dendrogram. Figure 3.29 demonstrates a dendrogram, used to ascertain proximity clusters of a colony via linking levels. The one shown, resulted from the datasets of the Frankfurt group. It revealed the two mother-infant pairs to represent the first two clusters (fig. 3.29, animals 1-4).

Dendrograms were calculated for all 3 colonies. The limit for the distance between cluster steps (fig. 3.29, dotted arrows and numerals) was defined to be bigger than 2. The shown dendrogram led to a 5-step division of the group, from the two clusters with minimal proximity indices (1+2 and 3+4) to an average p.i., involving the whole group.

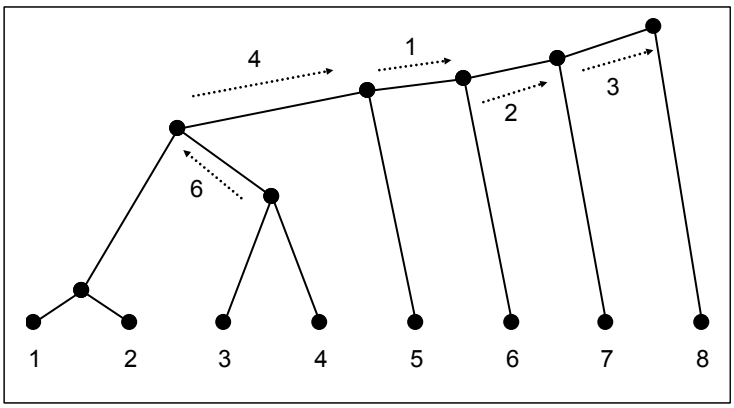


Fig. 3.29: Hierarchical cluster analysis (single link method): Dendrogram of inter-individual proximity indices with transformed cluster-group average values. dot between 1 and 2=minimum value, arrows and numerals=distance between average values (cluster steps); bottom numerals=individuals (in this case Frankfurt: 1=Ukela (♀), 2=Haiba (♀, infant of 1), 3=Natalie (♀), 4=Heri (♂, infant of 3), 5=Kamiti (♀), 6=Margrit (♀), 7=Salonga (♀), 8=Ludwig (♂)

With the aid of the dendrograms, clustering figures with linking p.i. levels were created for each group (fig. 3.30).

The core cluster of inter-individual spacing (highest p.i. values) in the Frankfurt colony consisted of the mother-infant dyad involving the youngest child. These two animals were linked at a level between 0.70 and 0.80. Another cluster comprised the other mother-infant pair, linked at a slightly lower level. The two mother-infant dyads were in turn linked with each other at a level between 0.40 and 0.50. The next cluster included all other females (cluster steps ≤2). The only adult male (Lu) tended to stay on the periphery and was linked to the rest in the last step, which resulted in an average total group value of 0.24.

The dendrogram of the Planckendael colony also led to a 5-step division of the group. Like in Frankfurt, the core cluster was represented by a mother and her child but they were linked to each other at a much lower level than the Frankfurt ones, namely around 0.22. No other dyadic cluster could be found. In a next step, the other Planckendael juvenile (Za) was linked to the first cluster, resulting in a cluster group average value of 0.16. Between 0.08 and 0.12 the next 4 animals of the group were linked in a two-step division (first Re and Ho, followed by Vi and Dj). The last step included the oldest male (Ki) and resulted in an overall average value of 0.07. Like in Frankfurt, also in Planckendael the most peripheral animal was an adult male with no mother in the group. The Planckendael female, having three sons in the colony (Ho) appeared "surrounded" by them: She was linked to the rest of the group after her youngest son, in one step with her oldest, and before her second eldest son.

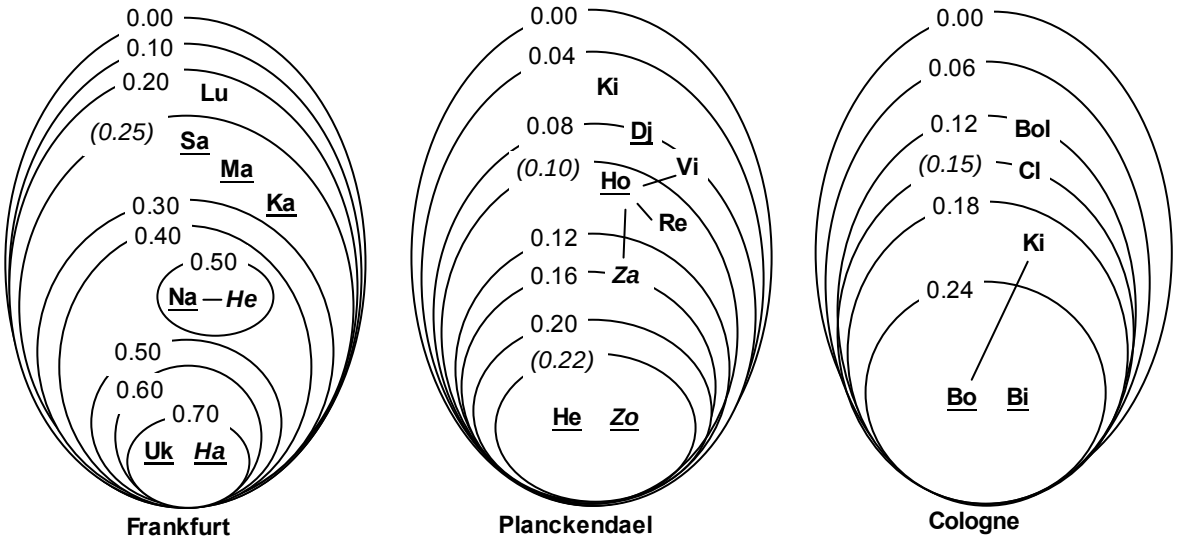


Fig. 3.30: Hierarchical cluster analysis of inter-individual proximity indices (p.i.) for 3 bonobo colonies (group average method is employed for linkage; letters=individuals (females=underlined, infants/juveniles=cursive, connecting lines=mother-son relationships); contour lines=p.i. of linking levels (intervals: left side=0.1, middle=0.04, right side=0.06); bottom to top=decrease of linkage

The dendrogram of the Cologne colony, which did not contain any youngsters, led to a 4-step division of the group. The central aggregation of the Cologne colony contained the two females of the group (Bo+Bi), linked to each other at a level which is much lower compared to that of the central aggregation in Frankfurt and yet a bit higher than the central mother-juvenile aggregation in Planckendael. The next to join the central aggregation was the adult son of one female (Ki) and another step included the oldest male (Cl). The most peripheral animal was again a male (like in Frankfurt and Planckendael), this time the youngest one. In Cologne, the final cluster-group average value, including all animals, was 0.12.

In summary, the central parts of a group included females and females with offspring respectively, whereas adult males, whose mothers were not in the group, made the most peripheral animals.

3.3 Activity budget

Activity budgets for all 3 colonies were generated and compared to see how the interactive behaviour was embedded into the overall behaviour of the animals. Therefore duration medians for certain activities were calculated and ratios were generated for them, referring to the median time an animal was observed for in each group. Only activities which could be found in every group were analysed in more detail and are shown in figure 3.31. Activities which did not occur in all colonies were e.g. a medical health training performed by the keepers, interactions with non-conspecifics, infant-related behaviours (suckling, carrying around or being carried around, mount-walking) or some individual fads like “painting with excrements” or “snorting air”. The remaining percentage of time spent on these other activities was highest in Frankfurt (around 20%): Only the Frankfurt colony had 2 dependent infants and in Frankfurt the medical health training was performed mostly in the afternoon, within the observation time. The chance to directly get in touch with non-conspecifics through the grid of the enclosure was also only given in Frankfurt. In Planckendael, around 10% of time was spent on other activities than mentioned below: Although the 2 juveniles were not totally dependent on their mothers anymore, they still showed suckling behaviour sometimes and were carried around from time to time. Additionally, some animals were observed while chasing rabbits on the outside island repeatedly or wading in the moat. In Cologne, the median of time spent on other activities was around zero percent, but two of the animals showed fads (“snorting air” and “stereotyping”) regularly.
For the Frankfurt colony, average values from the results of all 4 observation blocks were calculated as no significant differences could be found between them ($p>0.9$; Friedman Repeated Measures ANOVA on Ranks). All behaviours listed in table 2.1 were included in the interactive category, except for physical contact. For a description of the analysed solitary behaviours see Ethogram (chapter 2.3).

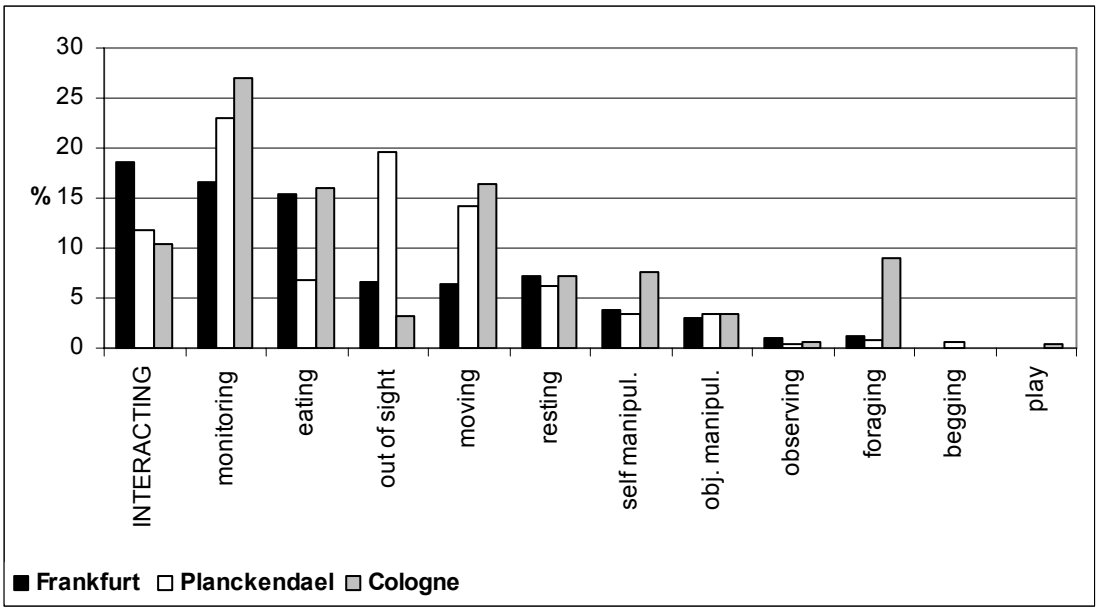


Fig. 3.31: Activity budgets in all 3 observed groups: rates of time an animal spent on different activities referring to the median observation time/animal. Frankfurt: n=8 animals, 19-20h/animal in block I-III and 4h/animal in block IV; Planckendael: n=8animals, 21h/animal; Cologne: n=5animals, 17h/animal).

