

SOCIAL RELATIONSHIPS IN CAPTIVE BORNEAN ORANGUTANS (*PONGO PYGMAEUS*)



Inaugural Dissertation
zur
Erlangung des Doktorgrades
der Mathematisch-Naturwissenschaftlichen Fakultät
der Universität zu Köln

vorgelegt von
Dorothee Claßen
aus Düsseldorf

Köln 2011

Berichtersteller:
(Gutachter)

PD. Dr. Thomas Ziegler

Prof. Dr. Ansgar Büschges

Tag der mündlichen Prüfung:

20.10.2011



“...when you look into the eyes of the orangutans there comes this moment when you get goosebumps, when you realise you are looking into the eyes of a person”

(Dr. Willie Smits)

Front cover: female orangutan Lotti, Cologne Zoo; this side: female orangutan Sandy and her newborn Samboja, Stichting Apenheul (FAQ: drawings by Dorothee Claßen)

CONTENTS

1. Introduction	1
1.1. Social life in primates	1
Social structure and social relationships	2
Social organisation	3
1.2. The orangutan, <i>Pongo</i> spp.	5
Status and distribution	5
Ecology	6
Ranging behaviour	7
Mating system	8
Social life	8
Inter-species differences in social organisation	11
Captive orangutans	12
1.3. Aim of the study	13
2. Animals and Methods	15
2.1. Animals and keeping conditions	15
Chester	16
Apenheul	17
Cologne	18
2.2. Methods	20
2.2.1. Data collection	20
2.2.2. Ethogram	22
2.2.3. Data analysis	24
3. Results.....	27
3.1. Activity profiles	27
Non-social activities in proximity	28
Aberrant behaviours	30
3.2. Social behaviour	31
3.2.1. Overview	32
3.2.2. Dyadic interactions	36
Female-female relationships	36
Male-female relationships	42
Male-male relationship	47
Adult-juvenile relationships	47
Juvenile-juvenile relationships	55
3.2.3. Triadic interactions	57
3.2.4. Long-term observations – Cologne	59
3.3. Spatial behaviour	66
3.3.1. Interindividual distances	66
Group average and sex-classes	66
Long-term observations – Cologne	68
3.3.2. Patterns of neighbourhood	71
Nearest neighbour distance	71
Proximity index	73
Sequence of neighbourhood	75

3.4. Long-term sampling of behaviours.....	76
3.5. Summary of results	81
4. Discussion.....	84
4.1. Sociability	84
4.2. The structure of social relationships	88
4.3. Fission-fusion tendencies.....	93
4.4. General conclusions.....	95
4.5. Future work.....	97
5. Abstract.....	99
6. Zusammenfassung.....	100
7. References	102
8. Appendix	113
9. Danksagung.....	123
10. Erklärung.....	124

TABLES AND FIGURES

Tab. 2.1: Keeping conditions overview	15
Tab. 2.2: Orangutans Chester Zoo	16
Tab. 2.3: Orangutans Stichting Apenheul.....	17
Tab. 2.4: Orangutans Cologne Zoo.....	19
Tab. 2.5: Ethogram - behavioural categories and included elements	23
Tab. 3.6: Frequency and duration of aberrant behaviours	31
Tab. 3.7: Interactions within female-female dyads.....	36
Tab. 3.8: Sociopositive interactions within female-female dyads	38
Tab. 3.9: Agonistic interactions within female-female dyads	39
Tab. 3.10: Interactions within male-female dyads.....	42
Tab. 3.11: Sociopositive interactions within male-female dyads	43
Tab. 3.12: Agonistic interactions within male-female dyads	45
Tab. 3.13: Interactions within the male-male dyad.....	47
Tab. 3.14: Interactions within female-juvenile dyads.....	48
Tab. 3.15: Sociopositive interactions within female-juvenile dyads	49
Tab. 3.16: Agonistic interactions within female-juvenile dyads	50
Tab. 3.17: Interactions within male-juvenile dyads.....	52
Tab. 3.18: Sociopositive interactions within male-juvenile dyads	53
Tab. 3.19: Agonistic interactions within male-juvenile dyads	53
Tab. 3.20: Interactions within juvenile-juvenile dyads.....	55
Tab. 3.21: Sociopositive interactions within juvenile-juvenile dyads.....	55
Tab. 3.22: Theoretically possible and observed number of triads	58
Tab. 3.23: Frequency of triadic interactions	59
Tab. 3.24: Comparison of frequency of interactions per observational method.....	78
Tab. 3.25: Comparison of duration of interactions per observational method	79
Tab. 8.26: Reciprocity indices per dyad	121
Tab. 8.27: Interindividual distances per dyad.....	122
Fig. 1.1: Orangutan distribution.....	6
Fig. 3.2: Activity profiles per group	28
Fig. 3.3: Non-social activity in proximity per group	29
Fig. 3.4: Non-social activities in proximity per group detailed	30
Fig. 3.5: Mean proportion of social activities per group.....	32
Fig. 3.6: Frequency and duration of social events between individuals per group.....	33
Fig. 3.7: Frequency and duration of social events between adult individuals	34
Fig. 3.8: Frequency and duration of social events between adult and juvenile individuals.	35
Fig. 3.9: Reciprocity of interactions within female-female dyads.....	41
Fig. 3.10: Reciprocity of interactions within male-female dyads.....	46
Fig. 3.11: Reciprocity of interactions within female-juvenile dyads.....	51
Fig. 3.12: Reciprocity of interactions within male-juvenile dyads.....	54
Fig. 3.13: Reciprocity of interactions within juvenile-juvenile dyads.....	56
Fig. 3.14: Types of triadic interactions	57
Fig. 3.15: Long-term series of interactions within female-female dyads	61
Fig. 3.16: Long-term observation of reciprocity within female-female dyads	62
Fig. 3.17: Long-term series of interactions within male-female dyads	64
Fig. 3.18: Long-term observation of reciprocity within male-female dyads	65
Fig. 3.19: Interindividual distances per group	66

Fig. 3.20: Distances between sub-/adult individuals per group	67
Fig. 3.21: Distances between sub-/adult individuals per observation period	69
Fig. 3.22: Development distances between adult females	70
Fig. 3.23: Development distances between sub-/adult males and females	70
Fig. 3.24: Nearest neighbour distance per group	71
Fig. 3.25: Nearest neighbour distance in sub-/adult individuals per group	72
Fig. 3.26: Nearest neighbour distance per observation period at Cologne	73
Fig. 3.27: Proximity index for female-female dyads and male-female dyads per group.....	74
Fig. 3.28: Proximity index per observation period at Cologne.....	75
Fig. 3.29: Probability of a neighbours' presence and absence within 3m radius per group.	76
Fig. 3.30: Activity profile Cologne per observational method	77
Fig. 3.31: Occurrence and time interval of grooming and approaching within 3-hrs units.	80
Fig. 3.32: Occurrence of grooming and approaching within 3-hrs units per dyad	81
Fig. 8.33: Facilities Chester Zoo	117
Fig. 8.34: Facilities Stichting Apenheul	117
Fig. 8.35: Facilities Cologne Zoo	118
Fig. 8.36: Long-term observations of dyadic interactions—adult individuals	119
Fig. 8.37: Long-term observations of dyadic interactions—adult and juvenile individuals.	120

1. INTRODUCTION

Primate social systems vary among and within species. This includes patterns of grouping, spacing, and mating patterns, as well as variability in patterns and quality of social relationships (Kappeler and van Schaik, 2002). The social systems of primates vary from the solitary organisation of some nocturnal prosimians to the complex systems in some monkeys and apes with animals that form temporal parties of variable composition (fission-fusion).

The social system of orangutans is regarded to be unique among diurnal anthropoids (Delgado and van Schaik, 2000). They live semi-solitary in the wild with great intra-specific flexibility in social organisation and association patterns (van Schaik *et al.*, 2004). According to van Schaik (1999) they are loosely organised in fission-fusion societies. However, even though several long-term studies have been carried out during the last decades, the social system in orangutans is still not well understood (Mitra Setia *et al.*, 2009; van Schaik, Marshall *et al.*, 2009). In addition, only a few studies have focused on the social abilities of orangutans in captivity so far. The present study intended to provide resources to fill this gap by investigating the socio-spatial relationships in different groups of captive Bornean orangutans.

The following chapter will first focus on general concepts and characterizations of sociality in primates, and then will focus on the state of knowledge in orangutans leading to the background of this study.

1.1. SOCIAL LIFE IN PRIMATES

The society of a species, also labelled as social unit or social system (Kappeler and van Schaik, 2002), is constituted by a set of individuals that interact regularly and do so more with each other than with members of other such societies (Struhsaker, 1969). According to Kappeler and van Schaik (2002), a species' social system is constituted by three discrete, interrelated components: the social structure (interfemale, intermale, intersexual relationships), the mating system (monogamy, polygyny, polyandry and polygyandry), and the social organisation, which describes the size, sexual composition and spatiotemporal cohesion of its society.

Social structure and social relationships

The social structure is defined by the quality, content, and patterning of social relationships between individuals and between societies (Hinde, 1975). The social structure is influenced by social factors and environmental variables (Crook, 1970). Furthermore, species-specific ecological and biological features (e.g. body-size) may influence individual ranging patterns within a population (Harcourt and Stewart, 1983). At the ultimate level, social relationships can be described as an investment, reflecting individual strategic goals (Kummer, 1978).

At the proximate level, social relationships can be described by the content and quality of interactions between individuals, and their relative frequency and patterning in time. Furthermore, interindividual distances can give clues on the quality of social relationships (Hinde, 1975). The quality of social relationships between and within sexes can be derived from the proportion of agonistic and affiliative behaviours (van Schaik, 1989), reflecting competition and cooperation, respectively (van Schaik *et al.*, 2004).

Close ties, often labelled as social bonds, between individuals are characterized by temporal synchronized activities (Hinde, 1975), spatial cohesion, and high levels of affiliative behaviours (e.g. grooming, spatial proximity). The strength of a social relationship can be evaluated by the frequency, duration, and the direction of interactions (both affiliative and agonistic). These parameters can be used to assess the degree of mutual attraction, tolerance and reciprocity between individuals (for a review see Silk, 2002).

Social relationships among individuals can be compared using the degree of complexity (uniplex vs. multiplex), reciprocity, stability (in terms of continuity and consistency) and dynamics (Hinde, 1979). The social partners influence each other's behaviour as well, resulting in complex, multilevel social networks (Aureli and Schaffner, 2002).

Concerning the social structure, there are species-specific differences referring to the distribution of the social relationships of a given quality among members of a social unit. According to van Schaik (1989) and Wrangham (1980), 'female-bonded' species like e.g. most *Macaca* spp. (van Schaik *et al.*, 1983) are characterized by female philopatry, well-differentiated allogrooming, spatial proximity and agonistic support ('alliances') between females, often based on kinship. In 'non-female-bonded' species like e.g. mountain gorillas (Harcourt, 1979), relationships between females are less differentiated and females can disperse more easily from their natal unit; often female-male relationships are more pronounced. In some species like chimpanzees (Bygott, 1979), males develop strong social

bonds among each other ('male-bonded') and are the philopatric sex (Wrangham, 1980). In other species, e.g. hamadryas baboons (Kummer, 1968), there are 'male-female bonds' within the social unit which continue beyond the females' reproductive phase (Walters and Seyfarth, 1986).

Social organisation

Three fundamental types of social organisation traditionally are distinguished, i.e. solitary and neighbourhood-systems, pair-living, and group-living (Kappeler, 1999; Kappeler and van Schaik 2002). According to socio-ecological models, group-living is suggested to have evolved as a cost-benefit optimisation process mainly affected by predation pressure and access to resources (van Schaik and van Hooft, 1983). Food distribution and abundance, predation risk and/or infanticide avoidance affect female dispersal, which in turn affects male distribution (van Schaik, 1989; Sterck *et al.*, 1997). The distribution and availability of food resources in relation to group-size and population-density affect competitive regimes in females, which in turn influence the patterns of social relationships.

In group-living species, two basic types of competition can be distinguished (see Walters and Seyfarth, 1986; van Schaik, 1989; Sterck *et al.*, 1997): 'contest' and 'scramble'. In a contest-competition situation, resources are more clumped and can be monopolized by individuals, alliances or groups. In a scramble-competition, availability of local resources is low, or sources are too scattered to be monopolised. In both types of competition, a possible way to reduce within-group competition is to adjust group-size. The adjustment may result in smaller groups of a species in a given environment (Dunbar, 1988), or in the temporary formation of smaller subgroups within a group or community (Kummer, 1971; Wrangham, 1979).

In most primate species, individuals live in permanent bisexual groups consisting of at least three adult individuals. There is a great diversity in species-specific group-demography referring to size, sex ratio and temporal stability (for detailed classifications see e.g. Vogel, 1975). In some species, spatiotemporal group cohesion is strong and remains constant (e.g. *Macaca* spp., Kappeler, 1999). In others, individuals are associated more loosely in 'open communities'. In such flexible societies, members split into smaller temporary subunits (also labelled 'parties' or subgroups) of variable size and composition, and merge again. This organisation is referred to as a 'fission-fusion' organisation (Kummer, 1971).

In fission-fusion societies, social organisation is so flexible that individuals belonging to the same community can rarely be seen all together (Aureli and Schaffner, 2005). The lack of permanent groups presumably is related to the combination of low predation risk and potentially strong feeding competition between females (van Schaik, 1989). Flexible subgroup-membership offers flexibility in exploiting and monitoring resources and allows the regulation of feeding competition (Kummer, 1971; Dunbar, 1988). It also requires complex cognition since rejoining conspecifics after lengthy periods of absence increases the needs for sophisticated navigation and renegotiating relationships (Russon and Begun, 2004).

The cognitive demands imposed by social complexity are suggested as an explanation for why primates have unusually large brains in relation to their body size; this proposal was formed to the social brain hypothesis (Jolly, 1966). In the phylogenetic context, hominid large brain and body size presumably co-occurred with slow life histories, prolonged immaturity, lower predation risk, flexible fission–fusion tendencies, stronger relationships with non-kin, and relatively high subordinate leverage leading to less rigid dominance and enhanced social tolerance (van Schaik *et al.*, 2004). Flexible fission-fusion tendencies would have favoured larger brains for more complex social problem-solving, and enhanced social tolerance may have further advanced cognition by enhancing conditions for socio-cultural learning (Russon and Begun, 2004).

For non-human primates, van Schaik (1999) distinguishes two types of fission-fusion organisation referring to whether its basic social units are represented by persisting subgroups, i.e. ‘group-based’ (e.g. geladas, Bergmann, 2010), or by single individuals, i.e. ‘individual-based’ (e.g. spider monkeys (Symington, 1990), chimpanzees (e.g. Nishida, 1968), bonobos (e.g. van Elsacker *et al.*, 1995), and orangutans (van Schaik, 1999)).

In a new framework, Aureli *et al.* (2008) propose to characterize any animal society by its degree of fission-fusion dynamics referring to the extent of temporal variation in spatial cohesion and individual membership in a group. The authors suppose two trajectories by which ‘higher fission-fusion groups’ could have evolved. On one route (‘A’), social relationships became increasingly valuable for mutual advantages through long-term associations. This permits the group members to remain together unless ecological pressures necessitate fissioning. On the other route (‘B’) ‘higher fission-fusion groups’ may have evolved from a solitary rather than a group-living condition. Intensified gregariousness does not require that increasingly differentiated social relationships and associations may have been short-lived. Resulting societies may shift into more cohesive if ecological conditions permit.

1.2. THE ORANGUTAN, *PONGO* SPP.

Within the taxonomic family of Hominidae (also known as great apes), orangutans are classified into the *Pongidae* subfamily. The last common ancestor of the orangutans split from the ancestors of the other three genera (chimpanzees, gorillas, humans) roughly 14 million years ago (Groves, 1989). Historically considered as subspecies, orangutans are classified as two separate species since the beginning of this century (Groves, 2001): the Bornean orangutan (*Pongo pygmaeus*) and the Sumatran orangutan (*Pongo abelii*). In Bornean orangutans, recent genetic and morphological analyses suggest at least three subspecies: *P.p. pygmaeus*, *P.p. wurmbii*, and *P.p. morio* (Groves, 2001; Goossens *et al.*, 2009).

Basic characteristics and the current state of knowledge will be described for free-ranging orangutans first, followed by a paragraph referring to orangutans under human care. Characteristics will refer to both Bornean and Sumatran orangutans since the classification into two species was only established in recent years. General patterns of social organisation seem to hold for both species; the suggested inter-species differences are described in a separated paragraph.

Status and distribution

Recent surveys provide evidence that an estimate of at least 54,000 individuals live on Borneo (Caldecott and Miles, 2005; Wich *et al.*, 2008) while the number is smaller on Sumatra with an estimate of 6,600 individuals. On both islands, the sizes of the wild populations are rapidly declining due to habitat loss (logging, fires), habitat fragmentation, hunting and capturing for pet trade. On the IUCN Red List, the status of Bornean orangutans is classified as endangered, Sumatrans as critically endangered (Ancrenaz *et al.*, 2008; Singleton *et al.*, 2008).

On Borneo, orangutan distribution is highly patchy (Fig. 1.1). Populations of *P.p. pygmaeus* are present in the northwestern part, *P.p. wurmbii* in central Borneo and *P.p. morio* in the northeastern part. Males are reported to wander into Brunei Darussalam occasionally (Goossens *et al.*, 2009). Wild Sumatran orangutans can only be found in the north of the island (Fig. 1.1), restricted to the provinces Aceh and North Sumatra.

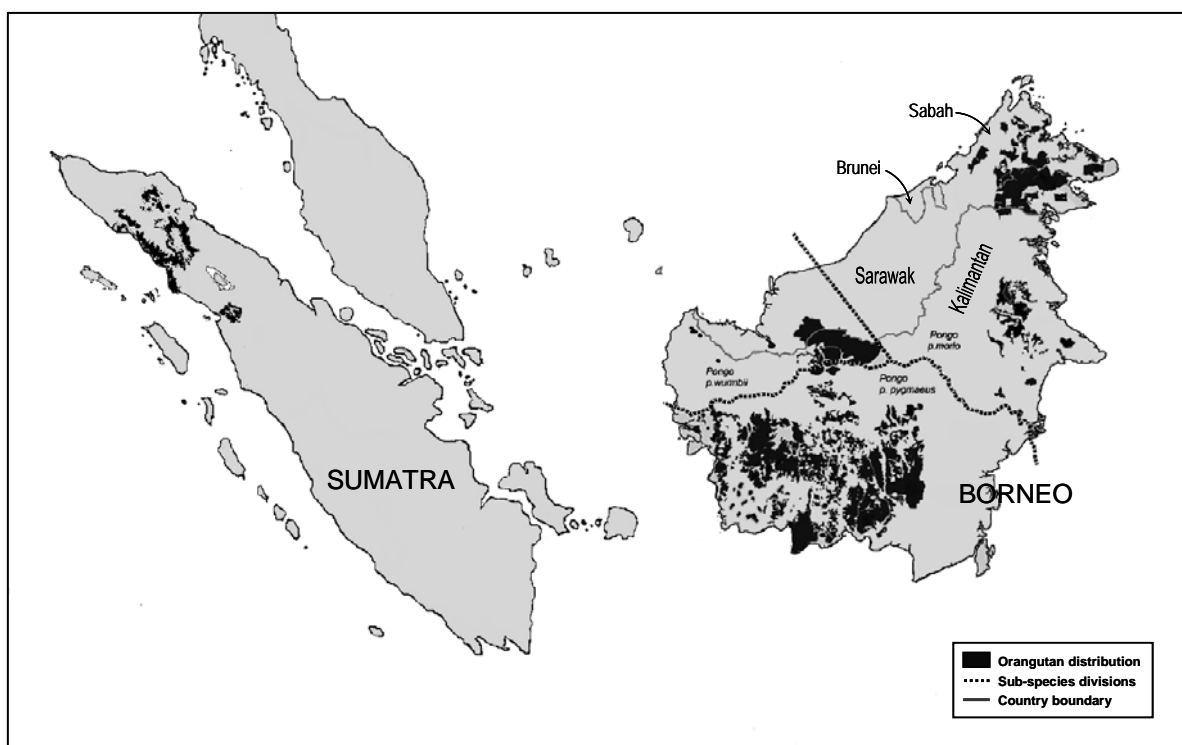


Fig. 1.1: Orangutan distribution

Data source of distribution adopted from Wich *et al.* (2008); for density and range type see Nellemann *et al.* (2007), and the IUCN Red List of Threatened Species, 2008 (www.iucnredlist.org). *P.p. pygmaeus*: northwestern part: Sarawak (Malaysia), northwest Kalimantan (Indonesia); *P.p. wurmbii*: central Borneo: south-west and Central Kalimantan (Indonesia); *P.p. morio*: northeastern part: east Kalimantan (Indonesia), Sabah (Malaysia). *Pongo abelii*: North Sumatran: Province of Aceh (Nanggroe Aceh Darussalam, Indonesia).

Orangutans mainly live in primary tropical rain forest and old secondary forest at low elevations that include peat swamp forests and lowland mixed dipterocarp forests (Rodman, 1988). Bornean orangutan density is low in most populations, ranging from 0.8 to 4.3 ind/km² on average (van Schaik *et al.*, 2005; Marshall *et al.*, 2007). On Sumatra, the average density seems to be slightly higher in similar habitats as on Borneo (Delgado and van Schaik, 2000; for a review see Husson *et al.*, 2009).

Ecology

Orangutans are the largest living arboreal primates with marked sexual dimorphism and male bimaturism. They are characterized by slow life-history patterns with long gestation periods, long inter-birth intervals, a late age of first parturition, long lasting associations of mothers with their offspring for at least six years, and longevity (for details see Wich *et al.*,

2004; van Schaik, Marshall *et al.*, 2009). Predation risk outside human threats is low on Borneo; on Sumatra the major predatory threat is constituted by tigers (*Panthera tigris sumatrae*) and clouded leopards (*Neofelis nebulosa diardi*). The absence of large terrestrial predators is probably one reason that Bornean orangutans are seen more frequently descending to the ground than Sumatran orangutans (Rijksen, 1978; Galdikas, 1988).

Orangutans consume more than 350 different species of plants but they are primarily frugivorous (about 60% of diet, see Wich *et al.*, 2006). Fruit availability varies seasonally and annually; ‘mast fruiting’ occurs at intervals of several years, i.e. every two to ten years (Knott, 1998a; Wich and van Schaik, 2000). During these periods, orangutans greatly exceed their caloric intake and are able to store additional fat reserves (Knott, 1998a).

Orangutans often rely on foods that are protected by physical defences like embedding matrices, spines, or protector ants, and therefore are difficult to process. Techniques for obtaining such difficult foods may involve flexible, manipulative sequences and tool use (Fox *et al.*, 1999; van Schaik *et al.*, 2003). Orangutans seem to use socially transmitted information in acquiring processing strategies, and probably also in cuing food location and availability (Russon, 2002). There are hints on the presence of socially transmitted behavioural innovations, i.e. some form of culture in feeding techniques, at least in some populations on Sumatra (van Schaik, Ancrenaz *et al.*, 2009).

Ranging behaviour

Dispersal patterns presumably represent a type of female philopatry (Rijksen, 1978; Galdikas, 1984; Singleton and van Schaik, 2002; Knott *et al.*, 2008): females tend to establish individual home ranges overlapping with or near to those of their mothers. Female home ranges vary from 3.5 to 6km² on Borneo (Galdikas, 1988; Knott *et al.*, 2008), and home ranges of even up to 8.5km² on Sumatra (Singleton and van Schaik, 2001). Within their home ranges, females seem to establish distinct core areas with only a minor degree of overlap (Knott *et al.*, 2008).

Mature males tend to disperse widely at maturity. A nomadic phase of roaming widely is suggested at some stage of (sub-) adulthood spanning a few years (Singleton and van Schaik, 2001; Utami-Atmoko *et al.*, 2009). Home range sizes of males are larger than those of females with estimates of minimum 25km² (Singleton and van Schaik, 2001). Individual home ranges seem to overlap considerably within and between sexes (Rodman, 1973; Horr, 1975; Galdikas, 1988; van Schaik and van Hooff, 1996; Knott, 1998b).

Mating system

The mating system of orangutans is promiscuous, characterized by female mate choice and strong inter-male contest competition (Rodman and Mitani, 1987; van Hooff, 1995; van Schaik and van Hooff, 1996). There are two morphs of sexually mature males in orangutans (bimaturism): ‘flanged’ males are twice the size of females, exhibit secondary sexual characteristics like long hair on the back, facial disk, flanges and a throat sac, and they are emitting ‘long calls’ (e.g. MacKinnon, 1974; Rijksen, 1978). ‘Unflanged’ males do not possess these features. The arrested development of secondary sexual characteristics is suggested to be an adaptation to stress avoidance against other flanged males during adolescence and sub-adulthood (Maggioncalda *et al.*, 2002). The timing and the duration of the maturational arrest seems to depend mainly on complex socioendocrine factors that are not yet fully understood (Maggioncalda *et al.*, 2002).

Both types of males are capable of reproducing (Utami *et al.*, 2002; Goossens *et al.*, 2006) whilst using different mating strategies. It has been suggested that flanged males use a ‘call-and-wait’ strategy (van Hooff, 1995) which involves the use of long calls to attract receptive females and to space out other males. Contrary, unflanged males actively seek and follow potentially fertile adult females and then try to mate and to maintain associations (Galdikas, 1985c; Mitani, 1990; van Hooff, 1995). Galdikas (1985b) and Mitani (1985b) found both flanged and unflanged males to force copulations with flanged males doing so mainly when not locally dominant.

Mating consortships may last up to few weeks in which flanged males were found to attempt maintaining exclusive access to a receptive female (Rodman and Mitani, 1987). Sexually active females (adult and adolescent) are assumed to prefer adult flanged males as mates (Schürmann, 1982; Galdikas, 1984). Flanged males in turn are assumed to be sexually more interested in adult females than in nulliparous/adolescent females (Schürmann, 1982; Galdikas, 1995).

Social life

Free-ranging orangutans spend most of their time solitarily, engaging in feeding, travelling, resting, and only occasionally associating with conspecifics in temporary parties (MacKinnon, 1974; Rijksen, 1978; Rodman, 1979; Galdikas, 1985a; Knott *et al.*, 2008). They are assumed to live in individual-based fission-fusion societies (van Schaik, 1999).

Social units can be recognized only by analysing long-term association patterns, if at all (van Schaik, *ibid.*).

Although orangutans have been observed for over three decades in several long-term studies, the knowledge – especially proximate aspects – about their social organisation is still limited (Delgado and van Schaik, 2000). The only more enduring social unit in the orangutan society seems to be the mother-infant bond: adult females stay with their dependent offspring for several years, and are sometimes also temporarily accompanied by an older sibling (e.g. MacKinnon, 1974; Horr, 1975; Rijksen, 1978; Galdikas, 1985a; Mitani, 1990). At one site on Sumatra, Singleton and van Schaik (2002) described a community consisting of ‘clusters’ of females with one adult male they all preferred as mate. At some other sites on Borneo there are hints that members of a local population may form loose communities and complex social networks of loose relationships (MacKinnon, 1974; Galdikas, 1985a).

Social interactions outside the mother-infant dyad, especially interactions with physical contact, seem to be rare between wild orangutans (Rodman, 1973; Rijksen, 1978; Galdikas, 1984; van Schaik and van Hooff, 1996). As mentioned by van Schaik *et al.* (2004), clear social bonds seem to be missing between adult individuals. Particular encounter behaviour, such as conspicuous greeting ceremony, between animals who meet each other after a period of separation is found to normally not occur (Rijksen, 1978). Grooming is reported anecdotally to occur between adolescent females (Galdikas, 1995), but generally it is described to be uncommon (van Schaik and van Hooff, 1996) or virtually absent (van Schaik *et al.*, 2004). In some studies, the pattern of individuals feeding and resting in spatial proximity (‘social feeding’, ‘social resting’) is regarded as social interactions (Riedler *et al.*, 2010) or is used as measures for affiliate relationships (Galdikas, 1984).

Associations of orangutans are defined by van Schaik (1999) and Knott *et al.* (2008) as such when individuals coordinate their movements within a distance of 50m between each other. Associations may contain all age/sex classes, with flanged males being the least sociable. Mean party size tends to be small, ranging between 1-4.25 individuals; larger aggregations may occur in large fruiting trees (Sugardjito *et al.*, 1987; van Schaik, 1999). Temporary parties (‘travel bands’, see te Boekhorst *et al.*, 1990) may last for some minutes, hours, or a few days up to maximally a few weeks; the frequency and duration of parties highly varies across the study sites (cf. MacKinnon, 1974; Rijksen, 1978; Galdikas, 1985a). Bornean orangutans were observed in association with conspecifics in a range of 0-40% of focal days

(Galdikas, 1985a; Sugardjito *et al.*, 1987; Mitani *et al.*, 1991), and Sumatran ones even in 57-80% (van Schaik, 1999). However, orangutans seem to do not encounter another conspecific every day (cf. Mitani *et al.*, 1991; Knott *et al.*, 2008). In their daily activity they spent below 1% on social activities (Knott, 1999).

Associations between adult females are found to be rare and not exceeding a few weeks (Rodman, 1973; Rijksen, 1978; Galdikas, 1984; van Schaik and van Hooff, 1996). Adolescent females seem to be the most gregarious age/sex class, participating in social groupings more often and for longer periods than others (Galdikas, 1995). Association patterns of adult female orangutans seem to be influenced by their age, reproductive status, age of dependent offspring, and probably relatedness, though kinship often is not fully known: descriptions range from active avoidance among some non-relatives (van Schaik, 1999; Knott *et al.*, 2008) to the formation of ‘nursery groups’ (Rodman, 1973; MacKinnon, 1974; Galdikas, 1984; van Schaik, 1999), to preferential associations among females relatives of a cluster (Singleton and van Schaik, 2002; Knott *et al.*, 2008).

The findings on female sociality indicate variable social relationships between females of a given study site, however, there are only little quantitative data: descriptions range from “indifference” (MacKinnon, 1974) over agonistic to affiliative (cf. MacKinnon, 1974; Rijksen, 1978; Galdikas, 1984; Rodman and Mitani, 1987; van Schaik, 1999). Some researchers suggest dominance relationships between certain females (Rijksen, 1978; Utami *et al.*, 1997; Knott *et al.*, 2008). At one site on Sumatra, Utami *et al.* (1997) described dominance hierarchies whereas Knott *et al.* (2008) did not determine a clear hierarchy for their site on Borneo. In none of the field studies either coalitions or alliances nor other indications for ‘supportive’ relationships have been found (for a review see van Schaik and van Hooff, 1996).

Referring to adult flanged males, several studies consistently show that they rarely encounter individuals of other age/sex classes (Rodman, 1973; MacKinnon, 1974; Galdikas, 1979, 1985b; Mitani, 1985b). They emit long calls, which might serve a spacing function between adult males (MacKinnon, 1974; Galdikas, 1983; Mitani, 1985a). Adult flanged males are reported to be highly intolerant of other flanged males and to have agonistic dominance relationships among each other (MacKinnon, 1974; Galdikas, 1985b; Mitani, 1985a). Playback studies by Mitani (1985a) on responses to long calls suggest individualised relationships. For some males, wounds and disfigurements from aggressive interactions have been

reported by Galdikas (1985b). However, Mitani (1990) assumed that direct confrontations or fights are often avoided.

Flanged males seem to be dominant over unflanged/subadult males but behave relatively tolerant if subadult males remain distant (Rodman, 1973; Galdikas, 1985b; Mitani, 1985b). Galdikas (1985b) found flanged males to be more aggressive in the presence of females in the form of chasing the other male, shaking branches, and emitting long calls. Subadult males are described to tolerate one another, and to occasionally form temporal associations during which they even engage in rough play interactions (Galdikas, 1985c).

Both adult and subadult males and adult females associate in consortships in the context of mating only (Schürmann, 1982; Galdikas, 1984). Galdikas (1995), however, found that subadult males and adolescent females may travel together for few weeks outside matings purposes. Male-female relationships are suggested to be individualised (van Schaik and van Hooff, 1996). Behavioural studies by Delgado and van Schaik (2000) on female responses to long calls showed that they avoided, approached or ignored the caller, depending on the social context and their reproductive status. During consortships, van Noordwijk and van Schaik (2009) and Schürmann (1982) observed some affiliative behaviours and instances of food sharing in the form of unopposed taking. However, van Schaik *et al.* (2004) assumed no consistent active affiliation to exist between males and females outside mating consortships.

Inter-species differences in social organisation

The two orangutan species show several phenotypic, behavioural, ecological and developmental differences e.g. in terms of diet, density, inter-birth intervals and culture (Wich *et al.*, 2009). Sumatran orangutans seem to be more gregarious than Bornean orangutans (Rodman, 1973; Galdikas, 1988; van Schaik, 1999; Delgado and van Schaik, 2000) due to both higher habitat productivity and orangutan density on Sumatra compared to Borneo. However, van Schaik *et al.* (2009) suggested that differences do not exist on the level of the social organization among the taxa but rather on a micro level adding up to substantial differences (for details see van Schaik *et al.*, 2009). For instance, in Sumatran populations, not only the density but also the size of female clusters tends to be larger, and encounters of individuals and party formation occur more frequently. In addition, associations involving adult females and

immature individuals tend to be more common and larger in mean party size (see review in Delgado and van Schaik, 2000).

Concerning socio-sexual strategies, Sumatran males seem to be capable of maintaining longer consortships, and forced copulations are reported to occur less often than in Bornean males (Galdikas, 1985c; Mitani, 1985b; Schürmann and van Hooff, 1986). Sumatran flanged males are assumed to have more stable dominance relationships and a more clearly identified dominant male being full-time resident in a local population. In Bornean flanged males, there is anecdotal evidence that they tend to be involved in escalated fights more often than Sumatrans (van Schaik *et al.*, 2009).

The cultural repertoires (e.g. tool using techniques) tend to be larger in Sumatran populations which might be due to the higher gregariousness involving greater opportunities for social transmission on Sumatra (van Schaik *et al.*, 2003).

Whether the inter-species differences and geographic variations can be linked to genetic differences and/or explained as local adaptations is still under discussion (van Schaik *et al.*, 2009). For both species it is assumed that they can not afford to live in permanent groups because their large body size entails high energetic demands for which ecological conditions are unfavourable due to widely dispersed food patches and seasonal fruit scarcities (Rodman, 1979; te Boekhorst *et al.*, 1990; Morrogh-Bernard *et al.*, 2009).

Captive orangutans

Orangutans have been kept worldwide in zoos since decades. The European Endangered Species Program (EEP) was established in 1989. At present, 155 Borneans (64.91) and 149 Sumatran (56.93) are held in 62 European zoos (Becker, 2009). On the population level, many of the adult females do not reproduce successfully and the total population still contains a high proportion of hand-reared animals. The population growth has stagnated since 1997 (Kaumanns *et al.*, 2004).

Captive orangutans are usually housed in stable groups the composition of which typically remains unchanged over years. Only few studies have been carried out about the social behaviour of orangutans under captive conditions (Bornean orangutans: Edwards and Snowdon, 1980; Poole, 1987; Beaver, 2000; Sumatran orangutans: Zucker *et al.*, 1986; Tobach *et al.*, 1989; Zucker and Ferrera, 1990; Zucker and Thibaut, 1995; Klein, 1999; Tobach and Porto, 2006). These studies revealed low rates of agonistic behaviour. Individuals were engaged in direct interaction much more often than their wild counterparts, and grooming was

not uncommon. In some groups, adult males were reported to engage in social interactions with females and juveniles often. Female-female and male-female social relationships showed a high degree of variability: some were affiliative, very few were (observably) agonistic, and some were “neutral” with individuals neither interacting sociopositively nor agonistically. However, recent hormonal analyses indicated that female Bornean orangutans tend to show a stress response when housed in permanent groups whereas Sumatrans do not (Weingrill and Heistermann, 2008). In a captive group of Bornean orangutans, Beaver (2000) assumed a correlation between social interactions and the level of abnormal stress-induced behaviour.

1.3. AIM OF THE STUDY

Derived from the spatiotemporal patterning in the wild, the social system of orangutans is classified as an individual-based fission-fusion system (van Schaik, 1999). Adult individuals are supposed to develop individualised relationships, and to form temporary parties with low rates of direct interactions (van Schaik and van Hooff, 1996; Delgado and van Schaik, 2000). In captivity, orangutans show higher rates of direct interactions. Edwards and Snowdon (1980) and Poole (1987) assumed that orangutans have the social potential to cope with the permanent presence of partners. Following the theoretical model of Aureli *et al.* (2008), orangutans might be described as a species with high fission-fusion dynamics. The findings on the behavioural ecology of orangutans as described above seem to be compatible with expectations derived from this concept. It is unknown, however, how orangutans regulate their social relationships on a proximate level under the situation of high fission-fusion dynamics and long periods of ranging solitarily. This includes both the patterning and structure of social relationships and possibly underlying mechanisms and principles.

The current study examined the socio-spatial relationships in zoo-living orangutans which are kept in groups on a proximate level, following the concept of social relationships by Hinde (1975). Different groups were chosen in order to obtain data from a larger sample size of individuals. It was assumed that the conditions of limited space, constant availability of food, and the permanent presence of partners may stimulate higher rates of social activities. This would allow describing detailed patterns of interactions, to draw inferences about possible underlying mechanisms and principles, and to investigate the persistence and form of fission-fusion tendencies.

This study aimed to contribute to the basic knowledge of the Bornean orangutan's social system, and sociality respectively. The study may convey resources concerning the question whether orangutans have the social potential to cope with the permanent presence of conspecifics under the limitations of captivity which may help to improve conservation oriented management. The results can also provide proximate referential data and inspiration for field studies.

The study examined the following issues and their underlying hypotheses based on the above described findings from the field and from previous captive studies:

- The individuals' sociability
 - ↳ the daily activity includes a high proportion of social activities
 - ↳ the frequency of agonistic interactions is low
 - ↳ atypical behaviours occur rarely
- The structure of social relationships
 - ↳ interactions between females occur more often than between males and females
 - ↳ physical contact is brief
 - ↳ physical contact occurs regularly but on a larger time-scale
 - ↳ triadic interactions are scarce
 - ↳ the quality of social relationships between adult individuals is maintained stable over time
- Fission-fusion tendencies
 - ↳ large interindividual distances alternate with spatial proximity
 - ↳ individuals 'associate' and 'split' on a regular basis with a short latency

2. ANIMALS AND METHODS

Observations were carried out at three different European Zoos: Chester Zoo (Chester, United Kingdom), Apenheul Primate Park (Stichting Apenheul/Apeldoorn, the Netherlands), and Cologne Zoo (Cologne, Germany). The colonies at Chester and Cologne lived under permanent and largely unchanged group-living conditions while the colony at Apenheul was kept under socially flexible conditions (separation management). The dataset comprised long-term observations at Cologne (June 2002 – Oct 2005) and shorter-time observations at Chester and Apenheul (two-month period each). Group compositions, keeping conditions, and procedures for data analysis are described in the following paragraph. Age class classifications are based on the definitions by Rowe (1996) and Kaplan and Rogers (2000).

2.1. ANIMALS AND KEEPING CONDITIONS

The three groups differed in their demography, husbandry, and the social management (see Tab. 2.1). At Cologne and Chester, individuals were kept in permanent groups. At Apenheul, the orangutans were kept in two or three subgroups, with the composition changing on a daily basis (separation management). At Chester, one individual was transferred to another zoo during the observation period. At Cologne, the group composition changed due to an animal transfer, one death, and independence of juveniles resulting in a change of subgroup-composition. Schematic plans of the enclosures are provided in the Appendix (Fig. 8.33–8.35).

	Chester	Apenheul	2002	Cologne 2003-04	2005
grouping	constant	flexible	constant	constant	constant
average density (ind/m ²)	0.008	0.009	0.011	0.010	0.008
average space (m ² /ind)	135.2	150.8	91.3	104.3	121.7
feeding	clumped	mainly clumped	scattered	scattered	scattered
enrichment	not daily	not daily	daily	daily	daily

Tab. 2.1: Keeping conditions overview

Climatic conditions of the indoor enclosures were similar in all facilities. The average density was calculated for the number of individuals per m² (ind/m²), and the amount of space per individual (m²/ind) respectively. ‘Not daily’ enrichment was provided every second to third day.

Chester

At Chester Zoo, two groups comprising two and three individuals were observed between May and June 2004. One group consisted of a subadult male – adult female pair; the other group comprised three maternally related sub-/adult females (Tab. 2.2). Except for the oldest adult female, all individuals were born at Chester Zoo and knew each other from infancy. The male-female pair was observed during 10 days; the male then was transferred to Norway and the remaining female was kept solitarily afterwards.

Identity	EEP no.	Age/sex class	Date of birth	Rearing	Parents (Sire; Dam)	Origin; comments
Martha (Ma)	806	AF	~1964	unknown	unknown	wild; multiparous
Sarikei (Sr)	1955	AF	22.11.1983	unknown	Dennis; Martha	Chester; primiparous
Leia (Le)	2760	SF	06.02.1996	mother	Anark; Martha	Chester; nulliparous
Matu (Mt)	2722	SM	26.11.1995	mother	Anark; Sarikei	Chester; transferred to Norway 17.05.2004
Pundu (Pu)	2261	AF	20.04.1989	mother	Anark; Lola	Chester; nulliparous

Tab. 2.2: Orangutans Chester Zoo

Age/sex classes: A=adult, S=subadult, J=juvenile, I=infant, M=male, F=female; EEP=European Endangered Species Program. Comments on the females' reproductive state refer to the time of this study.