The highest ratio of time spent on interactive behaviour was reached in Frankfurt, although the difference to the other two groups was not significant (One Way ANOVA, $p>0.05$). On average, an individual in this colony spent 19% of the time it was observed for on interacting, whereas this ratio was much lower in Planckendael (12%) and in Cologne (10%). Some ratios were quite similar in all groups, e.g. the amount of time spent on manipulating objects (3%) and the amount of time spent on resting (between 6-7%). Others were more similar in two groups but differed in the third: As expected, an animal in Planckendael had a higher ratio of being out of sight compared to the other two colonies, due to the huge outdoor enclosure which allowed the animals to completely move from sight for longer times. Self manipulating accounted for 3-4% of the time in Frankfurt and Planckendael but for 8% in Cologne. The amount of begging was zero in Cologne, supposedly due to the more difficult conditions for visitors to feed the animals in these enclosure. It reached nearly 1% in Planckendael which coincides with the observer's personal impression about the visitor's feeding behaviour. Another big difference existed concerning foraging behaviour: An animal of the Cologne group spent around 9% of time on foraging whereas this value was just around 1% in Frankfurt and Planckendael. The keepers in Cologne additionally fed extremely small food items thrown all over the enclosure, which caused the animals to spend a lot of time on searching for them e.g. between the wood wool. This could not be observed that regularly in Frankfurt and Cologne.

3.4 Artificial fission-fusion conditions

The last part of this chapter focuses on the Frankfurt group. The animals in Frankfurt were kept in an artificial fission-fusion system (separation management). The animals were usually kept in 2 subgroups, the composition of which was changed by the keepers on an optional basis. In order to investigate whether changes in behaviour occurred which might have indicated perceivable splitting tendencies for the keepers, datasets were used which included the first and the last 2 days of given subgroup constellations (with a minimum of 2 days in between).

	1	2	3	4	5
a	14/15.04.03	23/24.04.03	13/14.05.03	15/16.07.03	18/19.10.03
b	18/19.04.03	06/07.05.03	20/21.05.03	21/22.07.03	28/29.10.03
in between	2 days	11 days	5 days	4 days	8 days

Table 3.23: Analysed datasets of the Frankfurt colony: 5 time periods were found, for which the first (a) and the last (b) 2 days of given subgroup constellations were observable and which included at least 6 days.

A total of 5 time periods was analysed for the Frankfurt colony (table 3.23) in which subgroup changing's occurred at the beginning of an observation day and in which the last 2 days before a new change were also observed. Only time periods with at least 2 days in between were used. Rates of interactive and spatial behaviour were analysed and are referred to in the following. For this section, again all possible partner combinations of a subgroup were taken into account as a complex unit and described via the calculation of a "mean dyad". Table 3.24 shows the results regarding interactive behaviour and physical contact datasets. Subgroups were classified as I and II, with subgroup I being the one, including the only adult male.

Regarding interactive behaviour, median frequency values per dyad went down in 5 out of the 10 options (100% in one case,), stayed the same in 1 case and went up in 4 subgroups. Duration values went down in 6 subgroups (100% in one case) and went up 4 times. Thus, although no significant decreases could be detected, a slight tendency was visible for the subgroups to show interactive behaviour less frequently and for shorter durations after staying together with the same conspecifics for a while.

The datasets of being in physical contact revealed the following: In 4 subgroup settings, no physical contact could be observed, neither on the first nor on the last two days. Frequency values for a mean dyad decreased in 3 out of the remaining 6 cases, stayed the same once and increased in 2 cases. Duration values decreased in 4 cases, with three of them even significantly, and increased in 2 cases. Thus, if physical contacts occurred between the

animals of a given subgroup, a decrease particularly in the duration of these contacts after a while without a change in group composition was pronounced. The same analyses were done regarding spatial behaviour by means of spatial proximity indices (p.i., chapters 2.3 and 3.2).

Frankfurt		interactive behaviour						physical contact					
		f/h			min/h			f/h			min/h		
		a	b	si. d.	a	b	si. d.	a	b	si. d.	a	b	si. d.
1	SG I (n=1)	6.50	12.50	*	17.93	11.55	*	0.00	0.00	*	0.00	0.00	*
	SG II (n=15)	1.50	1.50	no	2.97	1.21	no	1.50	1.50	no	8.92	6.63	a>b
2	SG I (n=6)	4.23	3.00	no	1.41	1.55	no	0.50	0.00	no	3.63	0.00	a>b
	SG II (n=6)	3.25	3.00	no	1.35	0.79	no	0.75	0.50	no	1.02	0.25	no
3	SG I (n=1)	4.00	6.50	*	6.76	9.05	*	0.00	0.00	*	0.00	0.00	*
	SG II (n=15)	2.50	3.00	no	0.54	1.43	no	0.50	1.00	no	1.13	6.00	no
4	SG I (n=3)	2.50	0.00	no	0.21	0.00	no	0.00	0.00	no	0.00	0.00	no
	SG II (n=10)	6.50	5.75	no	4.47	4.64	no	3.25	3.50	no	5.38	9.17	no
5	SG I (n=10)	5.25	4.25	no	4.19	3.68	no	1.75	1.50	no	3.85	1.27	a>b
	SG II (n=3)	1.09	2.50	no	0.53	0.14	no	0.00	0.00	no	0.00	0.00	no

Table 3.24: Frankfurt: Interactive behaviour and physical contact per animal dyad (duration and frequency medians) after a change of composition and shortly before a new change. 1-5=analysed time periods; SG=subgroup (I+II); n=number of dyads per subgroup; a=2days after a change, b=2days before a new change; si. d.=significant differences found with Paired t-test respectively Wilcoxon Signed Rank Test ($p<0.05$), *=no statistical testing because of just one dyad

The proximity index for a mean dyad went down in 6 out of 10 subgroups tested. The decrease was significant in 4 cases (table 3.25). Thus regarding spatial behaviour, an obvious trend could be found for the animals to be in proximity to each other less often after a while of staying in an unchanged subgroup setting.

Frankfurt		spatial behaviour p.i.		
		a	b	si. d.
1	SG I (n=1)	0.37	0.28	*
	SG II (n=15)	0.41	0.26	a>b
2	SG I (n=6)	0.30	0.06	a>b
	SG II (n=6)	0.22	0.13	a>b
3	SG I (n=1)	0.17	0.15	*
	SG II (n=15)	0.22	0.25	no
4	SG I (n=3)	0.11	0.14	no
	SG II (n=10)	0.31	0.42	no
5	SG I (n=10)	0.38	0.30	a>b
	SG II (n=3)	0.14	0.21	no

Table 3.25: Frankfurt: Proximity index (p.i., median value) per animal dyad after a change of composition and shortly before a new change. 1-5=analysed time periods; SG=subgroup (I+II); n=number of dyads per subgroup; a=2days after a change, b=2days before a new change; si. d.=significant differences found with Paired t-test respectively Wilcoxon Signed Rank Test ($p<0.05$), *=no statistical testing because of just one dyad

A significant increase could never be found, neither for frequency and duration of interactive behaviour and physical contact nor regarding the spatial proximity index. Significant decreases occurred regarding the time spent in physical contact and regarding the proximity

index. They were found in the same 3 time periods (time periods 1, 2 and 5). Figure 3.32 demonstrates the results for these 3 time periods, showing all dyads from both subgroups.

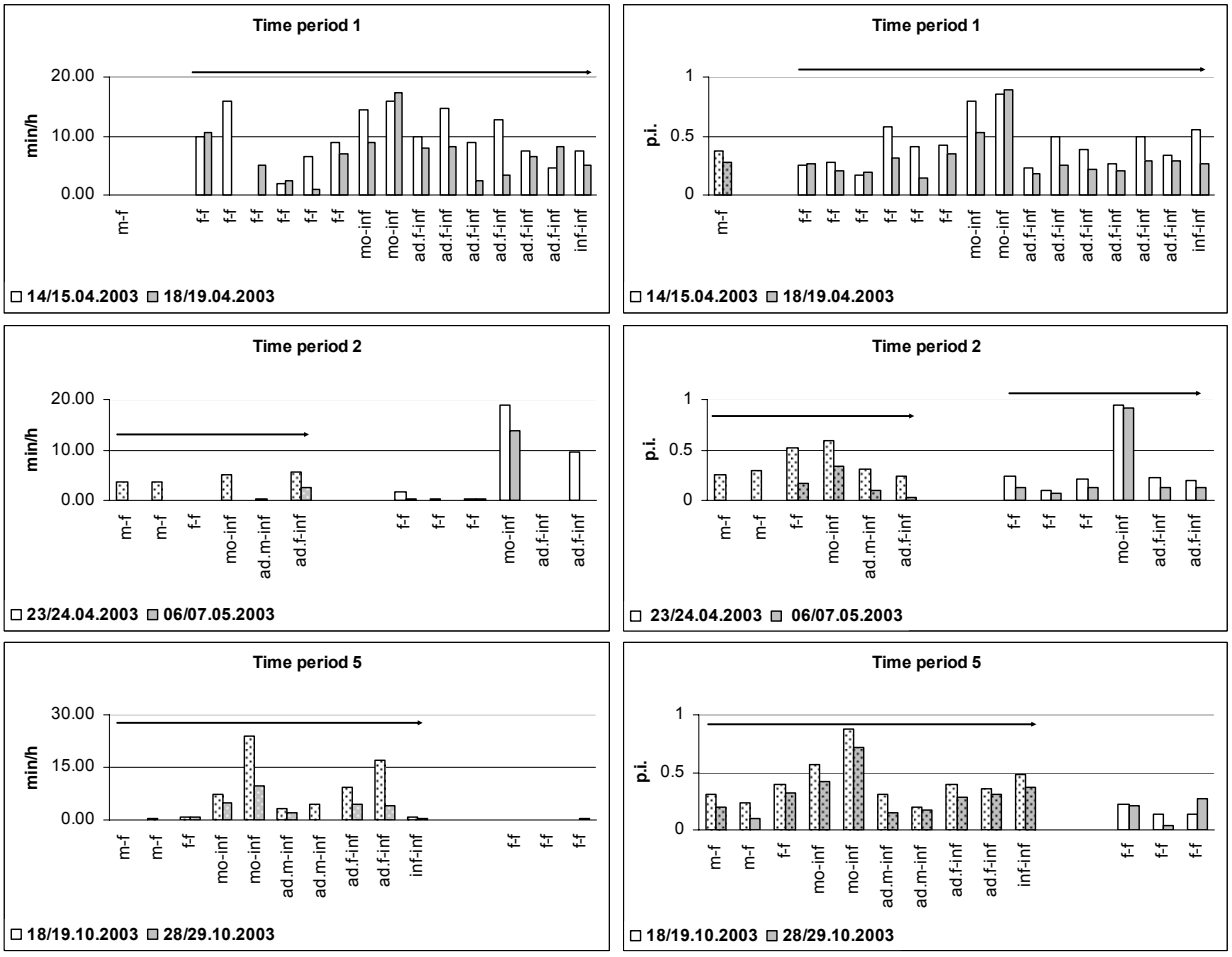


Fig. 3.32: Frankfurt: Duration of physical contact (min/h, left side) and spatial proximity index (p.i., right side) per animal dyad after a change of composition and shortly before a new change. white bars=first 2 days after a change, grey bars=last 2 days before a new change; bars with dots=subgroup 1, bars without dots=subgroup 2 arrows=significant differences found with Paired t-test respectively Wilcoxon Signed Rank Test ($p<0.05$)
dyads: m-f=male-female, f-f=female-female, mo-inf=mother-infant, ad.m-inf=adult male-infant, ad.f-inf=adult female-infant

In time period 1 (14/15.04+18/19.04.2003) subgroup 1 only existed of one male-female dyad so no statistical testing could be done. Physical contact could not be observed between these two animals at all, but their proximity index decreased after they were kept together for a while. Subgroup 2 involved 15 dyads. The duration of time spent in physical contact decreased in 10 out of these 15 dyads and the proximity index was found to be lower in 12 cases.

In time period 2 (23/24.04+06/07.05.2003), both subgroups included 4 individuals, which resulted in 6 animal dyads per subgroup. For the subgroup including the only adult male (subgroup1) a decrease of time spent in physical contact was found in 4 out of the 6 dyads and

the spatial proximity index actually decreased between all animals. In subgroup 2 a decrease of time spent in physical contact could only be observed in half of the dyads. Physical contact could not be observed within the other half at all, neither on the first 2 days nor on the last.
In time period 5 (18/19.10+28/29.10.2003), subgroup 1 was composed of 5 individuals, resulting in 10 dyads. A decrease in time spent in physical contact was found in 7 dyads and a decreased proximity index occurred in all 10 dyads. Subgroup 2 consisted of 3 animals, resulting in 3 possible dyads. Nearly no physical contact occurred between the animals of this subgroup. The spatial proximity index was lower in 2 of these dyads after the animals were kept unchanged for a while.
Generally, the results show that interactions tended to decrease while distances tended to increase. However, only datasets dealing with distances (physical contact, spatial proximity) revealed significant alterations.

Occasionally all animals were kept together during daytime. When such subgroup encounters occurred, ad libitum focal group sampling was used for the first 10-40 minutes with the aid of a voice recorder. An increased rate of moving, screaming and of sexual contacts could be observed in these time periods. Agonistic behaviours were nearly never observed during subgroup encounters.
Sexual contacts were analyzed with regard to their total amount of occurrence and attention structure. Only those encounters were taken into account, which were induced after at least one day of separation conditions. A total of 5 days was analyzed.

	time recorded	sexual contacts		
date	**(min)**	**total**	**max.**	**%**
10.05.03	10	7	Ka (♀)	100
12.07.03	30	3	Ka (♀)	67
13.10.03	15	6	Ka (♀)	100
12.11.03	25	7	Lu (♂)	71
17.11.03	40	13	Ka (♀)	77
Ø (f/10min)		**3.61**		

Table 3.26: Frankfurt: Sexual contacts during the first hour of subgroup encounters. total=total amount of sexual contacts observed; max=main participant; %=share of main participant in total amount; Ø=overall mean value

Subgroup encounters always led to an increased amount of sexual contacts. On average the elevated rate of 3.6 sexual contacts per 10 minutes was observed directly after the individuals were united. Referring to the attention structure of sexual contacts, it got obvious that the youngest adult female, which was introduced into the Frankfurt colony in 2002 (Ka) clearly took centre stage. During 2 out of the 5 analysed encounters this female was involved in

100% of all sexual contacts and during another 2 occasions she was involved in at least 65%. Only on 1 day (12.11.03, table 3.26) the adult male was involved in sexual contacts more prominently (71%). The pronounced role of the young, immigrated female as the most preferred partner for sexual interactions fits to the results found before, when analysing the datasets of a whole observation period (chapter 3.1.3).

Additionally, all datasets obtained via focal animal sampling (which started directly after the ad libitum sampling) were analyzed regarding interactive and spatial behaviour. This was done to test, whether any coherence between higher rates and a previous separation could be found for a given dyad. The 2 mothers were never separated from their infants and therefore the datasets from the 2 mother-infant dyads were excluded. At first, it was investigated whether an obvious maximum value of interactive and spatial behaviour could be found for each of the 26 dyads on one out of the 5 days. An obvious maximum (peak value) was defined to be at least 50% higher than all other values. Afterwards it was looked up if the peak value of a dyad was reached on a day following a separation of the 2 individuals. As an example, the following figure (fig. 3.33) demonstrates the obtained frequency rates of interactive behaviour for each of the 26 dyads on each of the 5 days of subgroup encounters.

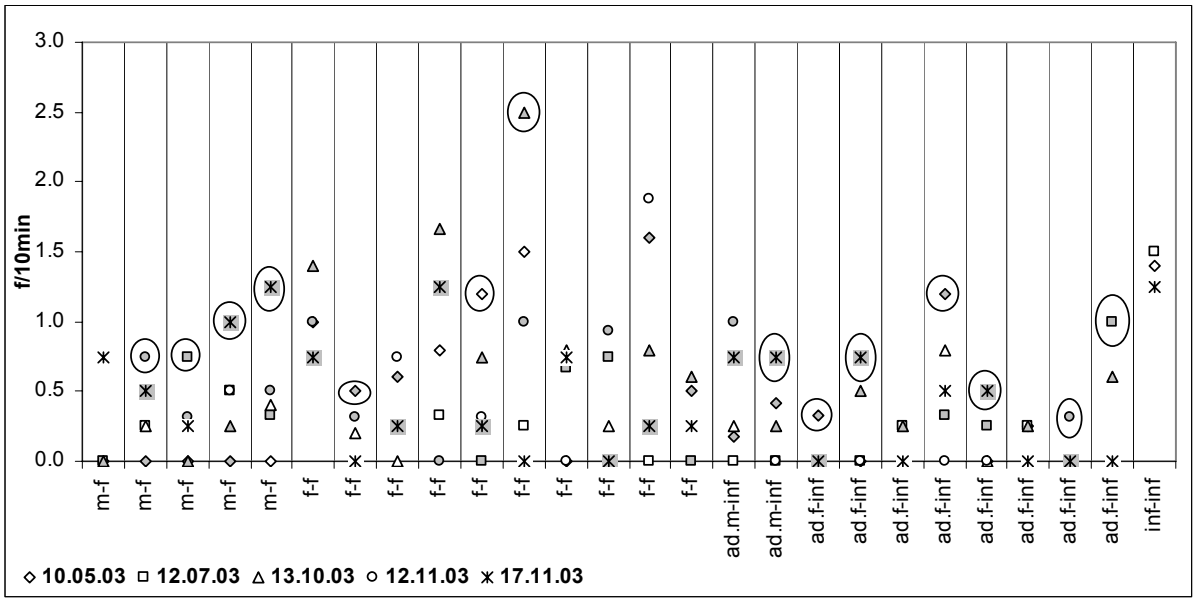


Fig. 3.33: Frankfurt: Frequency (f/10min) of interactive behaviour per animal dyad (n=26) on 5 days of subgroup encounters. different symbols=different days; highlighted in grey=value reached on a day after being separated; framed=clear peak value (≥50% higher than the others)
dyads: m-f=male-female, f-f=female-female, ad.m-inf=adult male-infant, ad.f-inf=adult female-infant, inf-inf=infant-infant

As can be seen in figure 3.33, the frequency of interacting within a dyad was quite variable between the analyzed 5 days of subgroup encounters, except for the 2 infants which always showed a relatively similar rate of interacting with each other. Around half of the dyads (14, framed) had a peak value on 1 out of the 5 different days. Most of these peaks (13, highlighted in grey) were reached on days following a separation of the involved individuals. Comparable results were also found regarding the duration of interactive behaviour, the frequency and duration of physical contact and regarding the spatial proximity indices (table 3.27).

	interactive behaviour		physical contact		proximity
n=26	**frequency**	**duration**	**frequency**	**duration**	**p.i.**
dyads with max.	14	18	14	16	12
separated before	13	13	11	10	10
%	**93**	**72**	**79**	**63**	**83**

Table 3.27: Frankfurt: Coherence between a higher rate of social and spatial closeness and a previous separation regarding 5 days of subgroup encounters. n=number of dyads (excluding the mother-infant ones); p.i.=proximity index; dyads with max.=number of dyads which had a peak value (≥50% higher than the other values) on 1 out of the 5 days of subgroup encounters; separated before=number of dyads whose participants were separated before reaching the peak value; %=resulting percentage

As can be seen in table 3.27, the majority of all dyads, which showed a peak value of interacting on 1 out of the 5 days of subgroup encounters, consisted of individuals, which were separated on the day before (93% regarding frequency and 72% regarding duration). This trend was also found for the datasets of physical contact (frequency=79%, duration=63%) and the datasets of spatial behaviour, analysed via proximity indices (p.i.=83%). So, if a given pair of individuals was interacting clearly more often or for longer durations or if it was found closer to each other on one of the subgroup encounter days, the chance that these animals had been part of different subgroups before was very high. Part-time separation seemed to abet a higher rate of social and/or spatial proximity between two animals when meeting again.

4. Discussion

This study deals with aspects of the social system of bonobos. It examines the social relationships in 3 groups of zoo-living individuals, on a descriptive and proximate level. Patterns of interactive and spatial behaviour were described and analysed with respect to the social structure within free-ranging bonobo communities and their fission-fusion social organization.

It was examined whether common traits found within the social relationships of zoo-living animals, would resemble known structural patterns found in free-living bonobos.
The amount of social and spatial proximity was analyzed with reference to different keeping conditions. A possible correlation between the artificial fission-fusion system (separation management) and the vitality of a group was examined.
The group kept under separation management conditions was investigated in greater detail, focussing on the observation of specific behavioural traits before and after rotations, to examine intrinsic fission-fusion motivations.

4.1 Methodological restrictions and effects of captivity

The number of groups and animals studied was quite low. Nevertheless, in all 3 groups at least some basic demographic structures were existent like animals of different ages and both genders or immigrated females, which, in sum, covered a relatively large spectrum of age and sex classes.
The evaluation of the artificial fission-fusion keeping strategy in Frankfurt was not optimal because subgroup alteration patterns differed somehow uncontrolled. The separation management schedule was, however, left uninfluenced by the observer because the investigations were intended to reflect the normal keeping conditions, including the changing patterns induced by the keepers based upon their personal “intuitions”.
Despite the differences regarding the general amount of space available for each colony, the keeping conditions of the groups also varied in terms of induced spatial crowding due to no outdoor access during cold periods. Although bonobos seem to be able to cope with limited spatial conditions to a certain extend via tension-reduction strategies (Sannen et al., 2004; Paoli et al., 2007), crowded conditions were also found to heighten the amount of aggression (Sannen et al., 2004; Planckendael colony during a crowded period in winter). The rate of

agonistic behaviours was lowest in Frankfurt and lower in Cologne compared to Planckendael, indicating no effect of restrictions of available space on aggression. However, it remains open whether the aggression rate in Cologne would have been even lower in the summertime with the animals being able to go outside. In Frankfurt, generally no differences were found regarding the interactive behaviour of the animals between the summer and the more crowded winter situation. But the average time an animal dyad spent in physical contact and its average proximity index dropped during the last two observation periods, which were conducted only inside. There may have been a negative influence of the more crowded situation on the "demand" of proximity. In Cologne, where observations were reduced to the indoor winter season, rates of physical contact were found to be lowest of all groups.

An omnipresent factor, influencing zoo-living animals are of course humans. Although most animals are generally familiar with humans, studies about captive chimpanzees revealed that intra-group aggression can increase in connection with prolonged personnel activity or the occurrence of unfamiliar persons (Lambeth et al., 1997; Maki et al., 1987). Uncontrolled distractions by humans, who actually often try to catch an ape's attention, may influence the ape's intra-species relationships. The animals of the Planckendael group were clearly influenced by visitors, trying to catch their attention by illicitly feeding them and the group was often found begging for food. Some of the observed agonistic behaviours occurred during these unbalanced feeding contests. In Cologne, some "permanent visitors" routinely tried to catch the animal's attention which mainly influenced the hand-raised male who often preferred to interact with humans rather than with his conspecifics. Interferences also did occur in Frankfurt, sometimes resulting in untypical behaviours like spitting against the visitors. Techniques to reduce the perceptible level of human activity together with enrichment or animal training procedures are discussed to be helpful in this regard (Lambeth et al., 1997), but will surely never be able to completely dispose these effects.