The orangutans were housed in a facility comprising three in-line indoor enclosures with two enclosures of 115.8m² each and a middle enclosure of 171.8m². At the two outer enclosures, the animals had access to outdoor islands of 391.3m², and 282.4m² respectively. A group of Sumatran orangutans was separately housed in the same facility, and all groups changed into a different enclosure each week to provide them balanced access to the outdoor islands. A series of interconnected night beds on ground level were situated under the visitors' walkway. The outdoor islands were available during the entire observation period. The orangutans were let out of their night beds in the morning at approximately 09:00 a.m. after cleaning the indoor enclosures and laying out a scatter feed (seeds, nuts, raisins, and primate pellets, or chopped vegetables). Fire hoses filled with peanut-butter, foliage and/or iced fruits were offered regularly around midday or afternoon. The animals were kept in the

indoor enclosures and islands between 09:00 a.m. and 04:00 p.m. At 04:00 p.m. the orangutans were confined to their night beds and given their main portioned feeds. The individuals remained in the night beds until the next morning. Manipulable objects (gunnysacks, paper) were provided periodically.

Apenheul

At Apenheul, a colony comprising ten individuals was observed between August and October 2005. The group consisted of an adult male, five adult females, one subadult female, two juveniles and one newborn (Tab. 2.3). Four of the six adult individuals were wild-born. The subadult female and the juvenile male were born at Apenheul. The hand-reared juvenile female was medicated with a pharmaceutical due to a birth defect. She had been integrated into the group at the age of 1½ years and received support by one of the adult females (Sandakan). At the time of this study, the adult individuals knew each other for 4-6 years. Two females knew each other from their previous institution before arriving at Apenheul.

Identity	EEP no.	Age/sex class	Date of birth	Rearing	Parents (Sire; Dam)	Origin, comments
Karl (K)	839	AM	~1961	unknown	unknown	wild; at Apenheul since 1999
Radja (Ra)	842	AF	~1963	unknown	unknown	wild; at Apenheul since 1999; lactating
Silvia (Si)	833	AF	~Dec. 1965	unknown	unknown	wild; at Apenheul since 1999; multiparous
Sandakan (Sa)	1881	AF	29.04.1982	unknown	Giles; Bali	Jersey; at Apenheul since 1999; lactating
Ralfina (Fi)	2123	AF	~1986	unknown	unknown	wild; at Apenheul since 2001; pregnant
Jose (Jo)	2516	AF	15.09.1992	unknown	Pi-ku; Barbara	Rotterdam; at Apenheul since 2001; nulliparous
Katja (Ka)	2806	SF	17.05.1997	mother	Karl; Radja	Apenheul; nulliparous
Binti (Bi)	2973	JF	11.12.2000	hand	Tuan; Ralfina	at Apenheul since 2002
Willie (Wi)	3055	JM	17.04.2002	mother	Karl; Radja	Apenheul
Samboja (Sm)	3219	IF	09.06.2005	mother	Karl; Sandakan	Apenheul

Tab. 2.3: Orangutans Stichting Apenheul

Age/sex classes: A=adult, S=adolescent to subadult, J=juvenile, I=infant, M=male, F=female; EEP=European Endangered Species Program. Comments on the females' reproductive state refer to the time of this study. The newborn female Samboja was not observed as focal animal.

The orangutans were kept in a facility comprising four indoor enclosures of 57.7-58.8m² each and four bipartite outdoor islands of 254.3-358.7m² each. Eight separation-rooms (10-15m² each) were attached to the indoor enclosures with some of the rooms being interconnected. The individuals had access to one of the outdoor islands per indoor enclosure. These islands were permanently available for the individuals during the observation period. When a subgroup consisted of more than five individuals, they had access to two indoor enclosures and two outdoor islands.

The orangutans were confined into the separation rooms for a first individual feeding at 08:00 a.m. while the indoor enclosures were cleaned. Throughout the day, three additional feedings consisting of vegetables, salad, fruit, cheese and/or bread were offered indoors at the grid to the keeper's area at around 12:00 a.m., 02:00 p.m. 04:00 p.m. Additionally, primate pellets and grains were provided periodically as scatter feeding or were hidden in enrichment constructs (feeding boxes, knot-holes). The individuals remained in the indoor enclosures from 09:30 a.m. over night until the next morning. The outdoor islands were available to 04:00 p.m.

After cleaning procedures in the morning, the sliding-doors connecting the enclosures and the separation rooms were opened and the individuals were able to move freely within the enclosures. Based on the keeper's assessment, sliding-doors were locked when the individuals seem to be relaxed in the given group-constellation. The subgroups then remained in their composition until the next day. When individuals indicated tendencies to change their subgroup (e.g. sitting and waiting at a sliding-door), the composition was altered during the day again.

Cologne

The group at Cologne Zoo was observed between June 2002 and July 2005. For the main part of the study period, i.e. September 2003 to December 2004, the group consisted of seven individuals: one adult male, four adult females and two juveniles. For other parts of observations, the group consisted of eight, and six individuals (Tab. 2.4). Except for the adult male, all animals were born at Cologne Zoo and knew each other since their birth and/or infancy. Hand-reared individuals were integrated into the group at the age of 1½ – 2 years.

Identity	EEP no.	Age/sex class	Date of birth	Rearing	Parents (Sire; Dam)	Origin; comments
Bornie (Bo)	1989	AM	18/03/1984	unknown	Pi-ku; Barbara	transferred from Antwerp in 1994
Lotti (Lo)	1125	AF	29/01/1971	hand	Eddi; Petra	Cologne; multiparous; receiving contraceptive
Tjintah (Tj)	1974	AF	01/05/1984	hand	Maias; Tjantike	Cologne; lactating
Suka (Su)	1975	AF	06/05/1984	hand	Yogi; Lotti	Cologne; nulliparous; died in 2005
Nony (No)	2045	AF	28/10/1985	hand	Jonny; Nonja	Cologne; lactating
Sandai (Sa)	2617	SM	20/08/1993	hand	Tuan; Lotti	Cologne; transferred to France in 2003
Barito (Ba)	2960	IM - JM	16/02/2000	mother	Bornie; Nony	Cologne
Bunyu (Bu)	2961	IM - JM	05/03/2000	mother	Bornie; Tjintah	Cologne

Tab. 2.4: Orangutans Cologne Zoo

Age/sex classes: A=adult, S=adolescent to subadult, J=juvenile, I=infant, M=male, F=female; EEP=European Endangered Species Program. Comments on the females' reproductive state refer to the time of this study.

The group composition changed during the study period due to a transfer and a death of an individual. The group was separated into two subgroups which were reunited at the last part of the study period, enabling the formation of four different sub-groupings:

- 1) summer 2002: 8 individuals were kept in one group (Bo, Lo, Su, Tj, No, Sa, Ba, Bu)
- 2) autumn 2003 – autumn 2004: 7 individuals were kept separately in two subgroups of composition “a” (Bo, Lo, No, Ba & Su, Tj, Bu)
- 3) autumn 2004 – winter 2004: 7 individuals were kept separately in two subgroups of composition “b” (Bo, Lo, No, Ba, Bu & Su, Tj)
- 4) summer 2005: 6 individuals were kept in one group (Bo, Lo, Tj, No, Ba, Bu)

The orangutans were housed in a facility comprising a 245m² large indoor and a 485m² outdoor enclosure. It was possible to divide the indoor enclosure in two separate enclosures of 100m² and 145m². The bigger enclosure was connected with the outdoor enclosure through a bridge. When divided into two separate subgroups, the group-members had visual access with each other through a large window. Four sleeping cages (total of 74.5m²) were connected with the indoor enclosure, freely accessible for the animals throughout the day. During cleaning hours and individual feeding, the animals were kept in the sleeping cages. The

outdoor enclosure was available during good weather conditions from spring to early autumn.

The orangutans were confined into the sleeping cages for a first individual feeding at 08:00 a.m. while the indoor enclosure was cleaned. At 10:00 a.m., the individuals were let out of the cages and were offered a scattered feed of vegetables in the indoor enclosure. They were given two more main feeds in the cages at 12:00 a.m. and 04:00 p.m. Additionally, the keepers scattered grains, rice or seeds four times a day and foliage was provided at the ceiling. Movable objects filled with food such as vulcanite-tubes were provided periodically, while manipulable objects (gunnysacks, paper, and footballs) were offered on a daily basis. The individuals remained in the indoor enclosure from 10:00 a.m. over night until the next morning. The outdoor enclosure was available to 04:00 p.m.

2.2. METHODS

The sampling methods and the parameters analysed were chosen with the focus on the basic characteristics of the social relationships: the quality, frequency, duration, and reciprocity of interactions, triadic constellations, and the degree of spatial cohesion. All these aspects were additionally examined for a long-term period of time, due to technical reasons at the Cologne group only. The assumed fission-fusion tendencies were analysed with the focus on the spatial behavioural patterns and supplemented by temporal patterns of 'meetings'. The groups were compared due to the different local keeping conditions and possible effects on the animals' behaviour.

2.2.1. Data collection

At all three zoos, behavioural data were collected using focal animal sampling with continuous recording (Martin and Bateson, 1986). All individuals were observed for the same amount of time per day using detailed paper-protocols. The newborn female at Apenheul (see Tab. 2.3) was not observed as focal animal. The daily order of focal animals was varied randomly but was balanced. 10-min units were used as focal animal time in all settings. In order to examine behavioural sequences on a larger time-scale, units of 3-hrs focal observations were conducted at Cologne additionally. To examine the spatial patterns, in all groups the locations of all individuals were mapped using instantaneous scan sampling (Martin and Bateson, 1986) at 10-min intervals before and after each focal observation. At Cologne, the

positions of individuals were scanned every 10 minutes throughout the whole observation period, i.e. also during the 3-hrs focal observations. At all three zoos, observations were carried out five-six hours daily between 10:00 a.m. and 04:00 p.m.

The dataset presented in this study was collected during a total of 313 observation days, consisting of a total of 1,598hrs of focal observation, and a total of 10,030 position scans.

At Chester, data were collected during four observation units for a total of 33 days. Observations comprised a total of 164hrs of focal animal sampling, which were 144hrs on the all-female group (48hrs/ind) and 20hrs on the male-female pair-group (10hrs/ind). A total of 1,087 position scans were collected, 327 of which included the pair-group.

At Apenheul, data were collected during two units of 30 consecutive days each. Observations comprised a total of 270hrs focal animal sampling (30hrs/ind) and a total of 1,757 position scans.

At Cologne, data were collected during a total of 220 days between June 2002 and July 2005. The main study period (September 2003 to December 2004) contained eight observation units consisting of 18 days each, and 15 days respectively, during which data were collected with 10-min focal time units (“AI-VIII”). These sessions were altered with eight periods (“BI-VIII”) during which behavioural data were collected using 3-hrs focal time units:

session	time period	session	time period
A 0	June – Aug 2002		
A I	Sep – Oct 2003	B I	Oct – Nov 2003
A II	Nov – Dec 2003	B II	Dec 2003
A III	Feb 2004	B III	Feb – Mar 2004
A IV	Mar 2004	B IV	Mar 2004
A V	Aug 2004	B V	Aug 2004
A VI	Oct 2004	B VI	Oct – Nov 2004
A VII	Nov 2004	B VII	Nov 2004
A VIII	Nov – Dec 2004	B VIII	Dec 2004
A IX	June – July 2005		

At sessions A0 and AIX, the individuals were kept all together in one group. At sessions AI-AVIII they were kept in two subgroups. During the gap between periods AIV and AV, one of the juvenile males was removed from one subgroup and introduced into the other one.

The outdoor enclosure was available at sessions A0, AV-VI, BV-VI, and AIX. At sessions V-VI, only the larger group had access to outdoors due to the subdivision of the enclosure.

Observations comprised a total of 828hrs via the 10-min focal units, and a total of 336hrs via the 3-hrs focal units (in sum 1,164hrs). Per individual, the 10-min sampling comprised observations of 120hrs/ind for six of the animals; the subadult male was observed for 6hrs and the female which died in 2005 for 102hrs. The 3-hrs sampling comprised 48hrs/ind. A total of 7,186 scans were collected. Session A0 comprised 304 scans, AIX comprised 666 scans, and A/BI-A/BVIII comprised 6,216 scans altogether.

2.2.2. Ethogram

The ethogram was based on behavioural descriptions by Rijksen (1978), Maple (1982), Poole (1987), and Liebal *et al.* (2006), and was supplemented by personal observations (Claßen, 2001). A set of 64 distinct social behavioural elements was used for observations. Additionally, a set of 27 non-social activities was used which were taken into account for analysis of activity profiles. Behavioural elements referred to in the text are given in italics.

For social activities, the identity of the sender and recipient as well as the identity of additionally involved partners were noted. An animal was recorded to be ‘out of sight’ when it was located in a sleeping cage and/or parts of its body were hidden by structures of the enclosure or by a conspecific so that his behaviour could not be recorded.

An abridged version of the ethogram is given in Tab. 2.5; detailed definitions of behaviours are provided in the Appendix (page 113 ff). For further analysis, the social behavioural elements were grouped into broader categories which were used in the results (see Tab. 2.5). The behaviours were scored as one event of defined duration, of endless duration respectively, until a break of at least 5 s or a switch to another class of behaviour occurred.

Based on descriptions by Riedler *et al.* (2010), a behavioural sub-category was furthermore used as intermediate between non-social and social elements, that was ‘*non-social in proximity*’: non-social activities were performed within arm’s reach to at least one other conspecific, then called e.g. *social feeding*, *social resting*. These behaviours may indicate social tolerance and attraction between individuals. For activity profiles these elements were included to the above-main category but they are also presented separately in Chapter 3.1.

Social activities	
<i>sociopositive</i>	<i>long physical contact</i> : allogroom*, sit in contact*, lean arm on*, embrace, tandem, social play contact* <i>short contact</i> : touch, make contact, kiss, beg, share/give food <i>without physical contact</i> : beg no-contact, share food no-contact, social play no-contact*, play-invitation interaction with newborn
<i>follow</i>	moving behind in a distance of 5 m max. into the same direction*
<i>approach</i>	approach with normal pace, advance with normal pace
<i>leave</i>	leave arm's reach with normal pace
<i>agonistic</i>	<i>mild dominant</i> : displace, scuffle, push back-contact, push back-no contact, grasp, draw, threaten/bite intention <i>serious dominant</i> : chase, bite, hit <i>mild submissive</i> : retreat from s.o., retreat without previous approach, give precedence to s.o., shrink back/flinch <i>serious submissive</i> : flee, flee without previous approach
<i>sexual</i>	genital inspection contact *, genital inspection no-contact *, positioning, copulation-trial*, copulation *, rape *, present, genital rubbing at s.o. *, urine drinking
<i>others</i>	pass by, graze, hold out hand, take food/food-object/object away, take food/object intention, teasing (hair-tease, pelt object/substrate at s.o.)
<i>maternal</i>	nipple contact, carry, collect, rest whilst clinging at the other's body
<i>triadic</i>	intervene interaction B-C, positioning between B-C, approach for support, displace B from C, grooming between A-B-C, contact between A-B-C, social play between A-B-C
<i>proximity</i>	stay within arm's reach without any other behaviour *
Non-social activities (outside arm's reach to another group mate)	
<i>locomotion</i> *	
<i>food-related</i> *	forage, hidden forage, carry food, feed / drink, hidden feed
<i>resting</i> *	rest, hidden rest, nesting
<i>manipulate</i> *	object manipulation, tool use
<i>autogroom</i> *	
<i>solitary/object play</i> *	
<i>visitor-directed</i> *	
<i>monitoring</i> *	monitoring surroundings, monitoring visitors in a distance >1.5m
<i>other</i>	urinate, masturbate*, self-inspection*, interactions with non-conspecific animals, display*, call, patrol
<i>aberrant behaviours</i>	biting off hair*, regurgitate ^a , lap pap, stereotypy*, coprophagy

Tab. 2.5: Ethogram - behavioural categories and included elements

Behaviours for which also the duration of the bout was recorded are marked by an asterisk; ^a: each case was recorded as a single event.

2.2.3. Data analysis

In order to investigate the individuals' sociability under group-living conditions and limited available space, activity profiles of social and non-social behaviours, the occurrence of *aberrant* behaviours, and the time spent on *non-social activities in proximity* were analysed.

To examine the structure of the social relationships the patterns of dyadic interactions were analysed. For each dyad, the mean hourly frequency and in some cases the duration (see Tab. 2.5) of each behavioural element was calculated. For comparisons of the groups, and certain classes of dyads respectively, dyadic values were averaged. Giving hints on whether pairs of individuals interacted with each other preferentially, the frequency of *grooming* was compared between dyads composed of adult individuals per group. For the male-female dyads at Apenheul and Cologne, this was also done for *sexual* interactions; in case of the Cologne group, only dyadic values of the periods in which individuals were kept in one large group were included. In order to examine whether the structure of social relationships changed in the course of time, long-term observations were carried out at Cologne during ten observations session including four different grouping situations (see Chapter 2.2.1.).

To assess whether a type of interaction was evenly distributed within dyads, a reciprocity index (see Silk *et al.*, 2006) was calculated for *grooming*, *touching* and *dominant/submissive agonistic* behaviours. The following formula (Silk *et al.*, 2006) was used:

$$(I_{a \rightarrow b}) / (I_{a \leftrightarrow b}) - (I_{b \rightarrow a}) / (I_{a \leftrightarrow b}).$$

This index also provides information about which of the partners was the more active participant. The index ranges from -1 to 1 with being 0 when the active-passive relation concerning a given type of interaction (I) was equally distributed between two partners (a, b), and being -1 and 1 when the interaction was completely performed by one of the partners actively.

A *triadic interaction* was defined as such when other partners joined in an interaction between the individuals A and B (e.g. intervention to aid in an *agonistic* interaction within 30 s; join in *grooming* bout between A and B by *grooming* or being *groomed*).

In case of the Cologne group, data from the 10-min units of focal observations were averaged over the sessions AI-VIII. The different sessions are presented separately in more detail as long-term observations. Data recorded via the 3-hrs focal units are presented in Chapter 3.4.

To make inferences about whether the spatial behavioural patterns resembled fission-fusion patterns, interindividual distances were calculated per dyad. In addition, to investigate an animals' neighbourhood irrespectively of another partners' identity, 'nearest neighbour distances' (White and Chapman, 1994) were calculated for every individual. In order to examine the neighbourhood in relation to another partners' age/sex class, a proximity index following Furuichi and Ihobe (1994) and Stevens *et al.* (2006) was calculated. The proximity index (P) for each dyad was determined by the number of 10-min scans in which the two partners were found within a distance of 3m from each other, divided by the total number of scans. Markov analysis (Martin and Bateson, 1986) following White and Chapman (1994) was applied to test whether the short-term sequence of the presence and absence of a neighbour within 0-3m was non-random. Supplementary, temporal patterns of 'meetings' were analysed using the dataset of 3-hrs focal observations from the Cologne group. The latency between two consecutive *grooming* events during a given 3-hrs unit, and *approaching* respectively, was calculated.

In order to identify differences between the groups in relation to local keeping conditions as well as age/sex class specific patterns, between-group and within-group comparisons were carried out. In case of dependent offspring (younger than five years, see Munn and Fernandez, 1997) and their mothers, the following *maternal* behaviours were included into the calculation of social activity rates, and into the category of *sociopositive* interactions respectively: *carry infant*, *rest in contact with mother/infant*, *take and hold infant/clinging at mother*, *nipple-contact*. They were however not analysed in further detail. Data from the male-male relationship at Cologne in 2002 are not included into figures and statistic analyses due to the lack of other male-male relationships to compare with, and due to the short-time period of observation. Essential aspects concerning this dyad are mentioned as referential data.

For age/sex class comparisons data were grouped into 6 categories of dyads: sub-/adult males, sub-/adult females, sub-/adult male and sub-/adult female, juveniles, sub-/adult female and juvenile, sub-/adult male and juvenile. The infants were included to the age class of juveniles in the analysis of behavioural data. For statistic testing of behavioural data, however, only dyads involving at least one sub-/adult individual and age/sex classes comprising at least two dyads were included, giving a total number of 62 dyads.

First analyses of spatial data revealed that the distances between dependent offspring and non-mothers highly corresponded to those between the mothers and non-mothers ($\tau=0.8773$, $p<0.001$). Thus spatial data from the mothers and their dependent offspring were lumped together. At Apenheul, a similar pattern applied for the hand-reared juvenile female and an adult female (dyad Sa-Bi); the latter was not the biological mother but was giving support to the juvenile, and their spatial data were highly correlated ($\tau=0.6816$, $p<0.001$). Values referred to in the text are abbreviated for the zoo-groups as follows: Chester=CE, Apenheul=AH, and Cologne=CN.

Behavioural data were computerised using the software 'Monkey Business' (© Weißhaar, 2004) which is a program for the structured storage of behavioural datasets. 'Monkey Business' enables various queries on datasets. Individual positions of the animals were computerised using the software 'Animal Tracker' (© Blessing, 2003) which calculates interindividual distances. For further analysis of behavioural and spatial data Excel 2003 (Microsoft® Corporation) was used. For statistic analyses SPSS 10.0 (© SPSS Inc., 1997) and SsS 1.1m (© Rubisoft, 1998-2005) were used.

Data were tested using Kolmogorov-Smirnov for normal distribution (significant level was set at $p<0.05$). When data were normally distributed, mean values and standard deviation were used; otherwise, median values, quartiles, minimum and maximum values were used. Significant differences between groups and age/sex classes were tested using One-way ANOVA (normal distribution) and the Kruskal-Wallis test (not normally distributed) with a post-hoc all pair-wise comparison (Tukey test, and Dunn's test respectively). An independent t-test and the Mann-Whitney U test were applied for comparisons between two units. To test for significant differences within age/sex classes and between dyads, the Friedman test and post-hoc all pair-wise comparison (Dunn's test) was used (see Siegel, 1988). In case of interindividual distances, comparisons between dyads were carried out when median distances differed for at least one metre.

For the long-term dataset from Cologne, paired-sampled t-tests, the Friedman test, and a Wilcoxon pair-wise comparison were applied for comparisons between the different observation periods and for comparisons between the two focal time methods.

Significant levels were all set at $p<0.05$. A trend was defined as a level of $p<0.1$ and is mentioned at the appropriate location.

3. RESULTS

The daily activity rates of the orangutans were analysed per group. The social relationships between the individuals in the observed groups are described comparatively with regard to characteristic aspects of interactive behaviour and spatial behavioural patterns. These aspects are presented for the Cologne group referring to the long-term series of observations additionally.

3.1. ACTIVITY PROFILES

An overview of the activity profiles per group is provided giving the amount of time individuals were engaged in social and non-social activities in the three zoos. Furthermore, the proportion of time the animals were engaged non-interactively but *within arm's reach* is described. Non-social activities were grouped into eleven broad categories. Social behavioural elements were clustered to 'social interactions'.

Individuals spent on average 15% of their time on social interaction (see Fig. 3.2; CE: 4%, AH: 15%, CN: 25%). Between-group comparison revealed that animals at Cologne spent significantly more time on social interactions than animals at Chester (One-way ANOVA: $F=4.333$, Tukey test CN vs. CE: $p<0.05$), but not significantly more time than those at Apenheul (Tukey test CN vs. AH and AH vs. CE: $p>0.2$). Individuals at Apenheul spent more time *sitting within another's arm's reach* (12% of time) than individuals at Chester but not more time than at Cologne (One-way ANOVA: $F=4.746$, Tukey test AH vs. CE: $p<0.05$, AH vs. CN: $p>0.1$). However, there was much individual variation within the groups especially referring to the time spent on social interactions (standard deviation of 10-15% at Apenheul and Cologne).

Concerning non-social activities, individuals spent the majority of their time on activities such as *resting* (20%), *feeding* (14%), and *monitoring* (13%) their surroundings. Comparing the groups, individuals at Chester and Apenheul spent more time on stationary behaviours (e.g. *resting*, *monitoring*, *autogrooming*) than individuals at Cologne and most of these differences were significant (One-way ANOVA and Tukey test, see Fig. 3.2).

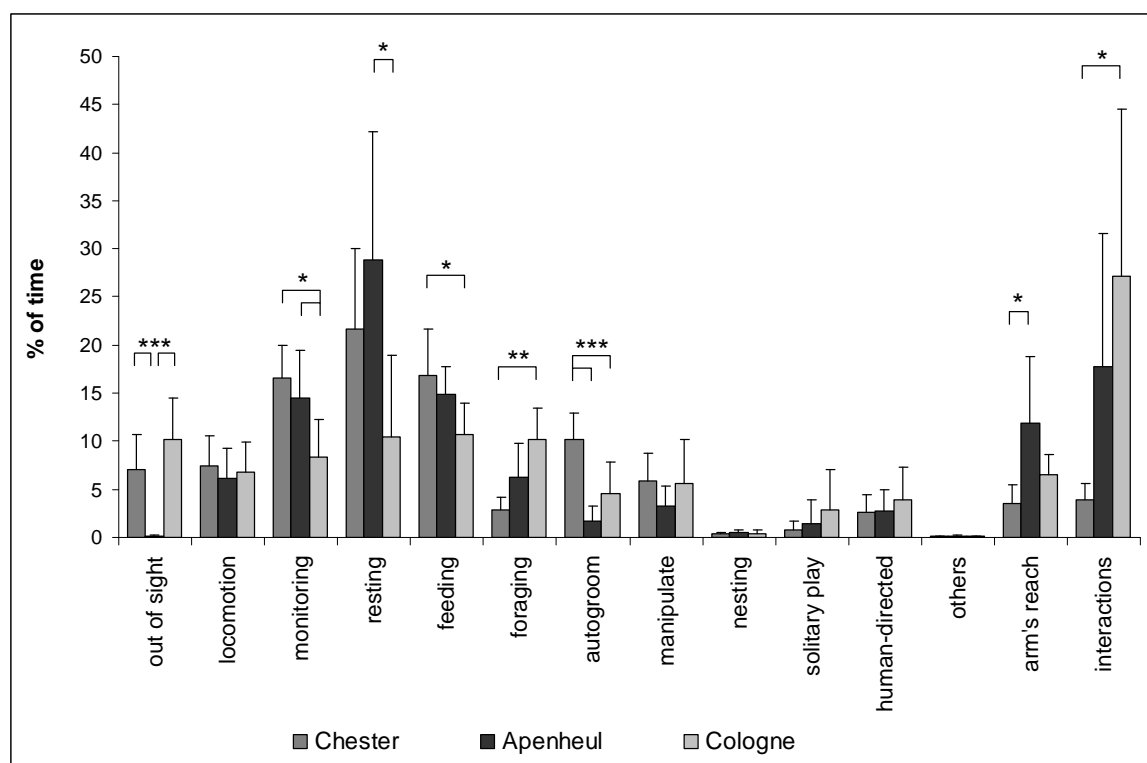


Fig. 3.2: Activity profiles per group

Percentage of time individuals spent on non-social and social activities is shown, averaged across all individuals. Mean values are given; error bars indicate the standard deviation. Mother-infant behaviours are included into the category of interactions. One-way ANOVA: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.005$.

Non-social activities in proximity

Extracted from the main categories of non-social activity described above, the proportion of those activities which were performed in proximity was calculated. Individuals spent 9-21% of their time on *non-social activities within another's arm's reach* (see Fig. 3.3). Although individuals of the Chester group spent compared to the other groups on average a relatively small amount of time on social interactions (cf. Fig. 3.2) they spent significantly more time on *social feeding*, *social resting*, or *social autogrooming* etc. (one-way ANOVA: $F = 5.791$, $p < 0.05$; Tukey-test CE vs. AH: $p < 0.1$, CE vs. CN: $p < 0.05$).

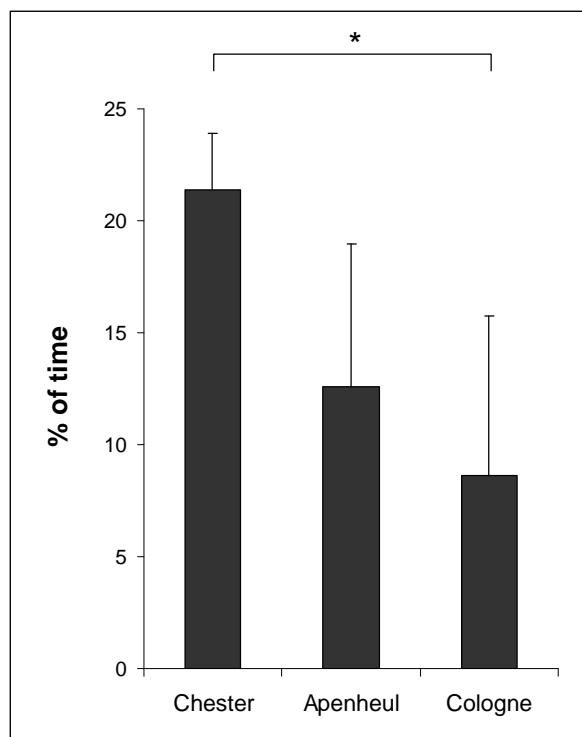


Fig. 3.3: Non-social activity in proximity per group

Percentage of time individuals spent on non-social activities within another's arm reach is shown, averaged across all individuals. Mean values are given; error bars indicate the standard deviation. One-way ANOVA: * $p < 0.05$.

A more differentiated picture of the types of behaviours exhibited within proximity is given in Fig. 3.4. In all groups, *social resting* made up the main proportion of time of all *non-social activities within another's arm's reach*. This tendency was most pronounced at Chester and Apenheul (CE: 56.7%, AH: 54.4%, CN: 27.2%). *Social feeding* frequently occurred in all groups as well, ranging between 37.5 – 41.7% on average; though individual variation was high (standard deviation: 14-18%).

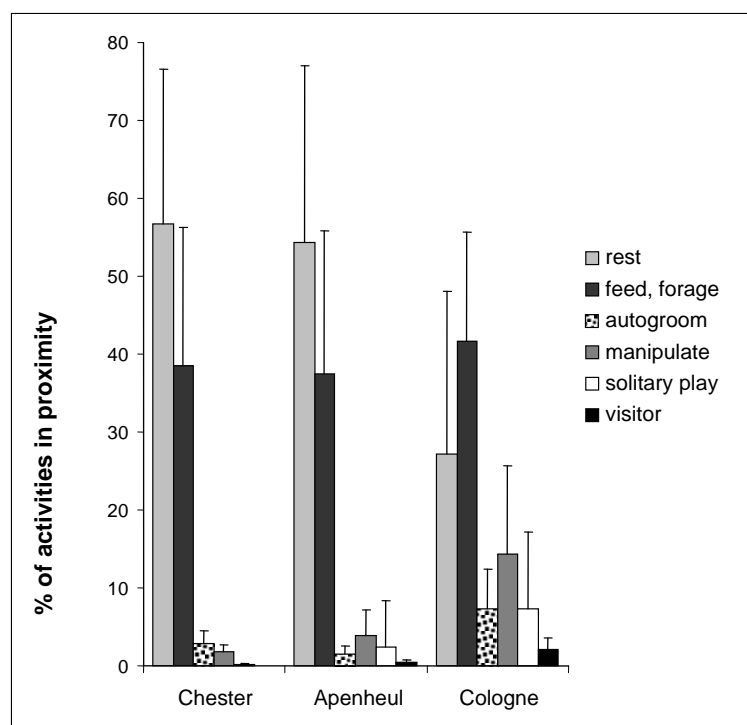


Fig. 3.4: Non-social activities in proximity per group detailed

Proportion of main non-social activities on the total of non-social activities within another's arm's reach is shown, averaged across all individuals per group. Mean values are given; error bars indicate the standard deviation.

Aberrant behaviours

Aberrant behaviours were observed in only a few individuals, mainly in female ones (Tab. 3.6). At Cologne, individuals showed *aberrant* behaviours most often, i.e. on average 1.9 times/h. Three out of four females *regurgitated* up to 4 times/h. In addition, one of the females sometimes *bit off her hair* and a second female showed *stereotype* locomotion almost 3 times/h. These females spent about 2%, and 3% respectively of their time on these *aberrant* behaviours. At Chester, individuals showed *aberrant* behaviours on average 0.2 times/h. *Stereotypy* was found in the oldest female with a low frequency and even less often in the subadult male. The subadult female was *biting off hair* only a few times (about 1 time/h). At Apenheul, *aberrant* behaviours were rarely observed, on average 0.03 times/h per individual.

		regurgitating, eating pap		stereotypy		biting off hair		biting off hair pre- sumed *		coprophagy	
		n/h	min/h	n/h	min/h	n/h	min/h	n/h	min/h	n/h	min/h
Chester	Martha			0.7	0.6						
	Sarikei										
	Leia					0.9	0.4	0.4	0.2		
	Matu			0.3	0.1			0.1	0.1		
	Pundu										
Apenheul	Karl	0.1	0.01	0.1	0.02						
	Radja										
	Silvia	0.1	0.03								
	Sandakan										
	Ralfina										
	Josje										
	Katja										
	Binti Willie									0.03	0.01
Cologne	Bornie										
	Lotti										
	Tjintah	4.1	1.5	2.8	2.1						
	Suka	0.3	0.1								
	Nony	4.6	1.4			0.7	0.9	0.4	0.4		
	Barito Bunyu	0.1	0.01								

Tab. 3.6: Frequency and duration of aberrant behaviours

Mean frequencies (n/h) and duration (min/h) of aberrant behaviours are shown per individual. A blank cell indicates that the behaviour was not observed during the observation period. *: the behaviour could not be observed reliably (see ethogram, pp. 113).

3.2. SOCIAL BEHAVIOUR

The patterns of social behaviour with regard to the overall social activity per group and per age/sex class composition of dyads are described. It is focused on the type of activity, and the overall frequency and duration of dyadic interactions. The dyadic interactions per age/sex class and individual are subsequently presented in more detail followed by a description of *triadic* interactions. A detailed picture of the interactive patterns between the individuals at Cologne for the long-term observations is given at the end of this chapter.

3.2.1. Overview

In all groups, the most frequent activities were *approaching* and *leaving* a partner (Fig. 3.5). Summed, these behaviours made up 59% at Chester, 45% at Apenheul and 40% at Cologne on the total number of social events within a given dyad. *Agonistic* interactions occurred much more rarely than *sociopositive* interactions, ranging between 6% at Chester and 3% at Apenheul and Cologne. Contrary, *sociopositive* interactions made up half of all interactions at Cologne (50%). *Maternal* behaviour made up 10% between the two mother-offspring dyads at Cologne, and 13% in the dyad at Apenheul. *Following* was rarely observed, as were *sexual* and *other* behaviours. The proportion of all these behaviours did not differ significantly between the groups (One-way ANOVA: $F=0.882 - 2.149$, all $p>0.05$).

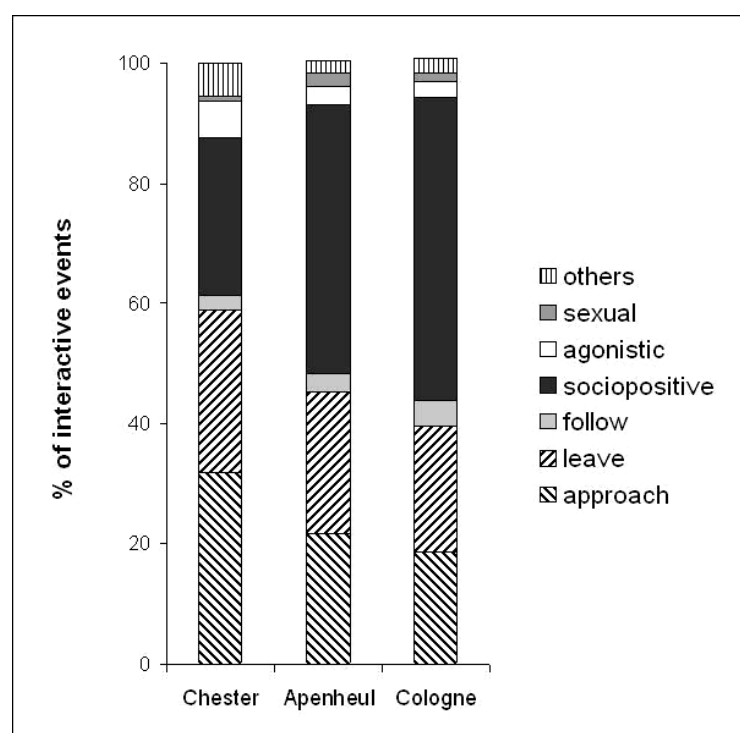


Fig. 3.5: Mean proportion of social activities per group.

Mean values for the proportion of social activities on the total number of interactive events are shown, averaged across dyadic values per group. Maternal behaviour was included to sociopositive behaviours. One-way ANOVA: all $p>0.05$.

Referring to the total frequency and duration of interactions (Fig. 3.6), partners of given dyad interacted on average 4.2 times/h and for 0.7 min/h with each other (median values and averaged across all dyads). Comparing the groups, individuals at Chester interacted almost

three times more often than animals at Apenheul and Cologne. Between-group comparison revealed significant differences neither in the frequency of interactions nor in the duration (Kruskal-Wallis: frequency: $H=2.191$; duration $H=1.131$; $p>0.05$). However, the variation between dyads and within a given dyad per time unit was high.

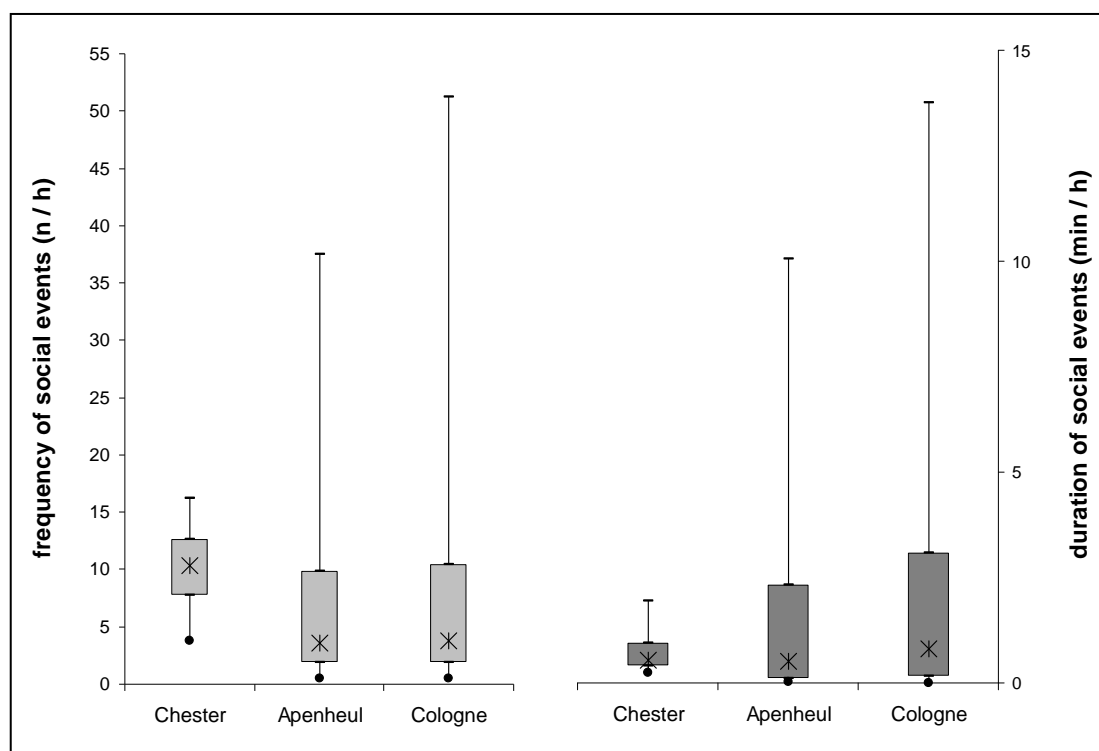


Fig. 3.6: Frequency and duration of social events between individuals per group.

Medians, quartiles, minimum and maximum values are shown, averaged across all dyads; left side= frequency medians (n/h); right side= duration medians (min/h). All types of dyadic interactions are summed including mother-infant behaviours; sit within arm's reach is not included. Kruskal-Wallis: all $p>0.05$.

Concerning dyads consisting of sub-/adult individuals (Fig. 3.7), females at Apenheul and Cologne interacted twice as often with another female than with a male, i.e. about 4-5 times/h (median values). In both groups, males and females interacted about 2 times/h with each other. Referring to the median duration of interactions, interactions between sub-/adult individuals were generally short. Females at Cologne spent on average 0.9 min/h on interacting with another female, at Chester only 0.5 min/h, and at Apenheul only some seconds. In all groups, interactions within male-female dyads lasted for a few seconds per hour. At Apenheul and Cologne, females interacted three times longer with another female than with

a male. At Chester, there were not that clear differences between the sex-classes, however, there was only one male-female dyad.