Although qualitative descriptions and interpretations from the wild regarding the social relationships of bonobos may be largely consistent with findings in captive settings, quantitative comparisons must be regarded carefully. The conditions in the wild do not allow continuous observations and numerical values are obtained differently compared to the daily close-up investigations in captive settings. Therefore, as also stated by de Waal (1990), some omissions and differences may be rather due to the detail in which captive animals are studied than to fundamental differences. But, within limits, comparisons can provide an important informative basis about the fundamental sociality of a given species and may also lead researchers to uncover subtleties that suggest hypotheses for field testing (King, 2004).

4.2 Results

With reference to the hypothesis, listed in chapter 1.5, 3 major results will be discussed in the following:

1. It was shown, that much of the descriptions and interpretations of social relationships in bonobos are consistent with this study's findings. Some additional patterns found deserve closer attention and further study.
2. Some important, mainly quantitative differences were found between the groups. As expected, the Frankfurt group, living under separation management conditions, turned out to be the liveliest.
3. Closer investigations revealed the artificial fission-fusion keeping strategy to be the most likely origin for the pronounced rates of social and spatial proximity in Frankfurt.

4.2.1 Patterns of social relationships

It seems that structural patterns of bonobo social relationships are relatively robust and not easily influenced by the conditions of captivity. Some aspects of the social relationships found and prevailing similarities to other studies will be discussed in greater detail in the following, mainly referring to reports of free-ranging animals.

Structural patterns of social relationships found in all 3 groups of zoo-living animals are comparable to the conclusions reached by researchers studying free-ranging bonobos, like Kano (Kano, 1987, 1990, 1992), Furuichi (Furuichi, 1989; Furuichi & Ihobe, 1994; Furuichi, 1997), White (White,1988, White & Chapman, 1994), Hohmann (Hohmann et al., 1999; Hohmann & Fruth, 2000, 2002, 2003).
The social relationships were predominantly of a sociopositive nature in all observed colonies. Agonistic behaviours were found infrequently (table 3.3), and even in the group where agonistic behaviours could be observed most frequently (Planckendael), they only accounted for 3.5% of all interactions (fig. 3.5). This fits with the assumption that bonobos are generally quite peaceful and tolerant apes, with a high rate of affiliative behaviours and a low potential for aggression (Kuroda, 1980; Kano, 1992; Furuichi, 1997).

As expected, highest dyad values of body contact were obtained by the mother-infant/juvenile dyads (tables 3.7, 3.8). Higher values of body contact with their mothers were found for the infants in Frankfurt (2-3 years of age), compared to the juveniles in Planckendael (6 years of age). In free-ranging animals, individuals start spending less time with their mothers upon reaching the juvenile stage (5-6 years of age), although they still remain relatively close (Kano, 1992). For the long-term observations in Frankfurt, a significant negative correlation was confirmed between an infant's age and the time it spent in physical contact with its mother (fig. 3.6). Both mother-infant dyads spent around the same amount of time in physical contact when the infants were about the same age. No comparative datasets could be found in other studies and the sample size in the present study was very low. More investigations in this regard could help to improve management schedules, e.g. by optimizing the amount of time a human should spend in body contact with an orphaned infant, without exaggerating the human-ape bond. Continuative studies could also help to detect problems within a given mother-infant dyad, or to optimize the monitoring of unrelated females, which may be good candidates for the adoption of an orphaned or neglected infant.

Infants and juveniles were found interacting with adults of both genders very frequently and seemed to play an important role as interaction and contact partners not only for their mothers (tables 3.4, 3.5). As most bonobo studies exclude infants and juveniles when investigating age-sex classes, little correlating datasets were found in the literature. Regarding other great ape species, Fossey (1979) stated that infants are strongly attracted to males in mountain gorillas and infants frequently followed, foraged and rested near males. This was also observed with the bonobos in Frankfurt and Planckendael, including long periods of social play between the adult males and the infants and juveniles. Although in great apes allocaring plays no major role, as the mother is the only individual nursing, and the main individual carrying the infant, some adaptive causes of allocaring, generally discussed for primates, are assumed to also fit with bonobos. Alloparenting behaviour allows individuals to practise caring for infants, it may enable an animal to gain access to group resources (like achieving better mating access to the mother), and it promotes the formation of social bonds (Ross & MacLarnon, 2000). Social play between the only adult male in Frankfurt and the two mother-dependent infants was sometimes found to facilitate friendly contacts like grooming or sitting in proximity between this male and the infant's mothers. For an example see Appendix (fig. 8.1). A mediating function of juveniles was also found by Pfalzer & Ehret (1995) in another captive bonobo group. In the Frankfurt colony, some incidents could be observed, in which the infant of an elderly female was of major interest for two younger females. Conflicts about

handling this infant repeatedly evoked social tensions between the two females, although one of them carried an infant herself (for a detailed description of such an incident see Appendix, fig. 8.2). Cheney (1978) observed a high proportion of agonistic interactions in free-ranging female baboons, as they competed with others over access to mothers and infants. According to the author, interactions with infants may be particularly important for female primates, if they constitute the stable core of the social group, which seems to be the case in bonobos. Additionally, for both genders, infants may provide a means by which groups are established, and by which the stability of a group's social structure may be perpetuated across generations (Cheney, 1978).

Among adults, females generally showed more interactive behaviour among each other than males did (tables 3.5, 3.6). Pooling the datasets of all three groups, only considering adult animals, revealed that a female-female bonobo dyad was more gregarious than a male-male one and significant differences regarding the time spent on interacting and being in physical contact were found (table 3.10; fig. 3.7, 3.8). No explicit comparable datasets were found in the literature regarding interactive behaviour as a main cumulative category. The findings presented here fit the assumption that intimate relations between females are an important feature of bonobo societies and that female bonobos are very sociable and cohesive, in contrast to males (Badrian & Badrian, 1984; Kano, 1992; White & Chapman, 1994).
The highest proximity index among adults was reached by an elderly female in each setting, whereas the lowest value was occupied by a male in all 3 colonies (fig. 3.26, 3.27, 3.28). Among males, adult sons reached higher proximity indices than males without a mother in the group (fig. 3.27, 3.28). Hierarchical cluster analysis revealed that the central part of each bonobo group observed, consisted of females and/or mothers with offspring, whereas males (without mothers in the group) were the most peripheral animals in each colony (fig. 3.30). A similar result was found by Furuichi (1989) regarding free-ranging animals, although he did not include infants and juveniles in his cluster calculations.

Regarding specific aspects of the social network, agonistic interactions were observed most frequently between the genders and second most frequently between males (fig. 3.22). Between females, agonistic interactions were found least frequently and between mothers and their adult sons, agonistic interactions were completely absent (tables 3.12, 3.13; fig. 3.22). Some studies on free-ranging animals found that agonistic interactions occurred most frequently between males (Idani, 1991; Furuichi, 1997). The lower rate of agonistic incidents

between males obtained in this study could be due to the fact that only in 2 out of the 3 groups studied more than 1 adult male was present. In one of these groups (Planckendael), 3 out of 4 males were siblings.

A trend was found for young individuals (5-10 years of age) to be involved in agonistic interactions more frequently than infants and older animals (table 3.21). According to Kano (1992), males from mid-adolescence into adulthood start to self-assert themselves and show a kind of rough behaviour, including repeated charging others. Idani (1991) found that young, immigrant females sometimes attacked or charged at younger males. Charging behaviour was most prominently observed in a young male in Planckendael, being 10 years of age. Females in this age class did show agonistic behaviours mostly against same-aged or younger individuals, with the rate being higher in the 2 young females, which were immigrants. However, because of the low number of animals per age and sex class, results must be assessed carefully.

In Frankfurt, the only adult male was the main target of aggression, receiving nearly all agonistic behaviours without acting agonistically himself (table 3.11; fig. 3.9). In Planckendael and Cologne, agonistic interactions were distributed more evenly (tables 3.12, 3.13; fig. 3.10, 3.12), but the only individuals being targets of aggression without acting agonistically themselves were also males. The assumption that males are more likely to be the victims of aggression and can even serve as "scapegoats" (Vervaecke et al., 2000a) is, therefore, strongly supported. For an example see Appendix (fig. 8.2).

The most prominent affiliative behaviour observed between the animals of each group was social allogrooming. Like reported for free-ranging animals (Badrian & Badrian, 1984), participants of social grooming included both sexes and all age-sex classes. The combined datasets revealed an average mother-adult son dyad to be involved in allogrooming most frequently whereas males were found to groom each other least frequently (fig. 3.22). Females were found grooming each other the second most frequently. These findings correlate with observations by Kuroda, (1980), Badrian & Badrian (1984) and Kano (1992) in free-ranging animals and with results by Stevens et al. (2006) regarding different captive settings.

Pooling the datasets and sorting all animals according to their age and sex revealed some tendencies regarding the ratio of grooming given and grooming received (table 3.21): As expected, an infant received more grooming than it gave. An adult female generally groomed more frequently and also received allogrooming more frequently than an adult male. In

contrast to the findings by Franz (1999), an adult female in this study did not generally receive more allogrooming than it gave, although this was found to be true for some (like the oldest female in Frankfurt, the 2 elderly ones in Planckendael and the younger one in Cologne).
In all 3 colonies, the main receivers of social grooming were females (tables 3.14, 3.15, 3.16). Although no rank relations were investigated in the present study, the finding that females received most allogrooming is congruent with the results by Franz (1999), who found that high-ranking adult females received most allogrooming in each of the zoo-living groups studied. Generally, in terms of distribution of social grooming, elderly females (≥ 20 years) played a major role in each colony (fig. 3.13, 3.15, 3.17).
Bidirectional allogrooming was generally rare and could only be observed between some of the animals (tables 3.14, 3.15, 3.16). It was mainly observed between females, and between mothers and their adult sons. It was less often found between unrelated males and females, although it did occur in some cases. In free-ranging animals, Ihobe (1992b) found no mutual grooming to occur between males, which is partly compatible with the results of this study, where it was observed only between the male half-siblings in Planckendael.

A tendency was observed, for the latest immigrated female of each colony to prefer one of the elderly females as a grooming partner (tables 3.14, 3.15, 3.16). These results fit to the assumptions about elderly females, being the specific focus of friendly contacts for young nulliparous, immigrated females in the wild ("specific senior females, SSF"; Furuichi, 1989; Idani, 1991). According to the authors, forming close associations with a SSF, most likely helps the immigrant to attain a stable position in the community. The selection of a SSF by a zoo-living female shortly after her "immigration" into a new colony, was also observed and described by Pfalzer & Ehret (1995). The fact that the immigrated female was groomed by the resident female much more frequently than vice versa in Cologne (table 3.16) may be due to the fact that only two females were present in Cologne, presumably pronouncing the role of the younger one as the only female interaction partner available.

All bonobos in all studied groups had sexual contacts with at least one conspecific (tables 3.17, 3.18, 3.19). Sexual contacts occurred between individuals of all age-sex classes, including infants and juveniles (fig. 3.19, 3.20, 3.21). Homosexual contacts were mainly observed between the females and occurred very frequently (GG rubbing). An increase of sexual contacts was related with an increase in social arousal, during feeding times (especially

when rare food items or enrichment tools were presented) or during the first hour of subgroup encounters in Frankfurt (see below). It was also observed terminating a conflict between two individuals, like described in the Appendix (fig. 8.2). The assumption that sexual behaviour (especially homosexual) in bonobos fulfil an important social function and can serve as a greeting, and to appease, reconcile and reassure in times of social tension (Kano, 1990, 1992; de Waal, 1989, 1995) was confirmed in this study.

If present, infants and juveniles were among the most active individuals regarding sexual contacts (tables 3.17, 3.18). They were found to perform sexual acts among each other very frequently but were also engaged in sexual contacts with adult animals. This was also found by de Waal (1990) studying a captive group and by Kano (1992) in free-ranging animals. The description by the latter author about infants, clinging to the back or belly of one partner of a copulating pair and waiting until it is "their turn" is comparable with the observations made in the Frankfurt colony. Additionally, the adult male in Frankfurt was also observed to "invite" the infants, which was also described in free-living animals (Kano, 1992).

Although no statistical differences occurred, the immigrated female had the most frequent sexual contacts in each group. All three of them were still nulliparous when observations took place and were a focus of sexual attention for other group members, regardless of age and gender (fig. 3.19, 3.20, 3.21). These findings are supported by the findings of Idani (1991) in free-ranging animals, who pointed out that nulliparous females copulated more frequently than parous females and immigrated females performed GG rubbing most frequently.

To sum up, as it was hypothesized, the social relationships found were manifold and clearly differed between animals of different age and sex classes. Many structural patterns, found in free-living bonobos, could be observed under the conditions of captivity. The more general conclusion that "the core of bonobo society is characterized by the presence of strongly bonded females and males associating with them" by Badrian & Badrian (1984) is largely supported. However, since some male-female relationships were also found to be pronounced, and the adult males with mothers in the colony were closely associated to the central cluster, the term "female-centred" species, as used by Stevens et al. (2008) seems to be more suitable.

Little information was found regarding the role of infants and juveniles as association partners for adults except in terms of parental care. Based on the present findings, it is proposed that these relationships also fulfil important functions in the bonobo society and need further attention.

4.2.2 Comparison of keeping conditions

Observational conditions between the three captive settings studied were quite comparable and the procedural method was identical for each of the observed groups. Some major, mainly quantitative, differences occurred between the different settings studied, overall following the proposed hypotheses.

The animals of the group, living under fission-fusion conditions (Frankfurt) were found to be the most socially active. Rates of social interactions and rates of physical contact were highest in this group (tables 3.1, 3.2; fig. 3.2, 3.4). Sociopositive and sexual behaviours took longest between the animals in Frankfurt whereas agonistic behaviours were extremely rare (table 3.3). Social interactions were pronounced in Frankfurt also regarding an animal's activity budget (fig. 3.31). The bonobos in Frankfurt were also found in spatial proximity to their conspecifics more often and for longer periods of time than the ones in Planckendael and Cologne (fig. 3.24). Hence, in spite of the fact that the availability of interaction partners was lowest in Frankfurt due to the consistent separation into smaller subgroups which, at the most, contained 4 adult animals at a time, the overall "social output" was highest in this colony.

Some significant differences occurred between the Frankfurt colony and the other two groups, whereas no significant differences were found between the two stable groups in any of the points mentioned. Therefore, the bonobos which were kept under artificial fission-fusion conditions clearly stuck out.

The lack of differences found between the Planckendael and Cologne colonies was, however, unexpected. Because living under the most spacious conditions, the Planckendael animals were expected to show some fission-fusion tendencies themselves. This was generally not the case, as all group members mainly stayed in the range of the observer's vision, although some diverse clustering tendencies could be recognized. Particularly the oldest adult male, being unrelated to the females, did show some more distinct fission tendencies, as he often left the others and remained absent for some hours. For an example see Appendix (fig. 8.4). A higher tendency for males to leave a party alone compared to females was also found in free-ranging animals (White, 1988). The leaving male in Planckendael was sometimes joined by the juveniles, another male or the young immigrated female but the latter normally rejoined the others within shorter time periods. It is assumed, that the amount of space together with the number of animals present was still not sufficient to allow for clear-cut separations and partner changes. The number of animals (n=8, including 2 juveniles) approximately equated the party sizes in free-ranging animals but, unlike in the wild, no other parties to fission and

fusion with, were present. The history and the demographic structure of the group are also guessed to have an influence, as e.g. 3 out of the 4 males present had the same mother, who was still present in the group. And although the outdoor enclosure in Planckendael was wide and structured, it was always possible for an individual to, at least, guess were the others must remain. Even in large, seminatural settings, members of a stable colony can never separate completely and the interplay between different relationships will always be present, prohibiting a clear-cut change in the partner spectrum. In contrast, free-living communities of bonobos are said to have a home range of at least 12 km^2 (Hashimoto et al., 1998) and splitting party members will presumably not have the chance to interact with the conspecifics left behind for some time. Furthermore, if two animals meet again, the actual party composition may be different compared to their last meeting, providing a diverse range of situational conditions and diversifications.

Closer investigations of fission-fusion situations could therefore only be made in Frankfurt. The number of animals present was in fact equal to the one in Planckendael, but the separation management created clear-cut fission and fusion situations with different partner spectrums at a time at a varying rate of alteration.

4.2.3 Influence of artificial fission-fusion conditions

Subgroup encounters in Frankfurt obviously led to a rapid increase of social arousal. The first minutes were characterized by loud vocalizations, swift movements and an enhanced rate of sociosexual contacts (table 3.26), which generally fits with descriptions about party encounters in free-ranging animals (Badrian & Badrian, 1984). De Waal (1989) argued that, if social tension has an independent effect on sexual activity, this effect should occur also when tension is unrelated e.g. to food. The subgroup encounters initiated by the keepers in the present study were only in some cases combined with feeding, therefore affirming a general effect of social tension on sexual activity (sociosexual behaviour).
Although some displaying behaviour occurred, no agonistic behaviours could be observed during the subgroup encounters. The probability of a dyad to show a noticeable peak value of social and spatial proximity on a subgroup encounter day was increased when these two animals were reunited. In a study on experimentally induced party encounters in chimpanzees, Okamoto et al. (2001) found that affiliative interactions between animals that had spent the weekend in different rooms were higher than between those, who stayed together before,

whereas aggressive interactions were not influenced by separation. Separations and reunifications are therefore assumed to have a positive effect on the livelihood of social relationships in both species.

Closer investigations within the different subgroups revealed that interactions tended to decrease after a while of unchanged subgroup compositions, while distances tended to increase (tables 3.24, 3.25). The bonobos seemed to experience a kind of "lack of interest" regarding interacting and being in touch with conspecifics after a while with only the same partners. This however was more pronounced in the datasets related with spatial behaviour.

It is assumed that an increase in spacing between the individuals of a given subgroup, resulting in a more general loss of group cohesion may be better detectable for the keepers than a more subtle change or decrease in interacting. The finding that the degree of spatial closeness in one or both subgroups was significantly lower in many cases just before the keepers decided to change the subgroup's compositions or induce subgroup encounters, fits with this assumption. As an example for the spacing of the animals on a day before a change compared to the situation at around the same time on the following subgroup encounter day see Appendix (fig. 8.3).:Keepers indeed may perceive these changes in proximity as a signal.

It may be that, in free-living individuals, the tendency to leave a party is also recognizable rather on spatial patterns than on social ones. This, however, may not easily be tested because of the observation conditions in the wild and because of the fact that free-ranging individuals possibly do not show a graduate separation, but just split.

In the wild, all members of a community mix freely in ever changing parties (de Waal, 1995) and except for mother-dependent offspring pairs, the individuals are assumed to be more unrestricted regarding wandering off or joining a party with a given conspecific or several ones. Only a small number of animals are living in zoological institutions worldwide (141, state 2003). Groups of bonobos in captivity are normally rather small with the group's composition being managed by human coordinators. Although a lot of attention is drawn on "creating" the right social grouping, patterns like different personalities and life histories of the subjects can only partly be considered. It seems likely, that individuals are sometimes forced to live with conspecifics, they would not have chosen as closer associates in a more self-determined situation. This also accounts for different subgroups: The keeper-induced splitting of a group in captivity can not be equated to the natural fission situation. The artificial fission-fusion system mainly follows the keeper's time and alteration schedules. Finding the right time for a change remains a personal matter of the current human carer (all

keepers asked said they do it "intuitively"). The keepers sometimes also arrange the subgroups according to management schedules (like keeping the only adult male together with at least one reproductive female). However, a certain degree of active participation on separation situations was found with the observed bonobos. On several occasions, the keepers did change their plans regarding subgroup compositions according to the animal's behaviours. If an individual was keen on joining a certain conspecific or subgroup, it normally achieved this goal. Active involvement in grouping decisions was also observed in Planckendael (pers. obs.), when the animals were confined to the different "night cages" e.g. during cleaning in the morning and was also stated by the management of the Milwaukee County Zoo (pers. com.).

Separation management can be particularly advantageous for some animals with special needs or for some individuals, who are more disregarded, social "outsiders" (pers. com. and pers. obs.). In the Milwaukee County Zoo, the oldest adult female, having some activity limiting health problems (hardness of hearing, blindness and epilepsy), is now only kept in small groupings on a daily basis to meet her social needs without overextending her social possibilities. Being separated in a subgroup with only one or two females at a time also advanced the introduction process of an unfamiliar, socially deprived adult male into the bonobo colony of the same zoo (Sandin, 2005). The only adult male in Frankfurt received more attention by some of the females, if he constituted the only interaction partner available. In addition, some dominance-subordinate relationships may alter with different group compositions, as found by Vervaecke et al. (1999) in an experimental set-up: An animal who agonistically dominated another in the whole-group situation was not dominant in a dyadic feeding test situation. Behaviours exhibited to specific partners are always affected by situational conditions, and therefore different interaction patterns can occur between the same pair of individuals (Kitamura, 1989). The only adult male, which was the most likely victim of attacks in the whole-group situations in Frankfurt, was rarely aggressed in a subgroup situation.

Applying part-time separations because of the social needs of specific animals is a more common feature within captive settings of bonobos but, until now, little attention was paid on the possible effects of artificial fission-fusion keeping patterns on the social life of the whole group. The present study revealed hints that separation management strategies may not only

be advantageous for some specific animals, but can rather stimulate the liveliness of a whole group.

Variances within the partner spectrum, as observed in free-ranging animals, may also help to avoid behavioural problems and more serious conflicts, which are assumed to be possible consequences of long-term stable groupings:
The separation management strategy was initiated in Frankfurt, after some severe outbreaks of aggression, directed against the only adult male of the group. Serious violent incidents are however untypical for bonobos, both in free-ranging animals (Kuroda, 1980; Kano, 1990; Hohmann & Fruth, 2003) and in captive ones (de Waal, 1989). A tentative explanation could be that, after a while of "social stagnation" due to an invariably partner repertoire, a kind of tense mood arises between the animals, which may suddenly "spark over" into aggression. As coalitions in bonobos seem to be more pronounced among females (Furuichi, 1997; Stevens et al., 2008) and males are more often said to be the victims of aggression (Vervaecke et al., 2000a), it seems reasonable that the most likely targets of attacks will be males. Furuichi (1997) reported that females sometimes allied with one another in the wild to attack males, but the ferocity of the attacks observed in Frankfurt was exceptionally severe. This may coincide with the assumption made by Vervaecke & van Elsacker, (2000), who argued that group stability as opposed to the normal fission-fusion pattern in the wild, may contribute to more pronounced differences in agonistic and competitive abilities and to a more pronounced expression of the effects of high female rank. Similar sounding, Stevens et al. (2008) stated: "The expression of dominance will undoubtedly be more rigid in captivity, where there are fewer competitors that are nearly always in the vicinity and similarly dominance styles may be more despotic to those in the wild". The establishment of definite linear dominance hierarchies, as found within some captive settings (Vervaecke et al., 2000b; Stevens et al., 2007), may already be an artefact of captivity, which does not accurately reflect the situation in the wild.
Another possible consequence of long-term stable grouping can be a kind of "social stagnation" linked with breeding problems. A study in the Cologne colony revealed the social relationships to be tense and unbalanced after a long period without any change (Haase, 2002). General activity levels were low and almost no sexual behaviour was observed. The situation significantly changed after an alteration in group composition (exchange of females). The relationships appeared to be more relaxed and outbalanced, significantly more sexual behaviour was shown and general activity levels were found to be much higher. In addition,

both animals of the long-time breeding pair in Cologne, which had stopped breeding for 15 years started to breed again. Some 3 years after the alteration, with the immigrant female and the hand-reared male of the group being old enough to reproduce in the meantime, the immigrant female gave birth for the first time, with the elderly male unexpectedly being the infant's father (genetically confirmed). A few weeks later, the elderly female unexpectedly also gave birth, with the subadult male being the infant's father. Resurgence in breeding after the introduction of an additional partner and the enhancement of cage space, was also found in a male Orang-utan (O`Donoghue, 1982). According to Carlstead & Shepherdson (1994), there is strong evidence that environmental stimulation, which increases activity and arousal, may benefit reproduction by promoting optimal neuroendocrine states required for adequate physiological and behavioural responsiveness.