Comparing female-female dyads between the groups, and male-female dyads respectively (Fig. 3.7), there were significant differences neither in the frequency of interactions (Kruskal-Wallis, CE vs. AH vs. CN: F-F: $H=1.226$; Mann-Whitney, AH vs. CN: M-F: $U=22.000$; $p>0.05$) nor in the duration of interactions (Kruskal-Wallis, F-F: $H=1.239$; Mann-Whitney, M-F: $U=23.000$; $p>0.05$).

Within-group comparison showed that there was much variation between female-female dyads and between male-female dyads. Statistic testing revealed significant differences between female-female and male-female dyads within a group neither concerning the frequency of interactions (Mann-Whitney, F-F vs. M-F: AH: $U=25.000$, CE: $U=16.000$; $p>0.05$) nor concerning the duration (Mann-Whitney, F-F vs. M-F: AH: $U=27.000$, CN: $U=18.000$; $p>0.05$).

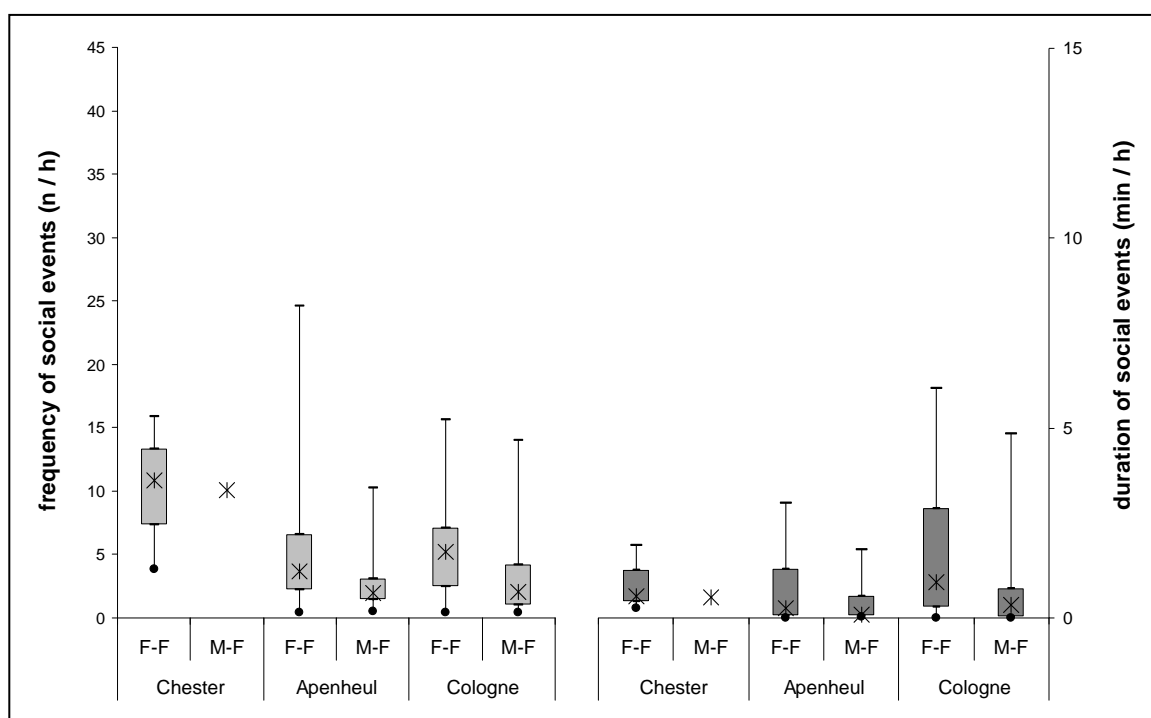


Fig. 3.7: Frequency and duration of social events between adult individuals.

Medians, quartiles, minimum and maximum values for female-female and male-female dyads are shown, averaged across the dyads of the respective sex-class; left side= frequency medians (n/h); right side= duration medians (min/h). All types of dyadic interactions are summed. Kruskal-Wallis and Mann-Whitney U for between-group and within-group comparisons: all $p>0.05$.

Compared to dyads composed of sub-/adult individuals, juveniles interacted much more often and longer with each other and also with sub-/adult partners at Apenheul and Cologne (Fig. 3.8). At Apenheul and Cologne, interactions in which juveniles were involved occurred on average 10.5 times/h and lasted for 3.4 min/h.

Between-group comparison of female-juvenile interactions, and male-juvenile respectively (Fig. 3.8), showed significant differences neither in the frequency of interactions (Mann-Whitney, F-J: AH vs. CN: $U=38.000$; M-J: AH vs. CN: $U=4.000$; $p>0.05$) nor in the duration (F-J: AH vs. CN: $U=38.000$; M-J: AH vs. CN: $U=1.000$; $p>0.05$). Among female-juvenile dyads there was much variation partly influenced by the mother-offspring dyads representing the maximum values of interactions. Within-group comparison of female-juvenile and male-juvenile interactions did not reveal significant differences either concerning the frequency of interactions (F-J vs. F-M: AH: $U=4.000$; CN: $U=7.000$; $p>0.05$) or concerning the duration (AH: $U=4.000$; CN: $U=8.000$; $p>0.05$).

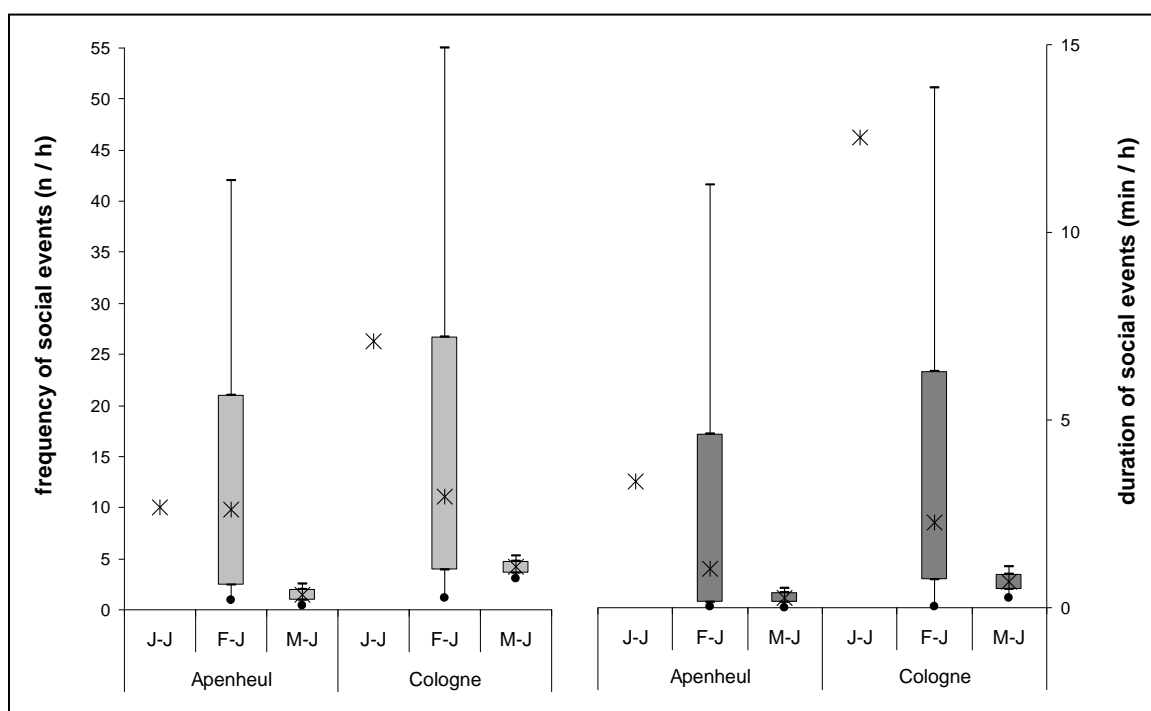


Fig. 3.8: Frequency and duration of social events between adult and juvenile individuals.

Medians, quartiles, minimum and maximum values for juvenile-juvenile, female-juvenile and male-juvenile dyads are shown, averaged across dyads of the respective age/sex class; left side= frequency medians (n/h); right side= duration medians (min/h). Data for female-juvenile dyads include mother-offspring dyads. All types of dyadic interactions are summed. Mann-Whitney U for within-group and between-group comparisons: all $p>0.05$.

Age and sex class comparison within the groups at Apenheul and Cologne (cf. Fig. 3.7, Fig. 3.8) revealed no significant differences in the median frequency of interactions and either in the median duration (Kruskal-Wallis, F-F vs. F-M vs. F-J vs. M-J: frequency: AH: $H=4.668$; CN: $H=5.350$; duration: AH: $H=4.918$; CN: $H=3.937$; all $p>0.05$).

3.2.2. Dyadic interactions

An overview of the interactions within a given dyad per age/sex class and per group is presented. The content of two pivotal behavioural categories, i.e. *sociopositive* and *agonistic* interactions, is described in more detail then. Additionally, active-passive relations within dyads are presented for these categories based on reciprocity indices (Appendix Tab. 8.26).

Female-female relationships

In all groups, sub-/adult females predominantly *approached*, *left* each other and interacted *sociopositively* (Tab. 3.7). At Chester, females *approached* each other significantly more often than females at Apenheul and Cologne (Dunn's test, $p<0.05$). In the latter two, partners *approached* and *left* one another 1.2 times/h each whereas at Chester females *approached* 3.5 times/h. Statistic comparison revealed almost no significant differences between the groups (except *approaching*, see Tab. 3.7).

	Chester		Apenheul		Cologne		sign. difference	
	n/h	min/h	n/h	min/h	n/h	min/h	n/h	min/h
approach	3.50	-	1.15	-	1.32	-	CE>AH, CE>CN	-
leave	3.08	-	1.23	-	1.19	-	no *	-
follow	0.24	0.03	0.07	0.01	0.10	0.04	no	CE>AH
sociopositive	2.65	0.35	0.93	0.17	2.26	0.82	no	no
agonistic	0.52	-	0.10	-	0.08	-	no	-
sexual	0.10	0.01	0.07	0.01	0.08	0.02	no	no
others	0.71	0.03	0.12	0.01	0.17	0.01	no	CE>AH, CE>CN

Tab. 3.7: Interactions within female-female dyads

Average median values of frequency and duration of female-female interactions per group are shown. Kruskal-Wallis and post-hoc Dunn's test for between-group comparison with $p<0.05$. *Kruskal-Wallis significant but post-hoc not significant.

Sociopositive interactions occurred more often than *approaches*, i.e. 2.0 times/h averaged across groups (Tab. 3.7). At Chester, where all three females were related, *sociopositive* interactions occurred neither much more frequently nor for longer duration than at Apenheul and Cologne where females were largely unrelated. At Cologne, where females spent the highest amount of time on *sociopositive* interactions, they did so less than 0.9min/h. At Apenheul, females just spent seconds on *sociopositive* interactions. Females rarely interacted *agonistically* with each other (mean, 0.2 times/h), most often at Chester.

Sociopositive

In almost all dyads, *touching* was the most frequent *sociopositive* interaction, with a mean rate of 0.7 times/h. *Begging* and *food-sharing* occurred in almost all dyads (mean, 0.3 times/h), most often between females at Apenheul (Tab. 3.8). *Grooming* (mean, 0.3 times/h) and *sitting in contact* (mean, 0.5 times/h) were most pronounced between females at Cologne, but differences between the groups were not significant (Kruskal-Wallis, $p > 0.05$).

Within all groups, there were one or two dyads in which partners frequently *groomed* (0.7 - 1.6 times/h), some dyads in which partners rarely *groomed* (0.03 - 0.33 times/h), and about one-third of dyads in which no *grooming* occurred (Tab. 3.8). At Cologne, Friedman test revealed no statistic differences between the dyads in the frequency of *grooming* ($F=8.731$, $p > 0.2$). At Apenheul and Chester, there were few significant differences. At Chester, the oldest female and her subadult daughter (Ma-Le) *groomed* each more often than they did with the other daughter, and sister respectively ($F=92.982$, $p=0.000$; Ma-Le vs. Ma-Sa: $Q=3.184$, Ma-Le vs. Sa-Le: $Q=3.001$, $p < 0.05$). At Apenheul, statistic differences were only found between the dyad with the highest *grooming* rate and one of the dyads in which no *grooming* was observed ($F=68.616$, $p=0.000$; Si-Jo vs. Ra-Sa: $Q=1.410$, $p < 0.05$). Within all groups, the mean duration of *grooming* did not exceed 0.9 min/h except of three dyads in total. The longest duration of *grooming* (2.8 min/h and 5.6 min/h) was found in two dyads at Cologne.

	F-F	groom		contact		social play		touch	beg, share food
		n/h	min/h	n/h	min/h	n/h	min/h	n/h	n/h
Chester	Ma-Sr			0.03	0.01	0.11	0.02	0.08	0.14
	Ma-Le	1.13	0.84	1.13	0.54	0.45	0.09	2.93	0.59
	Sr-Le	0.03	0.01	0.08	0.02	0.35	0.16	0.90	1.21
Apenheul	Ra-Ka	0.20	0.39	0.27	0.36			0.13	0.30
	Ra-Sa							0.10	0.10
	Ra-Fi								0.04
	Ra-Jo								
	Ka-Sa	0.25	0.06	0.45	0.12			0.60	0.30
	Ka-Fi								0.18
	Ka-Jo								
	Sa-Fi			0.17	0.11			0.42	0.20
	Sa-Si			1.75	0.77			3.13	0.13
	Sa-Jo	0.33	0.72	1.84	1.06	0.37	0.19	1.18	0.61
	Fi-Si	0.25	0.83	0.45	0.18	0.05	0.01	0.40	0.20
	Fi-Jo							0.33	
	Si-Jo	0.72	1.46	0.98	0.57	0.02	0.01	0.91	0.29
Cologne	Lo-No	1.56	5.58	0.41	0.09	0.02	0.01	0.65	0.14
	Lo-Su			0.17	0.11			0.25	
	Lo-Tj	0.25	0.35	0.54	0.23			0.67	0.22
	No-Su								
	No-Tj	0.10	0.05	0.87	0.42	0.72	0.48	0.92	0.54
	Su-Tj	0.84	2.82	0.90	0.33	0.04	0.03	2.11	0.50
Kruskal-Wallis H	1.583	1.508	0.638	0.200	7.311	6.916	1.609	2.582	
p	n.s.	n.s.	n.s.	n.s.*	CE>AH	CE>AH	n.s.	n.s.	

Tab. 3.8: Sociopositive interactions within female-female dyads

Mean frequency and duration per dyad are shown; a blank cell indicates that the behaviour did not occur during the observation period. Contact includes sit in contact and lay arm on shoulder; touching includes touch, make contact, kiss; beg and share food includes with and without contact. Kruskal-Wallis and post-hoc Dunn's test for between-group comparison with $p < 0.05$; for tendency of significance: * $p < 0.1$; n.s.: $p > 0.05$.

A similar pattern was found for *sitting in contact* (Tab. 3.8): frequencies ranged from less than 0.1 times/h up to 1.9 times/h in a few dyads; durations ranged from a few seconds to 1.1 min/h in maximum. Between females at Apenheul *sitting in contact* was exhibited more frequently and for a longer duration than *grooming*. Within all groups, there were some dyads in which partners did not *groom* at all but *sat in contact* on occasion.

Social play (of short duration) was observed in all three dyads at Chester, but only in a few dyads at Apenheul and at Cologne (Dunn's test, CE>AH, $p < 0.05$). There were only two out of 13 dyads in which no *sociopositive* interactions were observed at Apenheul, and one out of six dyads at Cologne.

Agonistic

Agonistic interactions of any type between females rarely occurred within all dyads; in three dyads they were observed not at all (Tab. 3.9). *Mild dominant* interactions were observed in most dyads (mean, 0.08 times/h). *Mild submissive* behaviours (mean, 0.13 times/h), e.g. *retreating*, occurred in all three dyads at Chester, and in about half of all dyads at Apenheul and Cologne. Statistic comparison between the groups revealed that *submissive* behaviours occurred significantly more often at Chester than in the other two groups (Dunn's test, $p < 0.05$, see Tab. 3.9).

	n / h per dyad	dominant		submissive		
		mild	serious	mild	serious	
Chester	Ma-Sr	0.06		0.44	0.02	
	Ma-Le	0.14		0.11		
	Sr-Le	0.13	0.02	0.61	0.20	
Apenheul	Ra-Ka	0.08		0.02		
	Ra-Sa			0.10		
	Ra-Fi	0.09		0.13		
	Ra-Jo			1.00		
	Ka-Sa	0.20		0.30		
	Ka-Fi			0.04		
	Ka-Jo					
	Sa-Fi	0.05				
	Sa-Si					
	Sa-Jo	0.29	0.04			
	Fi-Si	0.10		0.05		
	Fi-Jo	0.04				
	Si-Jo	0.07				
	Cologne	Lo-No	0.08			
		Lo-Su				
Lo-Tj		0.01				
No-Su		0.08				
No-Tj		0.07		0.06		
Su-Tj		0.31		0.01		
Kruskal-Wallis H	1.668	2.374	6.749	13.270		
p	n.s.	n.s.	CE>CN	CE>AH, CN		

Tab. 3.9: Agonistic interactions within female-female dyads

Mean values per dyad are shown; a blank cell indicates that the behaviour did not occur during the observation period. Kruskal-Wallis and post-hoc Dunn's test for between-group comparison with $p < 0.05$; n.s.: $p > 0.05$.

Serious agonistic interactions (e.g. *chase*, *flee*) were extremely rare (mean, 0.01 times/h; Tab. 3.9): at Cologne they were recorded during the observation period not once, at Apen-

heul they were recorded in one dyad only. At Chester, *serious agonistic* behaviours occurred in two out of three dyads of related females (mean, 0.08 times/h).

Both at Apenheul and Cologne, there were some dyads in which *dominant* but no *submissive* behaviour was exhibited; the other way round only occurred within three dyads at Apenheul. At Chester and at Apenheul, there was one dyad each within which females interacted *agonistically* clearly more often than within other dyads. In case of the Chester group, it was the mid-aged female and her subadult sister (Sr-Le). At Apenheul it was the oldest and the youngest adult female (Ra-Jo). In the latter case, however, females were kept together for a total of two hours only.

At Apenheul, a *serious* conflict once occurred in the evening outside the observation sessions between two of the females (Ra-Fi) such that the older female *chased* and *bit* the younger female (communicated by the keeper). The females were then separated over night but stayed in the same subgroup in the afternoon of the next day again, and no *agonistic* interactions were observed.

Reciprocity

Referring to the active-passive relation of *grooming* within female-female dyads, there was a clear tendency that in those dyads where *grooming* was performed, only one of the partners was the active one (Fig. 3.9; Appendix Tab. 8.26). *Touching* was distributed more reciprocal between partners. In all groups there was a tendency that females which were the more active partner in *grooming* also were more active in *touching*.

Referring to *agonistic* interactions, *dominant* and *submissive* behaviours were distributed unidirectional between partners with the exception of one dyad at Cologne (Su-Tj). In case of dyads where both *dominant* and *submissive* interactions occurred, they were performed in opposite direction. This turned out to be the case in about half of the dyads at Apenheul and at Cologne. In Chester, this pattern applied for all three dyads: the oldest female acted *dominantly* towards both of her daughters, and her older daughter did so towards her younger sister. In turn, the oldest female received *submissive* behaviours from both of her daughters, and the older daughter from her sister.