These findings, together with the results of the present study are compatible with the assumption that some animal species might actually need to experience some level of environmental novelty or uncertainty on a regular basis (Carlstead & Shepherdson, 1994).
The present results provide hints that for bonobos, a "stimulating" effect can be induced by separation management conditions. No indications were found for negative impacts regarding this keeping strategy. And, as associations are actually of a temporary character in free-living bonobos (de Waal, 1995), an intrinsic motivation for leaving and/or changing their interaction partners regularly may generally be given (apart from ecological reasons, chapter 1.3).

4.3 General conclusions

Great efforts are made to compensate for an animal's restrictions of captivity, e.g. by building bigger and more complex, naturalistic environments (Schreiber, 2004). In doing so, understanding the complex social processes that intervene between an animal's environment and its reproductive outcome is a basic demand of zoo-biologists (Carlstead & Shepherdson, 1994; Schürer, 2004). The results of this study may contribute in different ways:
They affirmed the assumption that bonobos seem to have a high adaptive potential as major aspects of the framework of bonobo social relationships seem to be realizable also in captive settings. Major parts of their behavioural repertoire observed in the wild can also be observed in captivity and bonding patterns found in zoo-living animals largely resemble those found in free-ranging individuals. This is compatible with findings by other researchers, comparing different captive settings (Franz, 1999; Stevens et al., 2008). It seems that many aspects of the

social structure in wild bonobo societies observed so far are important basic principles which belong to the animal's natural heritage.

However, the present findings revealed that different keeping strategies do have an influence on their social relationships and an artificial fission-fusion keeping strategy apparently increases the liveliness of a group. As bonobos are said to live in flexible fission-fusion societies in the wild, this aspect of their life may also be relevant regarding their natural heritage and an intrinsic need for changes seems to exist.

Although it is seems that animals living in stable groups can cope with the situation quite well and reproduction is generally said to be similar for wild and captive bonobos (de Lathouwers & van Elsacker, 2005), reproductive failures and problems like social stagnation or untypical outbreaks of aggression may be consequences of long-term stable grouping.

Already in 1995, van Elsacker et al. stated, that: "There is an immediate need to clarify useful concepts to create more natural social groupings of captive colonies of bonobos". It is assumed that a systematically performed separation management points into the right direction regarding captive fission-fusion species like bonobos.

For an optimal care, all institutions housing bonobos should combine their efforts in collaboration with SSP (Species Survival Plan) and EEP (European Endangered Species Program) coordinators to sustain and improve optimal management strategies and implement the best possible conditions in captivity. Allowing zoo-living species to "optimize" their relationships has to be of great interest in terms of conservation biology, because this is likely to result in optimization of life-history patterns that, in turn, may stabilize population dynamics on the long run (Singh & Kaumanns, 2005). The artificial fission-fusion system may not only be regarded as an additive and a more natural form of social enrichment carried out in some of the captive groups. More flexible keeping conditions may be beneficial for the whole captive population, especially on the long-term. Separation management schedules may not only be applied in terms of breeding or handling individuals with special needs, but also because they generally benefit the animal's social life, as they adapt their natural living conditions. This view is also shared by other institutions, like the Milwaukee County Zoo, housing the largest group of bonobos today (n=21), which are also kept in an artificial fission-fusion system (pers. comm.).

Particularly more long-term investigations on multiple groups and more comparisons with free-ranging individuals are needed regarding the social potential and possible social needs of primates living in fission-fusion societies, also taken into account other species (like chimpanzees, spider-monkeys and orang-utans). While more similarities can be found

between basic grouping patterns of both *Pan* species (Kano, 1987) and the spider monkey (McFarland Symington, 1990), orang-utan populations seem to lack a well-defined community in the wild and individuals often forage alone or in rather small "travel parties" (van Schaik, 1999). The orang-utan can therefore be regarded as the most individual-based fission-fusion species. Under the restricted conditions of stable-group husbandry, this may lead to social problems just as well. Despite the fact that reproduction is quite similar for wild and captive bonobos (de Lathouwers & van Elsacker, 2005), other captive populations, like the orang-utan one, do show more pronounced breeding problems (Kaumanns et al., 2004), assumedly related with social reservations.

The present study mainly serves as a model with implementation character, as it demonstrates for the first time, how flexible keeping conditions may help stimulating the social relationships of captive fission-fusion primate species.

5. Summary

The following study analyses the social relationships in zoo-living bonobos. The main aim of the study was to determine if there is a correlation between the vitality of a group, measured via the amount of social and spatial proximity between its members, and a keeping system which more closely resembles grouping patterns found in free ranging animals.

The behaviour and inter-ape relationships in three different zoo-living groups were studied, and compared to what is known of free-living bonobos. The knowledge base concerning free-living bonobos is limited compared to other great ape species. But, it is well documented that they live in flexible and fluid fission-fusion societies in the wild, in which members of the same community forage and travel in ever-changing parties. One of the groups studied (Frankfurt) was kept in an artificial fission-fusion environment, this group was compared to two others (Cologne and Plankendael) which were kept in constant groups. The question was, whether changing the group members often, as in Frankfurt, has a positive effect on the animal's social relationships, noticeable by a higher rate of social and spatial proximity.
Detailed analyses of the separation management strategy performed in Frankfurt were carried out. It was investigated whether all-animal encounters enhanced the social arousal and whether individuals, which were separated before tended to be especially attracted by each other. It was furthermore hypothesised that bonobos that spend some time together in a constant subgroup, show signs of social separation, indicating an intrinsic motivation to move on (fission). To test this, observation data taken form just after a fission-fusion "event" was compared to data form before such an "event", to see if the rearrangement of a group had a stimulating effect on the group dynamic.

The social patterns observed in the three groups investigated in this study correlate to what has been observed in free-living bonobos. This confirms the conclusion that captive bonobos display many of the social characteristics that have been observed in the wild. Many inter-ape relationships however, like these between juveniles and adults, have not been studied intensively and need to be studied in more detail.
The Frankfurt group, which was kept in the artificial fission-fusion system, showed increased values in social and special proximity, compared to the other groups which were kept in constant parties (Cologne and Plankendael). The amount of agonistic behaviour in this group (Frankfurt) was, in contrast, lower.

When being reunited, the animals mostly displayed an increase in socio-sexual behaviour, but rarely any aggressive behaviour. After a few days within the same subgroup the animals tended to display a decrease in social interactions and direct proximity to each other.

The results of this study confirm assumptions that bonobos have a great ability to adjust to captive conditions, and are able to display much of their natural behaviour in captivity (high adaptive potential). This being the case, affirms the assumptions that also zoo studies, are of invaluable importance towards understanding the social behaviour and social needs in this, the least studied, of the great apes. Future studies should aim to combine the two fields of study (zoo and field) to a greater extent.

This study could also prove important to zoos keeping bonobos and other fission-fusion species, as it clearly shows that the artificial fission-fusion system used in Frankfurt increases the vitality and social dynamic in this group. This also raises the question whether bonobos have an intrinsic drive to leave/join groups to maintain sociability. Keeping long-term vital social groupings is, however, of great importance regarding future conservation efforts.

6. Zusammenfassung

Die vorliegende Studie behandelt die sozialen Beziehungen von Bonobos in menschlicher Obhut. Ziel der Arbeit war, mögliche Zusammenhänge zwischen der Vitalität einer Gruppe, speziell der sozialen und räumlichen Nähe ihrer Mitglieder zueinander, und Aspekten einer flexiblen, der Situation frei lebender Tiere ähnlicheren Haltungsform zu untersuchen.

Verhaltensweisen und Beziehungsmuster in 3 verschiedenen Gruppen von Bonobos wurden analysiert und mit dem bisherigen Wissen über das soziale Leben dieser bislang am wenigsten erforschten Menschenaffenart verglichen. Dabei wurden vorwiegend Freilandstudien berücksichtigt. Das interaktive und räumliche Verhalten in einer der Gruppen, welche in einem künstlich induzierten "fission-fusion" System gehalten wurde (Frankfurt), wurde dem von konstanten Gruppen gegenübergestellt (Planckendael und Köln). Es sollte überprüft werden, ob ein relativ häufiger Partnerwechsel, wie er für frei lebende Bonobos beschrieben worden ist, erkennbare Auswirkungen auf die soziale Dynamik einer Gruppe hat. Für die Bonobogruppe, deren Mitglieder überwiegend in 2 variablen Untergruppen gehalten wurden, wurde im Anschluss überprüft, ob die Raten an sozialer und/oder räumlicher Nähe mit der Dauer ihrer jeweiligen Zusammensetzung abnahmen, was auf eine intrinsische Motivation in Richtung Auseinandergehen ("fission") hinweisen könnte. Zudem wurden Untergruppentreffen, bei denen alle Tiere zeitweise miteinander interagieren konnten, untersucht, um zu überprüfen, ob ein solches Zusammenkommen ("fusion") einen stimulierenden Effekt auf die Gruppendynamik hat, insbesondere auf die Interaktionsraten von Tieren, die vorher getrennt waren.

Strukturelle Beziehungsmuster, welche in allen 3 Zoogruppen gefunden wurden, entsprachen grundsätzlich dem bisher bekannten Bild des sozialen Lebens von Bonobos. Dies bestätigt die Erwartungen, dass diese Tiere auch in menschlicher Obhut viele natürliche Verhaltensmuster zeigen. Einige untersuchte Faktoren, wie die sozialen Beziehungen zwischen Jungtieren und Erwachsenen, sind bislang nur wenig berücksichtigt worden und bedürfen intensiverer Forschung.
Die Bonobogruppe, welche unter künstlichen "fission-fusion" Bedingungen gehalten wurde, zeigte eine deutlich erhöhte Rate an sozialer und räumlicher Nähe, verglichen mit den konstanten Gruppen. Die Rate an agonistischem Verhalten hingegen war in dieser Gruppe am

geringsten. Interaktives Verhalten hatte in Frankfurt auch einen größeren Anteil am Aktivitätsprofil, verglichen mit Planckendael und Köln.
Untergruppentreffen führten bei den Bonobos zu einem Erregungsanstieg, was vor allem an einer erhöhten Rate an sozio-sexuellem Verhalten zu erkennen war, aber nie zu einer erhöhten Aggressivitätsbereitschaft führte. Nach einigen Tagen ohne Veränderungen im Partnerspektrum, sank häufig die Interaktionsrate einer Untergruppe und die Tiere befanden sich weniger häufig in direkter räumlicher Nähe zueinander.