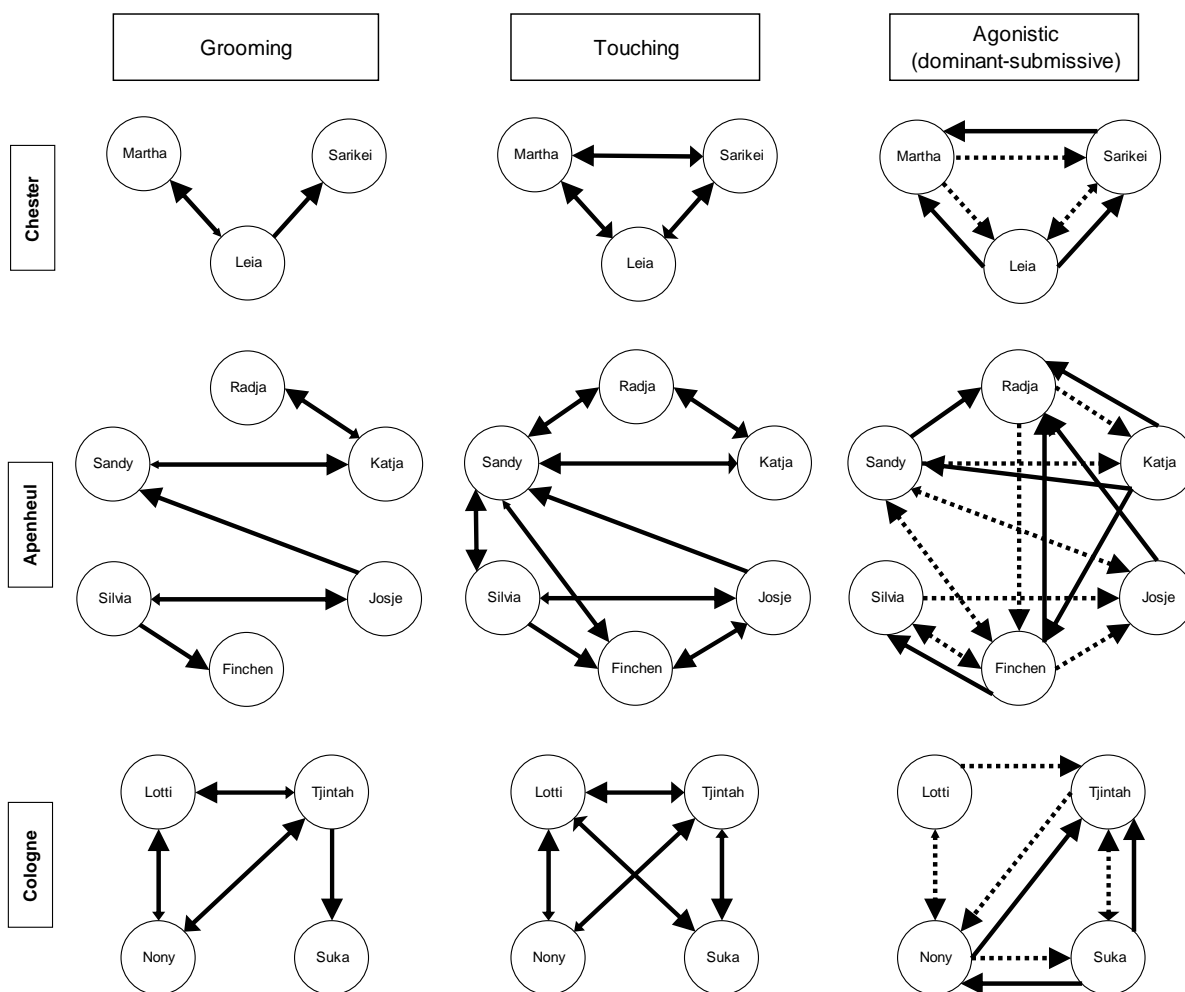


Fig. 3.9: Reciprocity of interactions within female-female dyads

The direction and degree of reciprocity of grooming, touching and agonistic behaviours within dyads is shown based on reciprocity indices (Tab. 8.26). The thickness of an arrowhead indicates the proportional contribution of the partners; line with one arrowhead = index was 1 or -1; line with two arrowheads of same thickness = index was 0. A lack of any arrow indicates that the behaviour was not observed between partners. Touching includes kiss and make contact. Agonistic behaviours: dominant = dotted line, submissive = solid line.

Combining the distribution of *grooming* and *agonistic* behaviours (Fig. 3.9), in dyads in which both occurred, the *groomer* received *dominant* behaviour from its partner. This was true for all dyads at Chester and Cologne and for most dyads at Apenheul. In the latter group, in three dyads (Sa-Ka, Sa-Jo, Ra-Ka) the *grooming* female received *dominant* behaviours as well. In another dyad (Si-Jo) the *groomer* was sender and recipient of *dominant* behaviour and receiver of *submissive* behaviours.

Male-female relationships

Sub-/adult males and females interacted rarely with each other and for short times only, especially at Apenheul and Cologne: interactions occurred 2 times/h in mean and lasted less than 0.5 min/h (Tab. 3.10). Statistic comparison revealed no significant differences in male-female interactions between Apenheul and Cologne in any behavioural category (Mann-Whitney U , all $p > 0.05$).

Within all groups, males and females predominantly *approached* and *left* each other (mean: *approach* 1.8 times/h, *leave* 1.5 times/h). *Sociopositive* interactions occurred 0.7 times/h in mean, which was three times higher than *agonistic* ones. At Chester, the only male-female pair interacted more often *sociopositively* than the male-female pairs at Apenheul and Cologne, but they interacted also more often *agonistically*.

	Chester		Apenheul		Cologne		sign. difference	
	n/h	min/h	n/h	min/h	n/h	min/h	n/h	min/h
approach	4.10	-	0.68	-	0.63	-	no	-
leave	3.20	-	0.54	-	0.65	-	no	-
follow	0.25	0.04			0.08	0.01	no	no
sociopositive	1.20	0.25	0.41	0.04	0.45	0.29	no	no
agonistic	0.75	-	0.17	-	0.13	-	no	-
sexual	0.05	0.01	0.03	0.004	0.05	0.01	no	no
others	0.50	0.03	0.13	0.01	0.06	0.003	no	no

Tab. 3.10: Interactions within male-female dyads

Average median values of frequency and duration of male-female interactions per group are shown. Mann-Whitney U for between-group comparison with $p < 0.05$.

Following was rare and even absent at Apenheul (Tab. 3.10). *Sexual* interactions were also rare in all settings (mean, 0.04 times/h). Within the groups at Apenheul and Cologne, there were no statistic differences between dyads (CN: $F=2.833$, $p > 0.5$; AH: $F=29.316$, $p=0.000$, post-hoc: K-Si vs. K-Ra: $Q=0.829$, $p > 0.05$). *Sexual* interactions consisted mainly of *genital examinations*. Unforced *copulations* were observed at Apenheul and Cologne; *raping* was only observed at Cologne. *Sexual* interactions involving the subadult male at Cologne were rare and did not include *copulations*. At Chester no *copulations* were observed.

Sociopositive

Within all groups, *touching* was the most frequent *sociopositive* interaction in all male-females dyads (mean, 0.4 times/h; Tab. 3.11) except one (Sa-Lo). *Begging/sharing food* was observed in most dyads but for relatively low rates, most often in Apenheul (Mann-Whitney *U*, AH vs. CN: $p < 0.1$, see Tab. 3.11). In a few dyads partners *groomed* (mean, 0.2 times/h) and/or *sat in contact* (mean, 0.6 times/h). *Social play* was observed in some dyads with a tendency to occur more frequently than *grooming* or *sit in contact*. There were no significant differences in any of the *sociopositive* interactions between the Apenheul and the Cologne group (Mann-Whitney *U*, all $p > 0.05$).

	M-F	groom		contact		social play		touch	beg, share food
		n/h	min/h	n/h	min/h	n/h	min/h	n/h	n/h
Chester	Mt-Pu	0.15	0.03	0.25	0.03	0.45	0.14	0.25	0.10
Apenheul	K-Ra					0.05	0.01	0.10	0.21
	K-Ka	0.26	0.08	1.18	0.40	1.03	0.81	2.00	0.77
	K-Sa							0.22	0.47
	K-Fi							0.04	
	K-Si			0.03	0.02			0.03	0.13
	K-Jo	0.09	0.49					0.09	0.28
Cologne	Bo-Lo	0.03	0.03	0.004	0.001			0.14	0.03
	Bo-Su							0.08	
	Bo-No	0.004						0.004	0.04
	Bo-Tj	0.15	0.50	0.06	0.02			0.43	0.03
	Sa-Lo								0.08
	Sa-Su	0.42	0.50	2.00	0.57	4.00	3.37	0.92	
	Sa-No			0.33	0.07	0.67	0.48	0.50	
	Sa-Tj			0.42	0.07	0.80	0.73	0.67	0.33
Mann-Whitney <i>U</i>		21.000	20.000	17.000	17.000	22.000	22.000	22.000	9.500
<i>p</i>		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.*

Tab. 3.11: Sociopositive interactions within male-female dyads

Mean frequency and duration per dyad are shown; a blank cell indicates that the behaviour did not occur during the observation period. Contact includes sit in contact and lay arm on shoulder; touching includes touch, kiss; beg and share food includes with and without contact. Mann-Whitney *U* for between-group comparison with $p < 0.05$; for tendency of significance: * $p < 0.1$; n.s.: $p > 0.05$.

In about half of all dyads *grooming* and/or *sit in contact* occurred (Tab. 3.11). But in most cases, *grooming* was rare (0.004-0.4 times/h) and short in duration (0.5min/h maximally). At Cologne, no statistic differences were found between dyads ($F=3.000$, $p=1.000$). At Apenheul, differences were found in only two cases: in the dyad composed of the adult male

and his subadult daughter *grooming* occurred more often than in two other dyads with no *grooming* ($F=180.457$, $p=0.000$; K-Ka vs. K-Fi: $Q=12.281$, K-Ka vs. K-Si: $Q=8.891$, $p<0.05$). A similar pattern was found for *sit in contact*: frequencies ranged from 0.004-0.4 times/h in few dyads with durations of only a few seconds to 0.6min/h maximally.

There was one dyad at Cologne, a hand-reared and related subadult male-female pair (Sa-Su), in which *sit in contact* occurred more often, i.e. 2.0 times/h. Also *social play* was much more pronounced between these two individuals. *Social play* was also observed within some other dyads: within the male-female pair at Chester; between the male and the oldest female (K-Ra) and the male and his subadult daughter (K-Ka) at Apenheul and within male-female dyads involving the subadult male at Cologne. In the latter group, *grooming* and *sitting in contact* could be observed more often between the adult male and a female than between the subadult male and a female, whereas *touching* and *social play* occurred more often in dyads involving the subadult male.

There was only dyad in total in which partners showed no *sociopositive* interaction other than *begging/sharing food*; this dyad was composed of the oldest female and her hand-reared subadult son (Sa-Lo, Cologne group).

Agonistic

Agonistic interactions between males and females occurred in most dyads but were rare in frequency (mean, 0.2 times/h; Tab. 3.12) and predominantly of a *mild* type. The highest frequency of *submissive* behaviours was observed in the male-female pair at Chester (0.6 times/h). Except of the latter, frequencies of *mild agonistic* behaviours were largely similar between the groups with a mean of 0.05 times/h in *dominant* interactions and 0.14 times/h in *submissive* ones. There were no significant differences in any of the *agonistic* interactions between the Apenheul and the Cologne group (Mann-Whitney U , all $p>0.05$).

		n / h per dyad	dominant		submissive	
			mild	serious	mild	serious
Chester	Mt-Pu		0.15		0.60	
Apenheul	K-Ra				0.05	
	K-Ka		0.26	0.05	0.15	
	K-Sa		0.002		0.11	
	K-Fi		0.04		0.31	
	K-Si				0.03	
	K-Jo			0.05		0.19
Cologne	Bo-Lo		0.02	0.004	0.08	0.07
	Bo-Su					
	Bo-No		0.01		0.19	0.02
	Bo-Tj		0.08		0.01	
	Sa-Lo					0.08
	Sa-Su					
	Sa-No		0.08		0.33	0.17
	Sa-Tj					
Mann-Whitney <i>U</i>			20.000	22.500	12.000	12.000
p			n.s.	n.s.	n.s.	n.s.

Tab. 3.12: Agonistic interactions within male-female dyads

Mean values per dyad are shown; a blank cell indicates that the behaviour did not occur during the observation period. Mann-Whitney *U* for between-group comparison with $p < 0.05$; n.s.: $p > 0.05$.

Serious agonistic behaviours (Tab. 3.12) were not observed at Chester and at Apenheul with the exception of one dyad (K-Ka). At Cologne, *serious submissive* behaviours were observed in half of all dyads (mean, 0.04 times/h); *serious dominant* interactions were observed in one dyad only (Bo-Lo) and extremely rare in frequency (0.004 times/h). *Mild dominant* and *submissive* interactions mainly occurred in dyads involving the adult male.

Reciprocity

At Apenheul and Cologne, *grooming*, *touching*, and *agonistic* interactions between males and females were largely unidirectional distributed (Fig. 3.10; Appendix Tab. 8.26). Between the male-female pair at Chester, *agonistic* interactions were unidirectional as well, but *grooming* and *touching* were performed reciprocally.

At Apenheul, *grooming* and *touching* was completely directed towards the male. At Cologne, *grooming* was directed towards the males as well but the distribution of *touching* between partners was more diverse: in two out of three adult male-female dyads, the male was the sender only. In dyads involving the subadult male, *touching* was more reciprocally distributed.

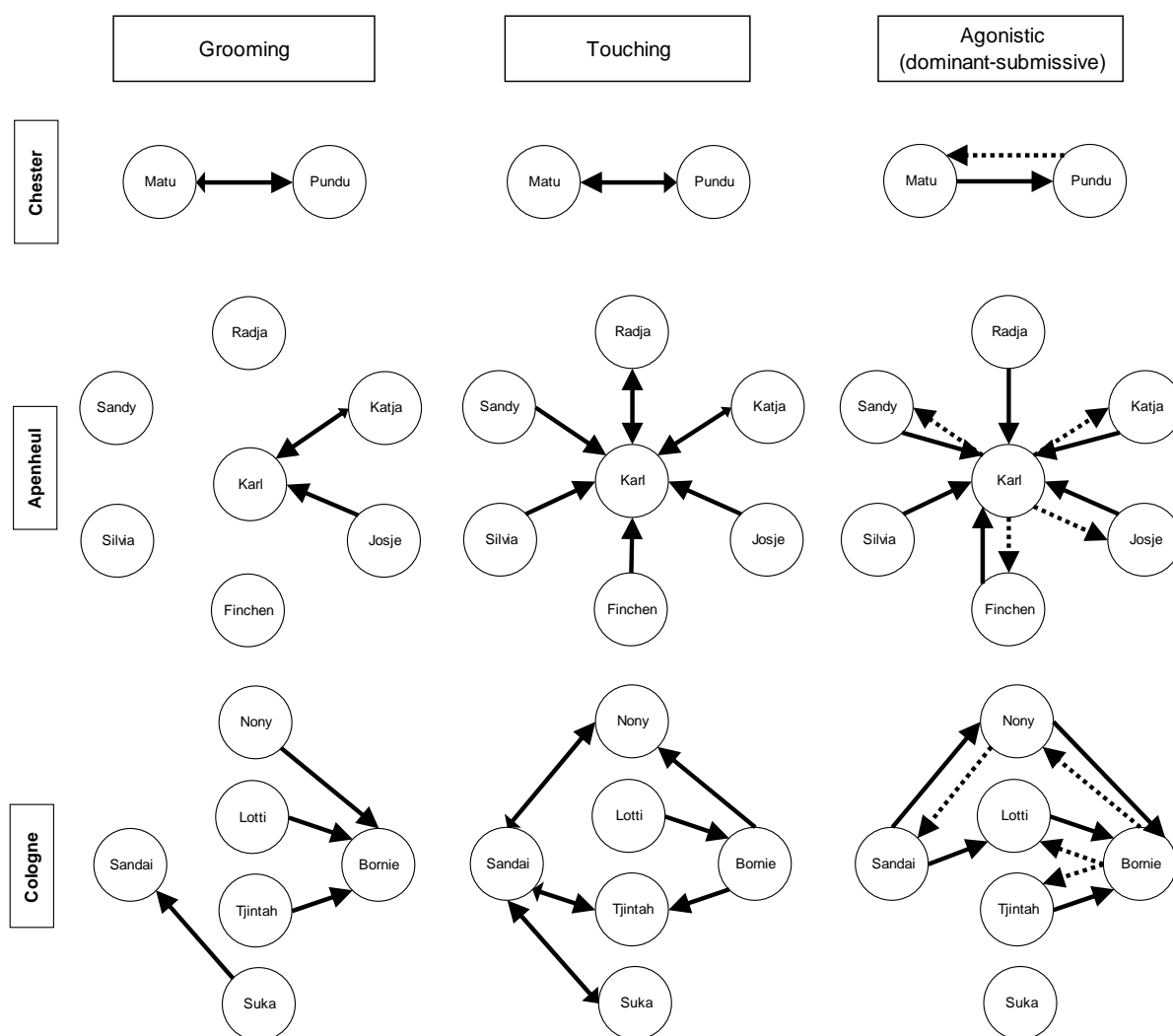


Fig. 3.10: Reciprocity of interactions within male-female dyads

The direction and degree of reciprocity of grooming, touching and agonistic behaviours within dyads is shown based on reciprocity indices (Tab. 8.26). The thickness of an arrowhead indicates the proportional contribution of the partners; line with one arrowhead = index was 1 or -1; line with two arrowheads of same thickness = index was 0. A lack of any arrow indicates that the behaviour was not observed between partners. Touching includes kiss and make contact. Agonistic behaviours: dominant = dotted line, submissive = solid line.

Referring to the reciprocity of *agonistic* interactions within male-female dyads (Fig. 3.10), *dominant* and *submissive* behaviours were unidirectional distributed between partners in all groups. In case of dyads where both *dominant* and *submissive* interactions occurred they were inversely directed. At Chester and Apenheul, the males were sender of *dominant* behaviours and females showed *submissive* behaviours. At Cologne, this pattern also applied for adult male-female dyads but not for dyads involving the subadult male. In the latter case,

the subadult male (Sa) showed *submissive* behaviours towards two females, one of which he also received *dominant* behaviours from (Sa-No).

Combining the distribution of *grooming* and *agonistic* behaviours in dyads where both behaviours occurred, the *groomer* received *dominant* behaviour from its partner in dyads at Chester and Apenheul, and in adult male-female dyads at Cologne.

Male-male relationship

Since there was only one male-male dyad (Cologne) during the first observation period, a short survey about their interactive pattern is provided (Tab. 3.13). Within this adult-subadult male dyad, only two types of interactions were observed: partners *approached* and interacted *agonistically*. *Sociopositive* interactions were not observed. *Agonistic* behaviours (0.5 times/h) occurred more frequently than *approaches* (0.3 times/h). Both types of interactions were unidirectional performed: only the adult male *approached* (all events were *advances*) and only the subadult male was sender of *submissive* behaviours. *Dominant* behaviours by the adult male directed towards the subadult were not observed.

	n/h	min/h				
approach	0.30	-				
leave		-				
follow						
sociopositive			dominant		submissive	
agonistic	0.50	-	mild	serious	mild	serious
sexual					0.33	0.17
others						

Tab. 3.13: Interactions within the male-male dyad

Mean values of frequency and duration of within-dyad interactions are shown; a blank cell indicates that the behaviour did not occur during the observation period.

Adult-juvenile relationships

Female-juvenile dyads

Referring to the relationships between sub-/adult females and juveniles (Apenheul and Cologne), sub-/adult females and juveniles predominantly *approached*, *left* each other and in-

teracted *sociopositively*, each about 3-5 times/h (Tab. 3.14). *Sociopositive* interactions tended to occur more frequently and for longer duration between females and juveniles at Cologne than at Apenheul. *Following* was observed occasionally (mean, 0.3 times/h). Females and juveniles rarely interacted *agonistically* (mean, 0.1 times/h). Statistic comparison revealed no significant differences between female-juvenile interactions at Apenheul and Cologne in any behavioural category (Mann-Whitney *U*, all $p > 0.05$).

	Apenheul		Cologne		sign. difference	
	n/h	min/h	n/h	min/h	n/h	min/h
approach	2.78	-	2.30	-	no	-
leave	3.06	-	2.57	-	no	-
follow	0.35	0.12	0.31	0.08	no	no
sociopositive	3.22	0.75	5.60	2.07	no	no
agonistic	0.15	-	0.12	-	no	-
sexual	0.02	0.005	0.08	0.01	no	no
others	0.25	0.01	0.15	0.005	no	no

Tab. 3.14: Interactions within female-juvenile dyads

Average median values of frequency and duration of female-juvenile interactions per group are shown. Mann-Whitney *U* for between-group comparison with $p < 0.05$.

Sociopositive

In almost all female-juvenile dyads, *touching* was the most frequent *sociopositive* interaction (mean, 1.9 times/h), followed by *social play* (mean, 2.3 times/h; Tab. 3.15). Mother-offspring pairs and some non-related female-juvenile pairs performed these behaviours most frequently. *Begging* and *food-sharing* occurred in almost all dyads, most frequently in mother-offspring dyads (Ra-Wi, No-Ba, Tj-Bu). *Grooming* and *sit in contact* were observed in half of the dyads at Apenheul and in almost all dyads at Cologne. *Grooming* and *contact* was most pronounced in mother-offspring dyads as well as in one subadult female-juvenile dyad at Apenheul (Ka-Bi). Within the other dyads, *grooming* and *sit in contact* occurred less than 0.8 times/h and lasted some seconds per hour only. There were no significant differences regarding any *sociopositive* interaction between the Apenheul and the Cologne group (Mann-Whitney *U*, all $p > 0.05$).

	F-J	groom		contact		social play		touch	beg, share food
		n/h	min/h	n/h	min/h	n/h	min/h	n/h	n/h
Apenheul	Ra-Wi	0.97	0.31	1.53	0.49	0.95	0.53	3.18	2.88
	Ra-Bi							0.05	
	Ka-Wi	0.52	0.10	0.53	0.09	6.28	4.73	2.77	0.58
	Ka-Bi	1.30	0.37	0.35	0.21	0.90	0.42	0.20	0.05
	Sa-Wi	0.45	0.07	0.35	0.08	3.95	2.90	2.70	0.70
	Sa-Bi	0.63	0.19	0.78	0.36	0.03	0.01	1.50	0.83
	Fi-Wi					0.26	0.06	0.53	0.22
	Fi-Bi			0.05	0.06			0.07	0.07
	Si-Bi								
	Jo-Wi			1.00	0.18	13.00	6.04	8.50	
	Jo-Bi		0.00	0.49	0.11	0.33	0.11	1.02	1.35
Cologne	Lo-Ba	0.11	0.03	0.59	0.12	2.36	1.23	2.05	0.16
	Lo-Bu	0.03	0.01	0.16	0.04	0.62	0.32	0.70	0.07
	No-Ba	1.68	1.54	3.48	1.06	3.68	2.62	4.49	7.30
	No-Bu	0.10	0.06	0.22	0.05	2.34	2.44	0.97	2.27
	Su-Ba							0.50	0.17
	Su-Bu	0.23	0.08	2.19	0.47	4.63	3.22	2.37	0.69
	Tj-Ba	0.01	0.003	0.19	0.05	0.74	0.69	0.69	0.42
	Tj-Bu	1.17	0.98	4.02	1.20	3.85	2.83	4.06	7.31
Mann-Whitney <i>U</i>	34.000	32.000	33.500	38.500	33.500	31.500	35.000	29.000	
<i>p</i>	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	

Tab. 3.15: Sociopositive interactions within female-juvenile dyads

Mean frequency and duration per dyad are shown; a blank cell indicates that the behaviour did not occur during the observation period. Contact includes sit in contact and lay arm on shoulder; touching includes touch, kiss; beg and share food includes with and without contact. Mann-Whitney *U* for between-group comparison with $p < 0.05$; n.s.: $p > 0.05$.

Agonistic

Agonistic interactions between sub-/adult females and juveniles occurred in most dyads (Tab. 3.16) but they were rare (mean, 0.3 times/h) and predominantly of a *mild dominant* type. *Submissive* interactions were observed in half of all dyads, appositely rather weak (mean, 0.08 times/h). *Serious agonistic* interactions were observed in only one dyad per group. Frequencies of *dominant* interactions in mother-offspring pairs did not differ much from most non-related pairs but both, the highest and the lowest frequencies of *mild dominant* interactions were observed between unrelated individuals. There were no significant differences in any of the *agonistic* interactions between the Apenheul and the Cologne group (Mann-Whitney *U*, all $p > 0.05$).

	n / h per dyad	dominant		submissive	
		mild	serious	mild	serious
Apenheul	Ra-Wi	0.10			
	Ra-Bi			0.15	
	Ka-Wi	0.17			
	Ka-Bi	0.45		0.65	0.05
	Sa-Wi	0.85		0.15	
	Sa-Bi	0.05		0.03	
	Fi-Wi	0.09			
	Fi-Bi				
	Jo-Wi	0.50			
	Jo-Bi	0.04			
	Si-Bi	0.13			0.13
Cologne	Lo-Ba	0.03			
	Lo-Bu	0.06			
	No-Ba	0.21		0.004	
	No-Bu	0.06	0.03	0.07	0.03
	Su-Ba				
	Su-Bu	1.52		0.29	
	Tj-Ba				
	Tj-Bu	0.70		0.01	
Mann-Whitney <i>U</i>		41.000	38.500	41.000	43.000
<i>p</i>		n.s.	n.s.	n.s.	n.s.

Tab. 3.16: Agonistic interactions within female-juvenile dyads

Mean values per dyad are shown; a blank cell indicates that the behaviour did not occur during the observation period. Mann-Whitney *U* for between-group comparison with $p < 0.05$; n.s.: $p > 0.05$.

Reciprocity

In both groups, *grooming* and *agonistic* interactions within female-juvenile dyads were largely unidirectional distributed when occurring (Fig. 3.11; Appendix Tab. 8.26). At Apenheul, juveniles were the sender of *grooming* in three out of five dyads. In one dyad (Ka-Bi), only the juvenile received *grooming* and in another dyad composed of siblings (Ka-Wi), partners mutually *groomed*. At Cologne, *grooming* was completely directed by adult females towards the juveniles except one dyad (Tj-Ba).

Touching was more reciprocally distributed between some partners; between other partners, however, *touching* was unidirectional. If *touching* occurred reciprocally, there was a tendency that juveniles contributed more than their sub-/adult partners. In both groups, dyads could be found in which only juveniles were sender of *touching*. At Cologne however, two dyads were found in which the adult individual was the only active part in *touching*.

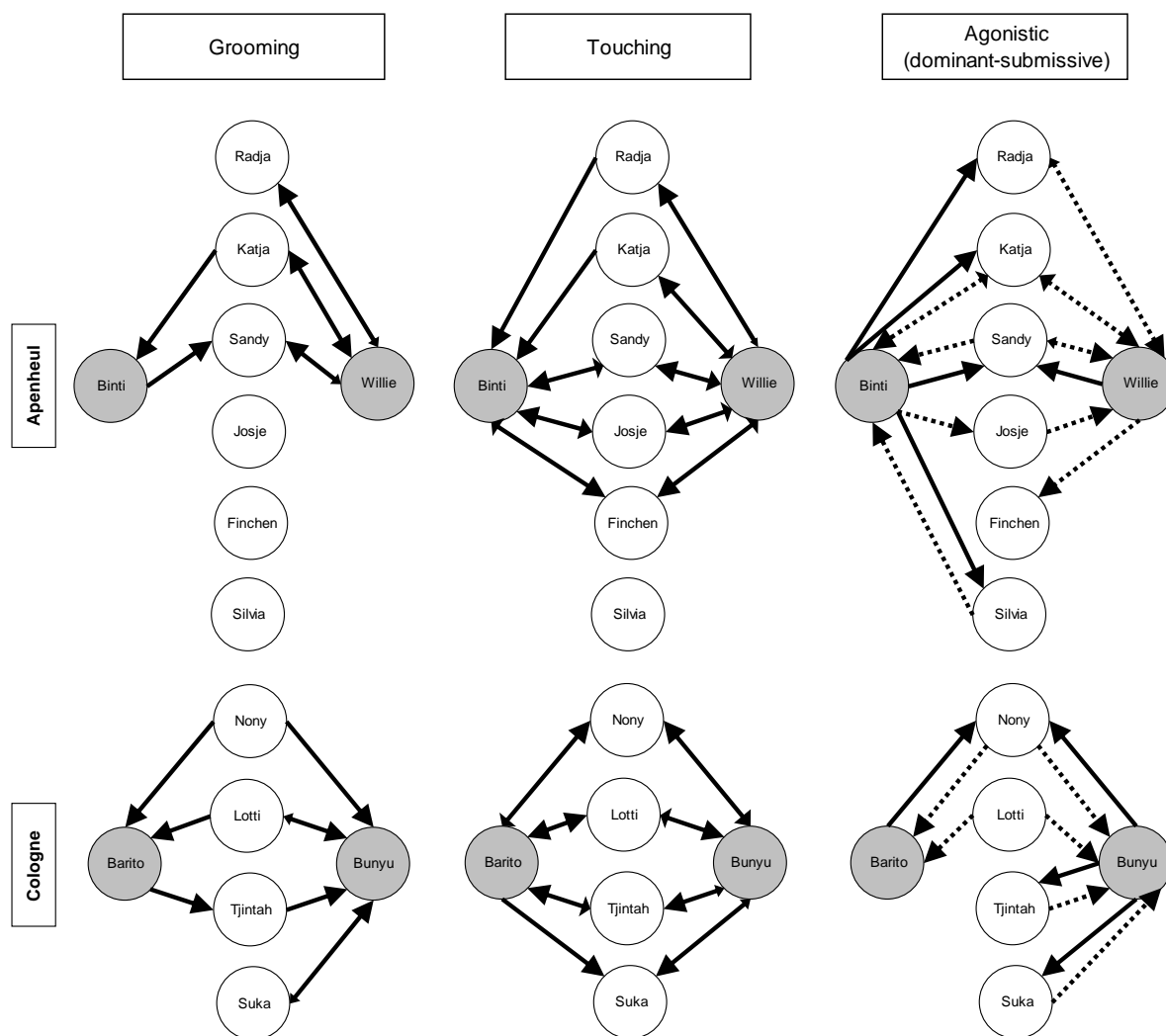


Fig. 3.11: Reciprocity of interactions within female-juvenile dyads

The direction and degree of reciprocity of grooming, touching and agonistic behaviours within dyads is shown based on reciprocity indices (Tab. 8.26). The thickness of an arrowhead indicates the proportional contribution of the partners; line with one arrowhead = index was 1 or -1; line with two arrowheads of same thickness = index was 0. A lack of any arrow indicates that the behaviour was not observed between partners. Juveniles = grey circles, adults = white circles. Touching includes kiss and make contact. Agonistic behaviours: dominant = dotted line, submissive = solid line.

Referring to the reciprocity of *agonistic* interactions within female-juvenile dyads (Fig. 3.11), *dominant* and *submissive* behaviours were unidirectional distributed between partners. In case of dyads where both *dominant* and *submissive* interactions occurred they were performed in opposite direction. With the exception of two dyads at Apenheul, *dominant* behaviours were completely directed by sub-/adult females towards their juvenile partners. *Submissive* behaviours were shown by juveniles. Combining the distribution of *grooming* and *agonistic* behaviours in dyads where both occurred, the two groups differed. At Apenheul, the *groomer* (mainly juveniles) only received *dominant* behaviour whereas at Cologne, the *groomer* (mainly adult females) also sent *dominant* behaviours.

Male-juvenile dyads

Referring to the relationships between sub-/adult males and juveniles, partners mainly *approached* (0.9 times/h), *left* each other (0.6 times/h) and interacted *sociopositively* (Tab. 3.17). *Sociopositive* interactions were observed most often in both groups with a mean rate of 1.0 times/h. They occurred three and accordingly seven times more often than *agonistic* ones at Apenheul and Cologne. In general, partners of a male-juvenile dyad at Apenheul interacted less often and for shorter duration than partners at Cologne. *Following* was observed a few times in both groups. At Cologne, some *sexual* interactions occurred. Statistic comparison revealed no significant differences between male-juvenile interactions at Apenheul and Cologne in any behavioural category (Mann-Whitney *U*, all $p > 0.05$).

	Apenheul		Cologne		sign. difference	
	n/h	min/h	n/h	min/h	n/h	min/h
approach	0.75	-	0.98	-	no	-
leave	0.18	-	0.96	-	no	-
follow	0.05	0.01	0.12	0.02	no	no
sociopositive	0.38	0.23	1.69	0.60	no	no
agonistic	0.13	-	0.24	-	no	-
sexual			0.002	0.00	no	no
others	0.04	0.001	0.18	0.01	no	no

Tab. 3.17: Interactions within male-juvenile dyads

Average median values of frequency and duration of male-juvenile interactions per group are shown. A blank cell indicates that the behaviour did not occur during the observation period. Mann-Whitney *U* for between-group comparison with $p < 0.05$.

Sociopositive

In all male-juvenile dyads, the most frequent *sociopositive* interactions were *social play* (mean, 0.6 times/h) and *touching* (mean, 0.3 times/h; Tab. 3.18). *Sit in contact* occurred in almost all dyads (mean, 0.2 times/h) whereas *grooming* and *begging/sharing food* was only performed within two dyads at Cologne. *Social play* was more pronounced between males and juveniles at Cologne than at Apenheul. At Cologne, *grooming* was observed in dyads involving the adult male only, lasting for a few seconds per hour. *Touching* also occurred more often in these dyads than in dyads involving the subadult male. There were no significant differences in any of the *sociopositive* interactions between the Apenheul and the Cologne group (Mann-Whitney *U*, all $p > 0.05$).

	M-J	groom		contact		social play		touch	beg share food
		n/h	min/h	n/h	min/h	n/h	min/h	n/h	n/h
Apenheul	K-Wi			0.15	0.04	0.51	0.42	0.05	
	K-Bi							0.04	
Cologne	Bo-Ba	0.05	0.01	0.11	0.02	0.22	0.16	0.64	0.04
	Bo-Bu	0.24	0.07	0.13	0.03	1.09	0.85	0.75	0.13
	Sa-Ba			0.42	0.08	0.88	0.66	0.17	
	Sa-Bu			0.25	0.05	0.75	0.55	0.25	
Mann-Whitney <i>U</i>		2.000	2.000	2.000	2.000	1.000	1.000	0.000	2.000
p		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

Tab. 3.18: Sociopositive interactions within male-juvenile dyads

Mean frequency and duration per dyad are shown; a blank cell indicates that the behaviour did not occur during the observation period. Contact includes sit in contact and lay arm on shoulder; touching includes touch, kiss; beg and share food includes with and without contact. Mann-Whitney *U* for between-group comparison with $p < 0.05$; n.s.: $p > 0.05$.

Agonistic

In both groups, *dominant* and *submissive* interactions occurred in dyads involving the adult male (Tab. 3.19). They were predominantly of a *mild* type and rare (mean, 0.08 times/h). Only a few cases of *serious submissive* behaviours within the adult-juvenile male dyads were observed at Cologne. There were no significant differences in any of the *agonistic* interactions between the Apenheul and the Cologne group (Mann-Whitney *U*, all $p > 0.05$).

	n / h per dyad	dominant		submissive	
		mild	serious	mild	serious
Apenheul	K-Wi	0.10		0.05	
	K-Bi	0.03		0.11	
Cologne	Bo-Ba	0.01		0.12	0.01
	Bo-Bu	0.10		0.07	0.01
	Sa-Ba				
	Sa-Bu				
Mann-Whitney <i>U</i>		3.000	4.000	3.000	4.000
p		n.s.	n.s.	n.s.	n.s.

Tab. 3.19: Agonistic interactions within male-juvenile dyads

Mean values per dyad are shown; a blank cell indicates that the behaviour did not occur during the observation period. Mann-Whitney *U* for between-group comparison with $p < 0.05$; n.s.: $p > 0.05$.

Reciprocity

In both groups, *grooming* and *agonistic* interactions were unidirectional performed if they occurred (Fig. 3.12; Appendix Tab. 8.26). *Touching* was unidirectional performed at Apenheul and within two dyads at Cologne. Within the other two dyads at the latter site, *touching* was distributed more reciprocally between partners. Both *grooming* and *touching* were shown by the juveniles directed to the sub-/adult males.

Referring to *agonistic* interactions, *dominant* and *submissive* behaviours were unidirectional distributed between partners in both groups. At Cologne, *dominant* and *submissive* interactions were performed in opposite direction with the adult male sending *dominant* behaviours and the juveniles behaving *submissively*. At Apenheul, *submissive* behaviours were also shown by the juveniles directed to the adult male. However, the adult male also received *dominant* behaviours from the juvenile male. When combining the distribution of *grooming* and *agonistic* behaviours at Cologne, the *groomer* (juveniles) received *dominant* behaviour from its partner.

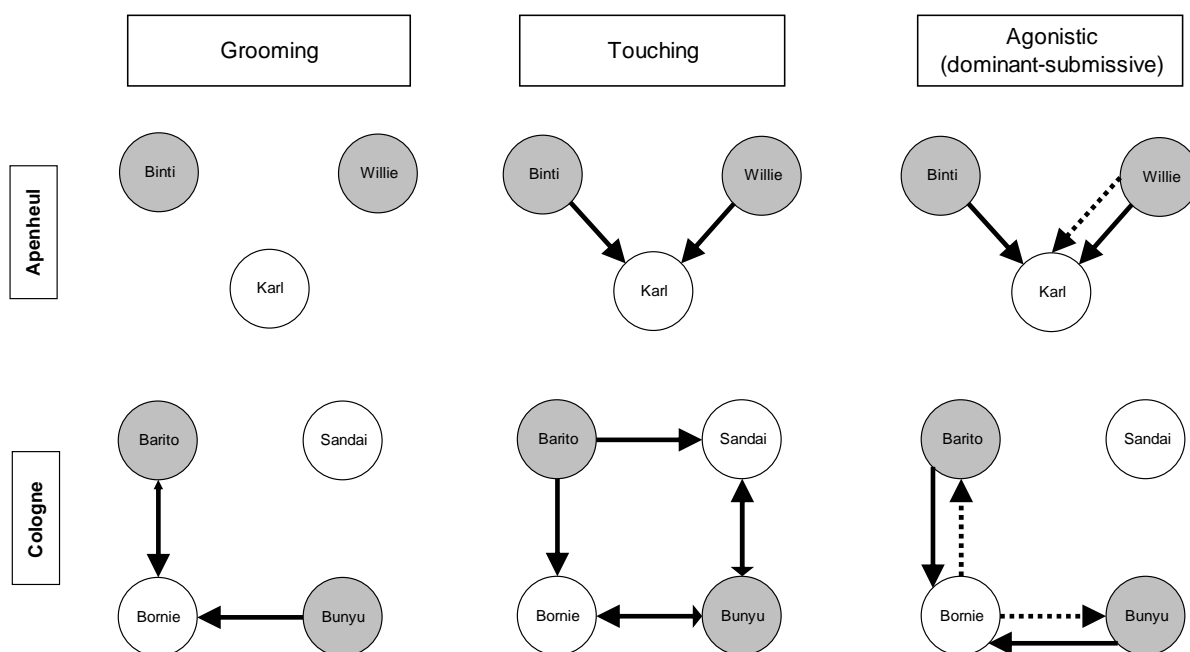


Fig. 3.12: Reciprocity of interactions within male-juvenile dyads

The direction and degree of reciprocity of grooming, touching and agonistic behaviours within dyads is shown based on reciprocity indices (Tab. 8.26). The thickness of an arrowhead indicates the proportional contribution of the partners; line with one arrow = index was 1 or -1; line with two arrowheads of same thickness = index was 0. A lack of any arrow indicates that the behaviour was not observed between partners. Juveniles = grey circles, adults = white circles. Touching includes kiss and make contact. Agonistic behaviours: dominant = dotted line, submissive = solid line.

Juvenile-juvenile relationships

The two juvenile-juvenile pairs at Apenheul and Cologne predominantly interacted *sociopositively* (mean, 9.6 times/h; Tab. 3.20). *Following* was rare, as were *agonistic* and *other* interactions. At Cologne, the two male juveniles generally interacted much more often than the male-female pair at Apenheul did, spending about 20% of their time interacting with each other.

	Apenheul		Cologne	
	n/h	min/h	n/h	min/h
approach	2.10	-	4.67	-
leave	2.60	-	5.85	-
follow	0.20	0.04	0.43	0.13
sociopositive	5.00	3.24	14.69	12.08
agonistic		-	0.07	-
sexual			0.46	0.11
others	0.05	0.003	0.13	0.005

Tab. 3.20: Interactions within juvenile-juvenile dyads

Average mean values of frequency and duration of juvenile-juvenile interactions per group are shown. A blank cell indicates that the behaviour did not occur during the observation period.

Sociopositive

Sociopositive interactions between the juveniles mainly consisted of *social play* (mean, 7.4 times/h) which occurred over three times more often and for longer duration at Cologne compared to Apenheul (Tab. 3.21). Both pairs sometimes *groomed* each other and gently *touched* whereas *begging* occurred between the male juveniles at Cologne only.

	J-J	groom		contact		social play		touch	beg, share food
		n/h	min/h	n/h	min/h	n/h	min/h	n/h	n/h
Apenheul	Wi-Bi	0.25	0.03	0.20	0.03	3.45	3.13	1.10	
Cologne	Ba-Bu	0.86	0.38	1.19	0.22	11.27	11.43	1.34	0.05

Tab. 3.21: Sociopositive interactions within juvenile-juvenile dyads

Mean frequency and duration per dyad are shown; a blank cell indicates that the behaviour did not occur during the observation period. Contact includes sit in contact and lay arm on shoulder; touching includes touch, kiss; beg and share food includes with and without contact.

Agonistic

At Apenheul, no *agonistic* interaction between the juveniles was observed. At Cologne, the males *pushed-back* one another a few times (0.069 times/h).

Reciprocity

Between juveniles, *grooming* and *touching* were reciprocally distributed to a certain extent (Fig. 3.13; Appendix Tab. 8.26); *agonistic* interactions were unidirectional performed. At Cologne, the juvenile contributing more to *grooming* and *touching* received *dominant* behaviour (here: *push-backs*) by its partner.