Die Ergebnisse dieser Arbeit sind kompatibel mit Annahmen, dass Bonobos ein hohes Anpassungspotential besitzen und bei geeigneter sozialer Gruppierung auch in Menschenobhut ihr natürliches Verhaltensrepertoire zeigen können. Da viele strukturelle Ähnlichkeiten zwischen den Beziehungen von zoolebenden und wildlebenden Tieren existieren, können Zoostudien dazu beitragen, soziale Beziehungsmuster dieser am wenigsten bekannten Menschenaffenart genauer zu analysieren. Zukünftige Untersuchungen sollten beide Forschungsbereiche (Zoo und Freiland) stärker kombinieren.
Auf der Ebene des Managements von Zoopopulationen konnte die vorliegende Studie erste Hinweise liefern, dass eine dem Freiland nachempfundene, flexible Haltung der Tiere in wechselnden Untergruppen einen stimulierenden Effekt auf die Vitalität einer Gruppe haben kann. Bonobos scheinen ein intrinsisches Bedürfnis nach sozialer Abwechslung zu besitzen. Institutionen, die Bonobos (und andere "fission-fuson" Arten) halten, sollten ein möglichst flexibles Haltungssystem in Erwägung ziehen, vor allem in Hinblick auf langfristig vitale soziale Gruppen und deren artgerechter Haltung in menschlicher Obhut.

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8. Appendix

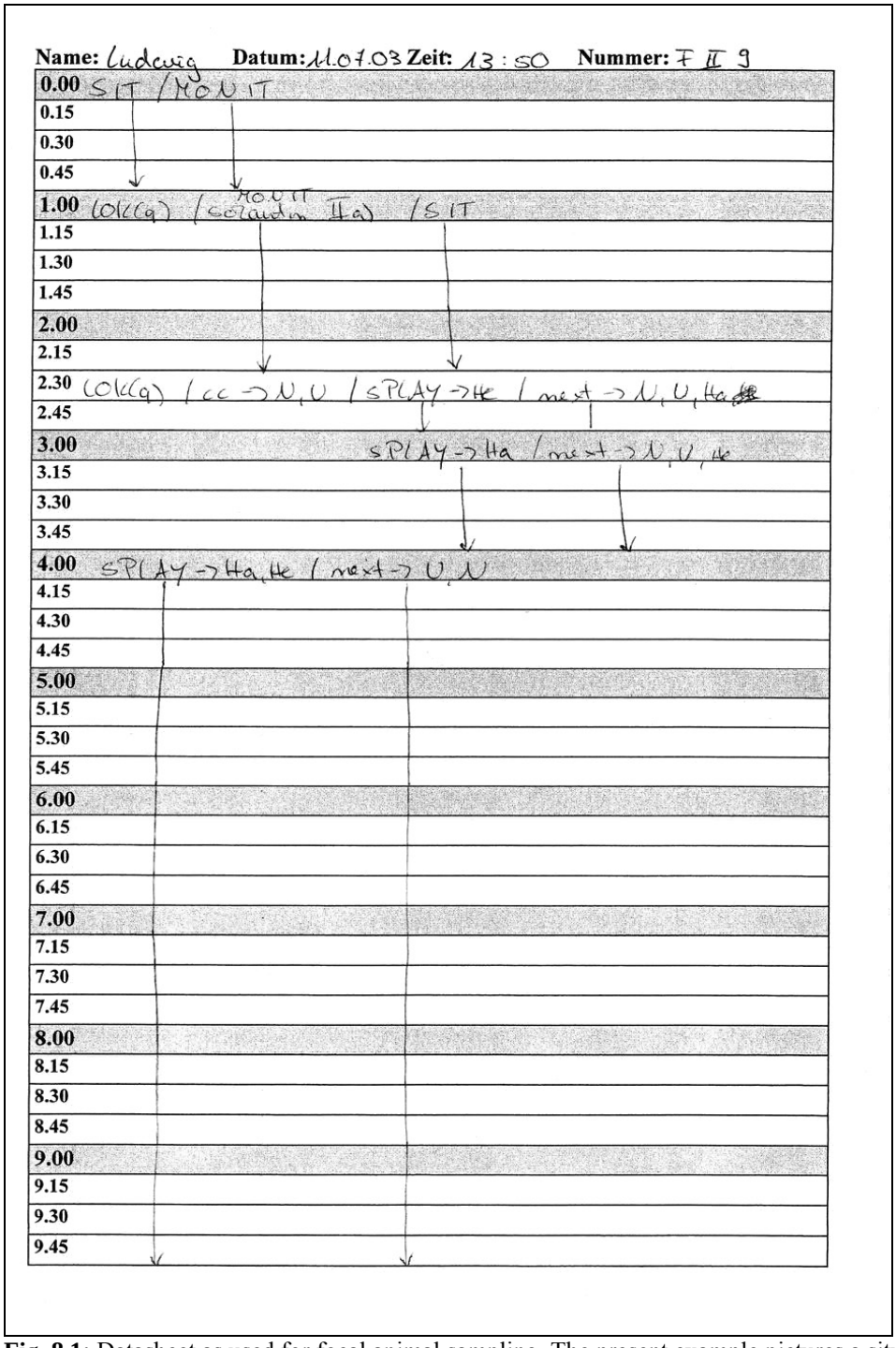


Fig. 8.1: Datasheet as used for focal animal sampling. The present example pictures a situation in which the only adult male of the Frankfurt colony (Ludwig) came close to 2 females (N=Natalie, U=Ukela) and kept proximity to them via playing with their infants (He=Heri, Ha=Haiba).
Used abbreviations: SIT=sitting, MONIT=monitoring, LOK(q)=moving quadruped, cc=coming close, sPLAY=social play, next=being in proximity (≤ 1m, around arm reach)

Friday, 18th July 2003

subgroups: Lu, Ma, Sa / Na+He, Uk+Ha, Ka

10:50-11:30

-Na+He sit in contact, next to Uk+Ha
-female Uk grasps Na's infant He with one hand and keeps holding his arm
-female Ka comes close and also clings to He with one hand
-He's mother Na takes her infant but Uk and Ka keep on holding He with one hand each as he clings to his mother's belly
-the three females sit in physical contact to each other, with He being on his mother's belly and Uk and Ka clinging to him with one hand each
-a kind of tense mood arises and all bonobos start screaming for a few seconds
-Na disconnects her infant from Uk and Ka and moves away
-as He moves alone again, Ka approaches him and grasps his arm again
-Na comes close and disconnects her infant again
-a few seconds later Ka again approaches He and starts playing with him for a few seconds but then moves away
-approx. one minute later Ka follows He but Na takes him to her belly
-Uk and Ka both come close to Na+He and start clinging to the infant again
-all animals move and start screaming, this time very loudly
-Uk and Ka release He, approach each other and start GG rubbing ventro-ventrally
-after the GG rub the tension seems gone and no further conflict occurred

-the tense situation also influenced the second subgroup: particularly the oldest female Ma watched the scene nervously, had short hand-contacts with Na through the grids of the enclosures several times and aggressively chased the male Lu once

Fig. 8.2: Description of a tense situation within the Frankfurt colony, which resulted from the struggle between 2 adult females concerning the contact to another one's infant. Incidents similar to this happened on several occasions. Abstract compiled with the aid of the appropriate focal animal datasheets and notes from a personal diary.
animals: Na=Natalie (♀), Uk=Ukela (♀), Ka=Kamiti (♀), He=Heri (♂, infant of Na), Ha=Haiba (♀, infant of Uk), Lu=Ludwig (♂), Ma=Margrit (♀), Sa=Salonga (♀)

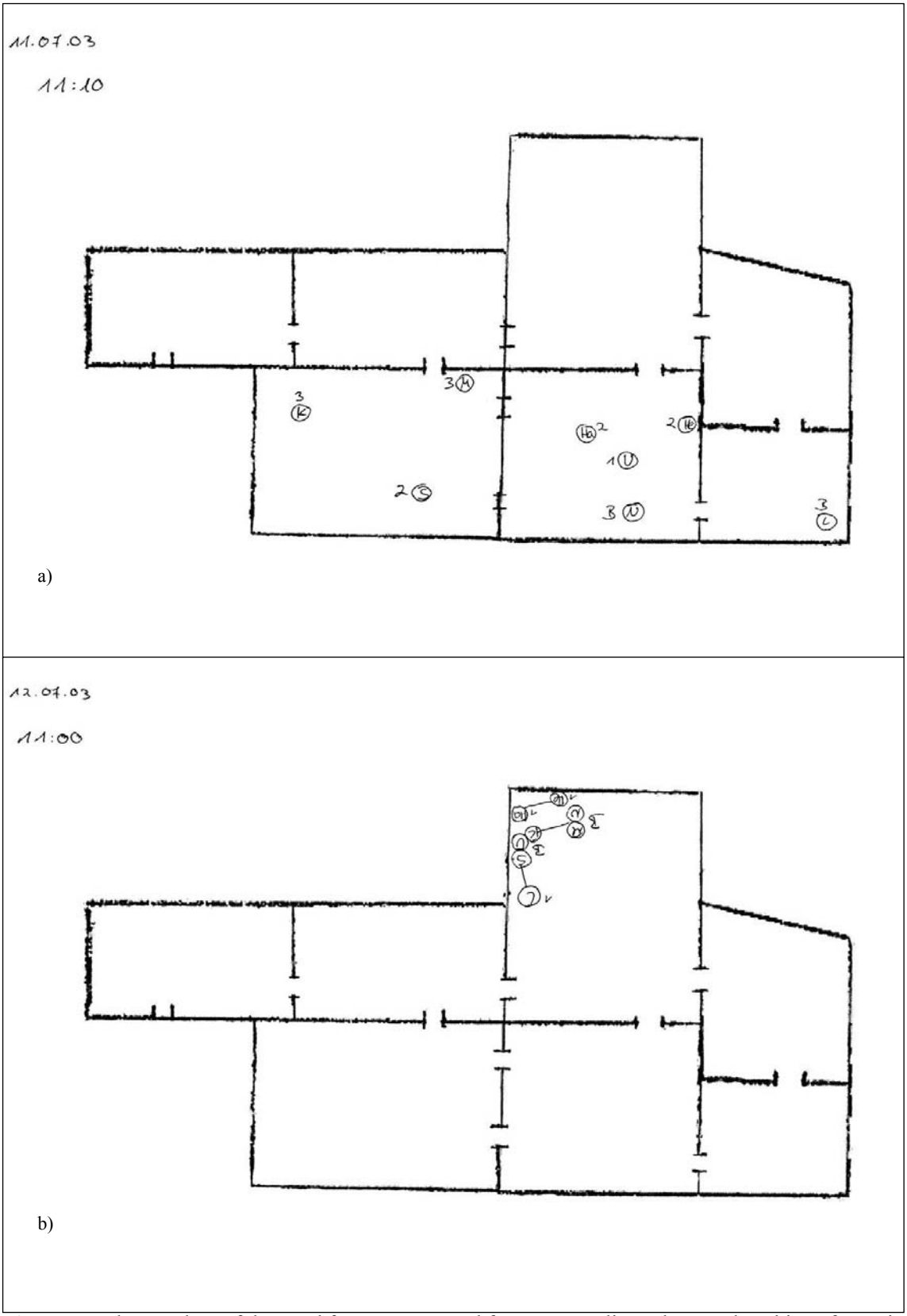


Fig. 8.3: Enclosure plans of the Frankfurt group as used for scan sampling. The actual position of an animal was marked with its first name's letter and a surrounding circle. The present plans give an example of the animal's distribution: a) after a long-term constant subgroup situation and b) around the same time of the following subgroup encounter day
numerals=different levels of height. B=being on the ground, connecting lines= within proximity (≤1 meter)
animals: L=Ludwig (♂), M=Margrit (♀), S=Salonga (♀), N=Natalie (♀), U=Ukela (♀), K=Kamiti (♀), He=Heri (♂, infant), Ha=Haiba (♀, infant)
lower parts=indoor enclosures, upper parts=outdoor enclosures

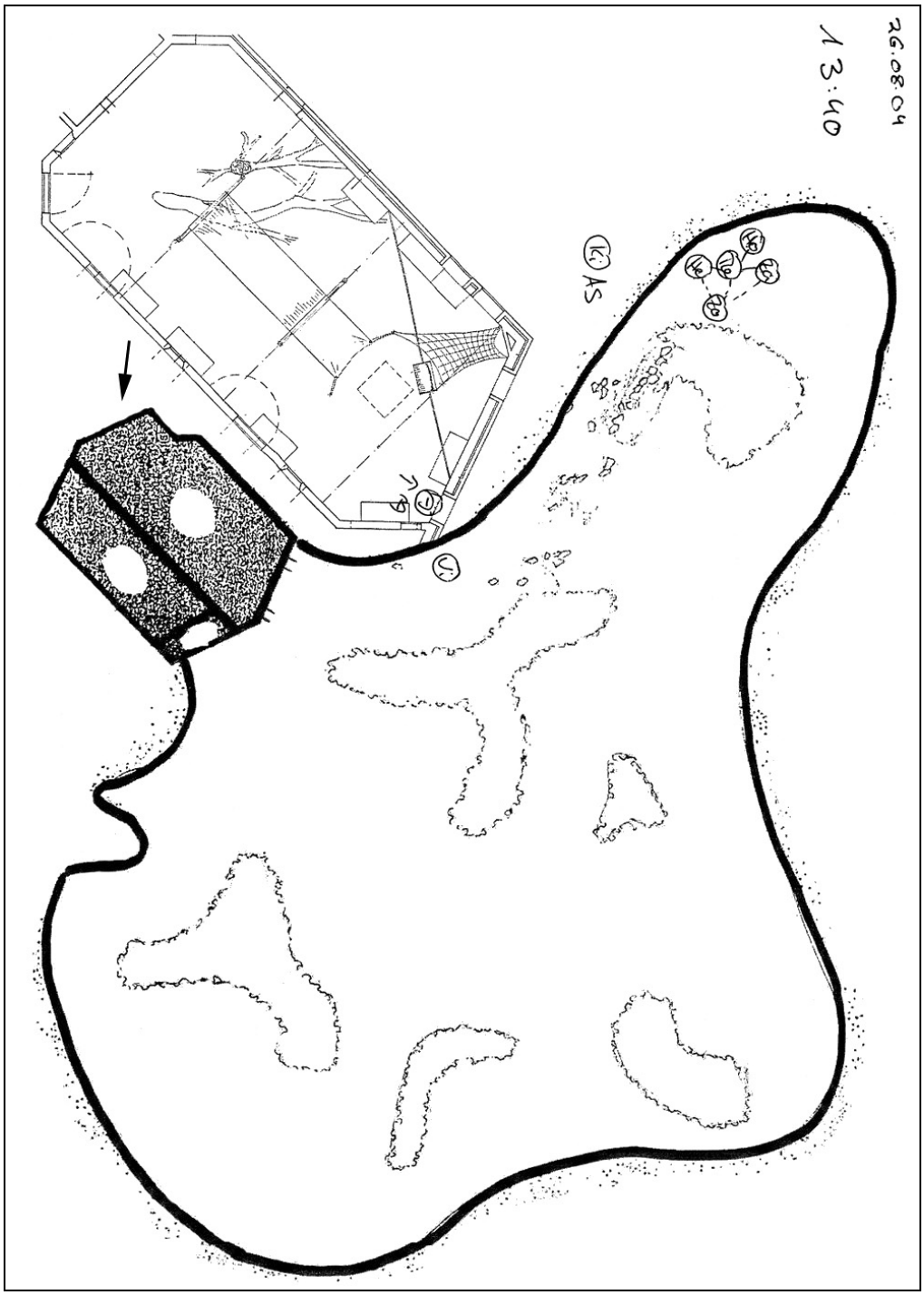


Fig. 8.4: Enclosure plan of the Planckendael group as used for scan sampling. The actual position of an animal was marked with its first name's letter and a surrounding circle. The present plan pictures a typical distribution, with the oldest male (Ki) being on the other side of the island. "Missing" animals were placed outside the enclosures and marked as out of the observer's sight (AS).
connecting lines=within proximity (≤1 meter), dotted lines=within a 5 meter radius
animals: Ho=Hortense (♀), He=Hermien (♀), Dj=Djanoa (♀), Zo=Zomi (♀, juvenile), Ki=Kidogo (♂), Re=Redy (♂), Vi=Vifijo (♂), Za=Zamba (♂, juvenile)

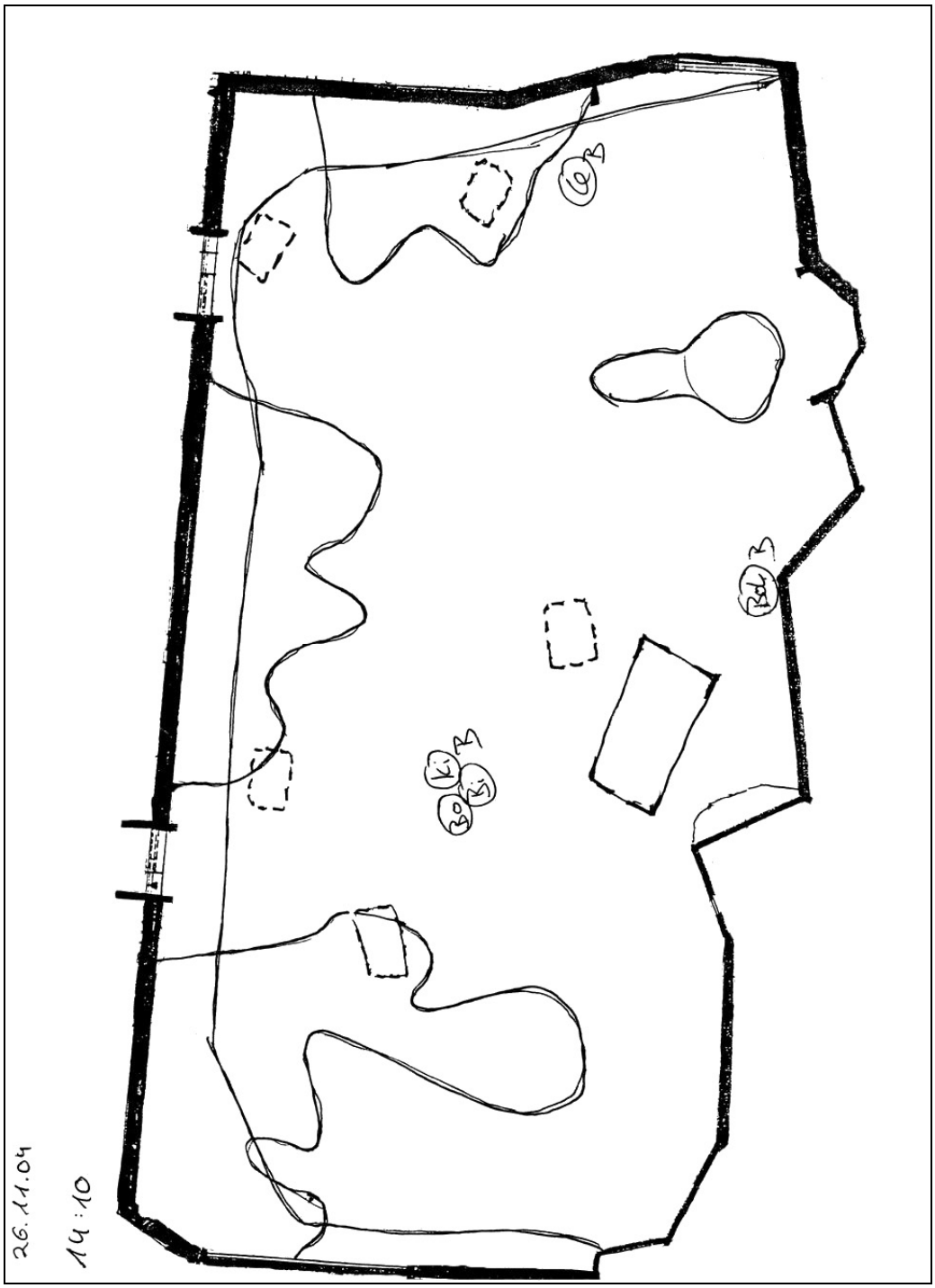


Fig. 8.5: Enclosure plan of the Cologne group as used for scan sampling. The actual position of an animal was marked with its first name's letter and a surrounding circle. The present plan pictures a typical distribution, with the only 2 females (Bo and Bi) and Bo's adult son (Ki) being in contact to each other (mostly observed in connection with social allogrooming).
animals: Cl=Clyde (♂), Ki=Kindu (♂), Bol=Bolombo (♂), Bo=Bonnie (♀), Bi=Binti (♀)

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1995 – 2001	Studium an der Universität Ulm im Fach Biologie, Diplom
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2001	Diplom in den Fächern Zoologie (Hauptfach), Ökologie, Medizinische Mikrobiologie und Betriebswirtschaft
2003-2008	Promotion im Fach Biologie an der Universität Ulm in Zusammenarbeit mit dem Zoologischen Garten Köln unter wissenschaftlicher Betreuung von Prof. Dr. G. Ehret und Dr. W. Kaumanns

Publikationen

Poster Präsentationen:

09.-12.08.05 1th Congress of the European Federation for Primatology/ 9. Tagung der Gesellschaft für Primatologie (Göttingen, Germany)

KIESSLING S, KAUMANNS W, HAASE D, CLASSEN D (2005): Social relationships in zoo-living bonobos, Pan paniscus. (Abstract). Primate Rep. 72: 53

CLASSEN C, KAUMANNS W, KIESSLING S (2005): Social relationships in zoo-living Bornean orang-utans (Pongo pymaeus). (Abstract). Primate Rep. 72: 24

07.-10.10.07 6th International Zoo and Wildlife Research Conference on Behaviour, Physiology and Genetics (Berlin, Germany)

KIESSLING S, KAUMANNS W, CLASSEN D: Artificial fission-fusion conditions versus stable-group conditions: A comparison between captive groups of bonobos. (Abstract). Conference contributions, IZW: Pgs. 123

CLASSEN D, KAUMANNS W, KIESSLING S: Every once in a while: Patterns of spatial behaviour in two captive groups of Bornean orangutans. (Abstract). Conference contributions, IZW: Pgs. 61

Eidesstattliche Erklärung

Hiermit erkläre ich, die vorliegende Dissertationsarbeit selbständig angefertigt und keine anderen als die in der Arbeit aufgeführten Hilfsmittel verwendet zu haben. Wörtlich oder inhaltlich übernommene Stellen wurden als solche gekennzeichnet.

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