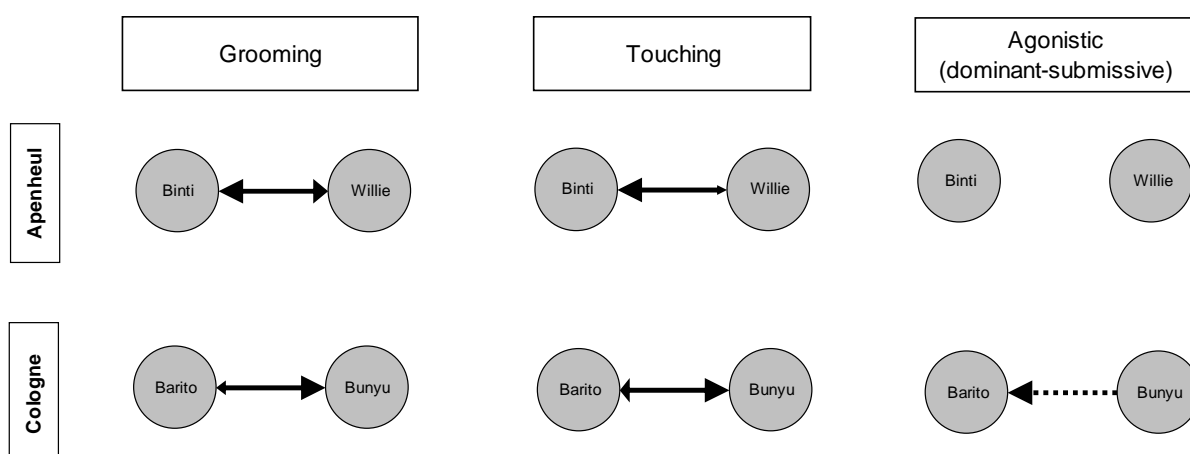


Fig. 3.13: Reciprocity of interactions within juvenile-juvenile dyads

The direction and degree of reciprocity of grooming, touching and agonistic behaviours within dyads is shown based on reciprocity indices (Tab. 8.26). The thickness of an arrowhead indicates the proportional contribution of the partners; line with one arrow = index was 1 or -1; line with two arrowheads of same thickness = index was 0. A lack of any arrow indicates that the behaviour was not observed between partners. Touching includes kiss and make contact. Agonistic behaviours: dominant = dotted line, submissive = solid line.

3.2.3. Triadic interactions

Interactions involving more than two partners were examined to make inferences about the network of social relationships. Interactions involving three individuals occurred in all groups. In total, eight different types of *triadic* interactions were observed (Fig. 3.14), most of them within the Cologne colony only. Frequencies of *triadic* interactions (total: CE=0.03 times/h, AH=0.3 times/h, CN=1.7 times/h) were low with the exception of *A approaches B which is interacting with C*. The latter interaction occurred 0.18 times/h within the Cologne group; at Chester and Apenheul frequencies were much smaller (CE: 0.002 times/h, AH: 0.09 times/h). Half of the eight observed *triadic* elements included *sociopositive* interactions between the participants (e.g. *A is groomed by B and C*, *A plays with B and C*), but all of them were observed at Cologne only. Another three elements tended to be *agonistic*; one of these occurring in all three groups was *A displaces B from C*.

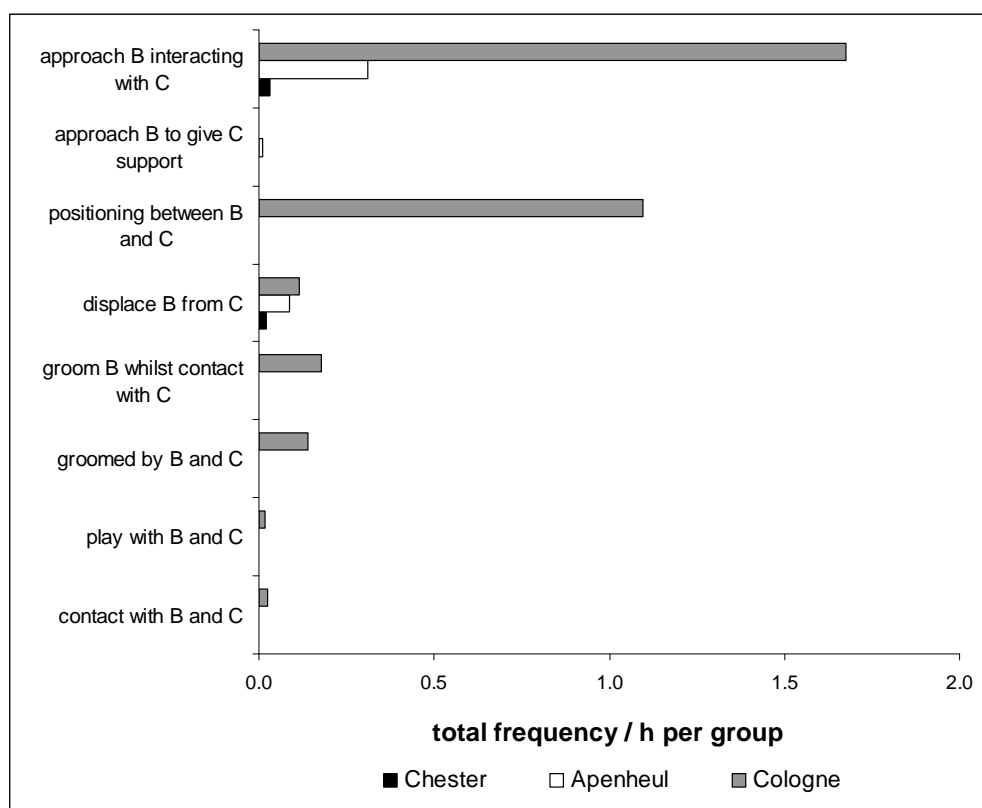


Fig. 3.14: Types of triadic interactions

The total frequency of all observed different types of triadic interactions per group is shown, expressed in events/h.

In relation to the number of theoretically possible triadic combinations, juveniles were often involved in *triadic* interactions at Apenheul and Cologne (Tab. 3.22). There was a small number of triads composed of only sub-/adult individuals within which *triadic* interactions were observed.

composition of triads	Chester	Apenheul		Cologne	
	only sub-/adults	only sub-/adults	sub-/adults and juveniles	only adults	adults and juveniles
theoretically possible No. of triads	4	210	294	120	216
observed No. of triads	3	2	19	11	66

Tab. 3.22: Theoretically possible and observed number of triads

The possible and observed number of triads per group in relation to the age class composition is shown. The theoretical number of possible triads within the groups was calculated via the binomial coefficient. To refer to the order within a triad (i.e. animal A, B, C), the falling factorial was adapted.

In most cases a *triadic* interaction took place only once or twice within the whole observation period; total frequencies had values of 0.002 and 0.003 times/h and type of triad (Tab. 3.23).

Concerning the age/sex class of participating individuals, sub-/adult females were most often observed in *positioning* themselves between two other individuals, in *displacing* a partner from another one, and in being *displaced* by a partner. At Cologne, adult females were also most often the active part in *grooming a partner whilst having contact to another one* and in *sitting in contact with two partners*.

Grooming and *social play* involving three individuals at a time was observed at Cologne only, and adult females and juveniles were the participating partners with the exception of one instance.

involved partner			positioning between B + C	approach B interacting with C	approach B to give C support	displace B from C	groom B in contact to C	groomed by B + C	play with B + C	contact with B + C
A	B	C								
CHESTER										
F	F	F		0.031		0.021				
APENHEUL										
F	F	F				0.011				
F	F	M		0.011						
F	F	J		0.044	0.011					
F	J	F		0.011		0.056				
F	J	J				0.022				
J	F	F		0.200						
J	F	M		0.011						
J	J	F		0.011						
J	F	J		0.022						
COLOGNE										
F	F	F		0.065			0.006			
F	F	M	0.006							
F	M	F	0.061	0.111						
F	M	J					0.002			
F	F	J		0.252		0.058	0.075	0.139	0.002	0.006
F	J	F	0.114	0.330		0.027	0.018			0.008
F	J	J		0.051			0.008			0.003
M	F	F		0.056		0.003				
M	F	J		0.011		0.008	0.006			
M	J	F		0.030			0.005			
J	F	F		0.309		0.003	0.040		0.006	
J	F	M		0.021						
J	M	F	0.002	0.052			0.014		0.003	
J	J	F		0.074			0.007		0.003	
J	J	M		0.015						
J	F	J		0.120		0.011			0.003	0.006
J	M	J	0.003	0.041		0.003				0.003

Tab. 3.23: Frequency of triadic interactions

The frequency of triadic interactions per hour and per group is shown. Values give the sum of all events between triads of the respective age/sex class of individuals involved. F=sub-/adult female, M=adult male, J=juvenile. Blank cells or missing triads of a given composition indicate that the behaviour did not occur during the observation period.

3.2.4. Long-term observations – Cologne

The development of the relationships between those adult individuals which were together for at least two different sessions in the same (sub-) group is described via three behavioural elements: *grooming*, *touching* and *agonistic* interactions. In the latter, all behaviours referring to this category were summed. For male-female dyads, the occurrence of *sexual* behav-

our over time is presented additionally. The mean frequency and duration of the total of social interactions within each of the dyads is given in the Appendix as referential data (Fig. 8.36, Fig. 8.37).

Female-female dyads

Referring to *sociopositive* and *agonistic* behaviours, the interactive pattern between adult females (Fig. 3.15) differed between sessions with a tendency of longer-lasting *grooming* when kept in subgroups and lower frequencies of interactions after reunion of subgroups. With the exception of the latter, frequencies of *approach* and *leave* largely remained on a constant level. Females *groomed* and *touched* each other at all sessions, while *agonistic* interactions were completely absent at some of them.

Regarding the two dyads where partners were kept together during the whole observation period (Fig. 3.15), in one dyad (Su-Tj) the total frequency of interactions considerably increased after the colony was separated into two subgroups. The frequency and duration of *grooming* continuously increased over time. During the first period following the removal of the juvenile male (AV), the females *touched*, *approached* and *left* each other more often. During the subsequent periods, the frequency of interactions decreased again.

Within the second dyad (Lo-No), the frequency of *groom*, *touch* and *agonistic* interactions changed much neither under more spacious conditions nor after introduction of the juvenile male. However, the duration of *grooming* increased after splitting of the colony (AI) and rapidly decreased again after the subgroups were reunited (AIX).

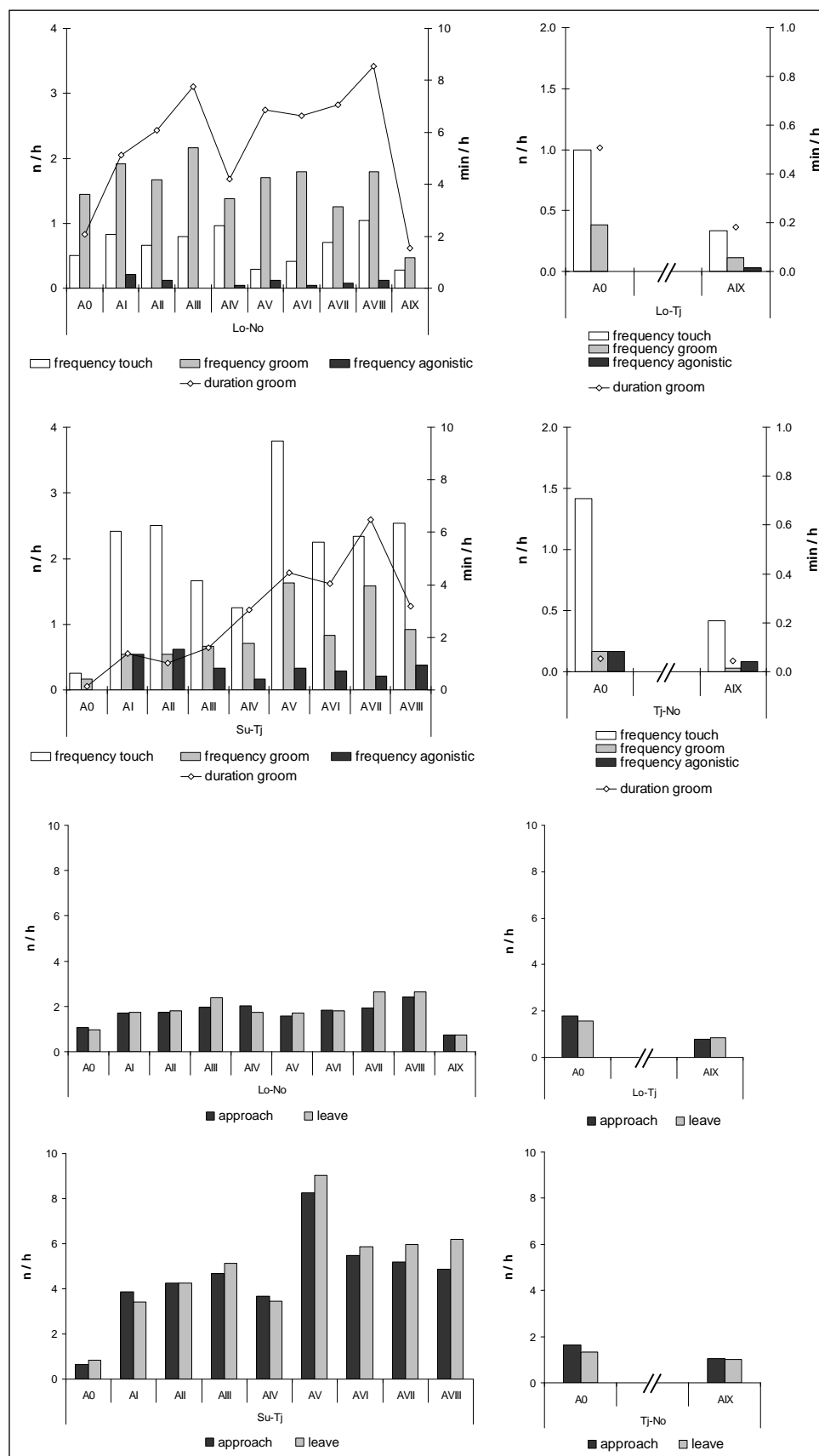


Fig. 3.15: Long-term series of interactions within female-female dyads

Mean frequencies of groom, touch, agonistic behaviours, approaches and leavings are shown per dyad and per observation period in which animals were kept in the same (sub-) group. The mean duration of grooming (min/h) is presented as open rhombus and line additionally.

Concerning the dyads where partners were not kept together over the whole observation period (Lo-Tj, Tj-No; Fig. 3.15), frequency of *grooming* and *touching* were smaller after subgroup-reassembly (AIX) compared to the period three years before (A0) when the females were also kept together in one large group. The frequency of *agonistic* behaviours slightly decreased in one dyad whereas in the other dyad it slightly increased.

Active-passive relations of *grooming*, *touching* and *agonistic* interactions within female-female dyads were largely stable regarding the different observation periods (Fig. 3.16). However, in one dyad (Lo-No) the *grooming* relation switched from period A0 (2002) to AI (2003). At the beginning of observations, the oldest female (Lo) mainly *groomed* the younger one and from the next period on, the younger female was the more active *groomer*. The degree of unidirectional *grooming* performed by the younger female increased successively in the course of time.

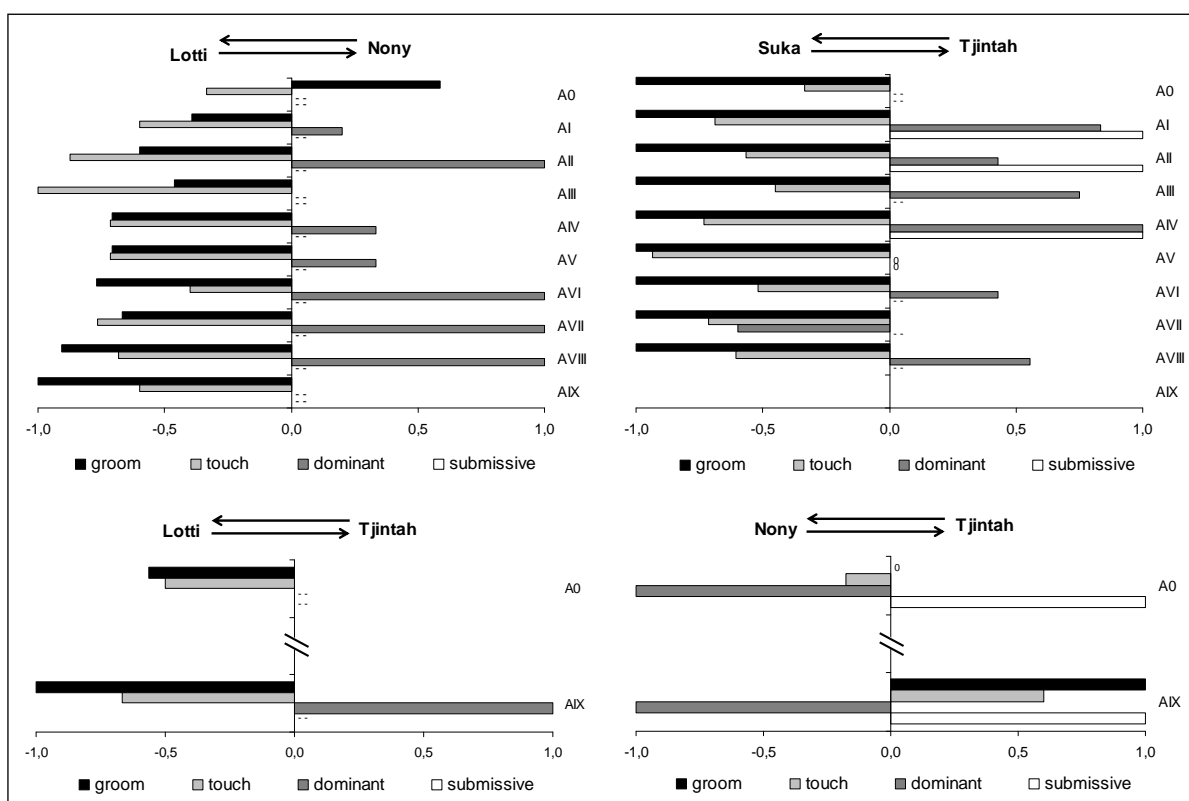


Fig. 3.16: Long-term observation of reciprocity within female-female dyads

Reciprocity indices of groom, touch, dominant and submissive interactions are shown per dyad and per observation period in which animals were kept in the same (sub-) group. Index value of 0 = both partners contributed equally to the behaviour; index value of -1 and 1 = the behaviour was completely performed one of the partners actively.

Referring to *agonistic* interactions, active-passive relations of *dominant* and *submissive* behaviours did not differ much between those sessions in which they occurred (Fig. 3.16). One partner was the main sender of *dominant* behaviours though in some sessions both partners contributed to *dominant* interactions. In the dyads where *submissive* behaviours occurred (Su-Tj, No-Tj) they remained unidirectional performed and the senders' identity did not change between sessions.

As qualitative annotation, few weeks after the study period, between two of the females (Lo-No) the relationship unexpectedly changed into more agonistic. There were instances of *serious* conflicts such that the younger female (which became pregnant) *chased* and *bit* the older female. The females were then separated and new subgroups were established.

Male-female dyads

Referring to the interactive pattern between the male and the females (Fig. 3.17) for which interactions were observed rarely in general (cf. Tab. 3.10 ff.), *sociopositive* interactions occurred highly inconstant over time with a tendency that *grooming* and *touching* peaked in few periods and were lacking in others. *Agonistic* interactions occurred during the entire observation period; rates decreased after the introduction of the juvenile male into the subgroup and after reunion of subgroups. Frequencies of *approaching* and *leaving* remained on a more constant level with a tendency to decrease after the introduction of the juvenile male. In one out of three dyads, partners interacted *sexually* during the entire observation period. In the other two dyads, *sexual* interactions occurred in only one period each.

Considering the dyads where partners were kept together over the whole observation period (Bo-Lo, Bo-No; Fig. 3.17), in one dyad (Bo-Lo) *touching* peaked in the session after the colony was split into subgroups and *grooming* occurred (AI). In the following periods, *touching* continuously decreased over time. *Grooming* peaked in frequency and duration in period AIII and was absent in all other periods. In this dyad, partners *approached* and *left* each other less often after the introduction of the juvenile male (AV-AVIII). *Sexual* interactions occurred in almost all periods (mainly *genital examination* by the male and *presenting* by the female), most often after the colony was split. In the other dyad (Bo-No) few bouts of *grooming* and *touching* occurred in only one period each. After splitting into subgroups, *agonistic* interactions initially increased and then decreased in the course of time. In this dyad, partners *approached* and *left* each other most often in periods AIII-V, at other periods frequencies did not change much. *Sexual* interactions occurred in period A0 only including a case of forced *copulation*.

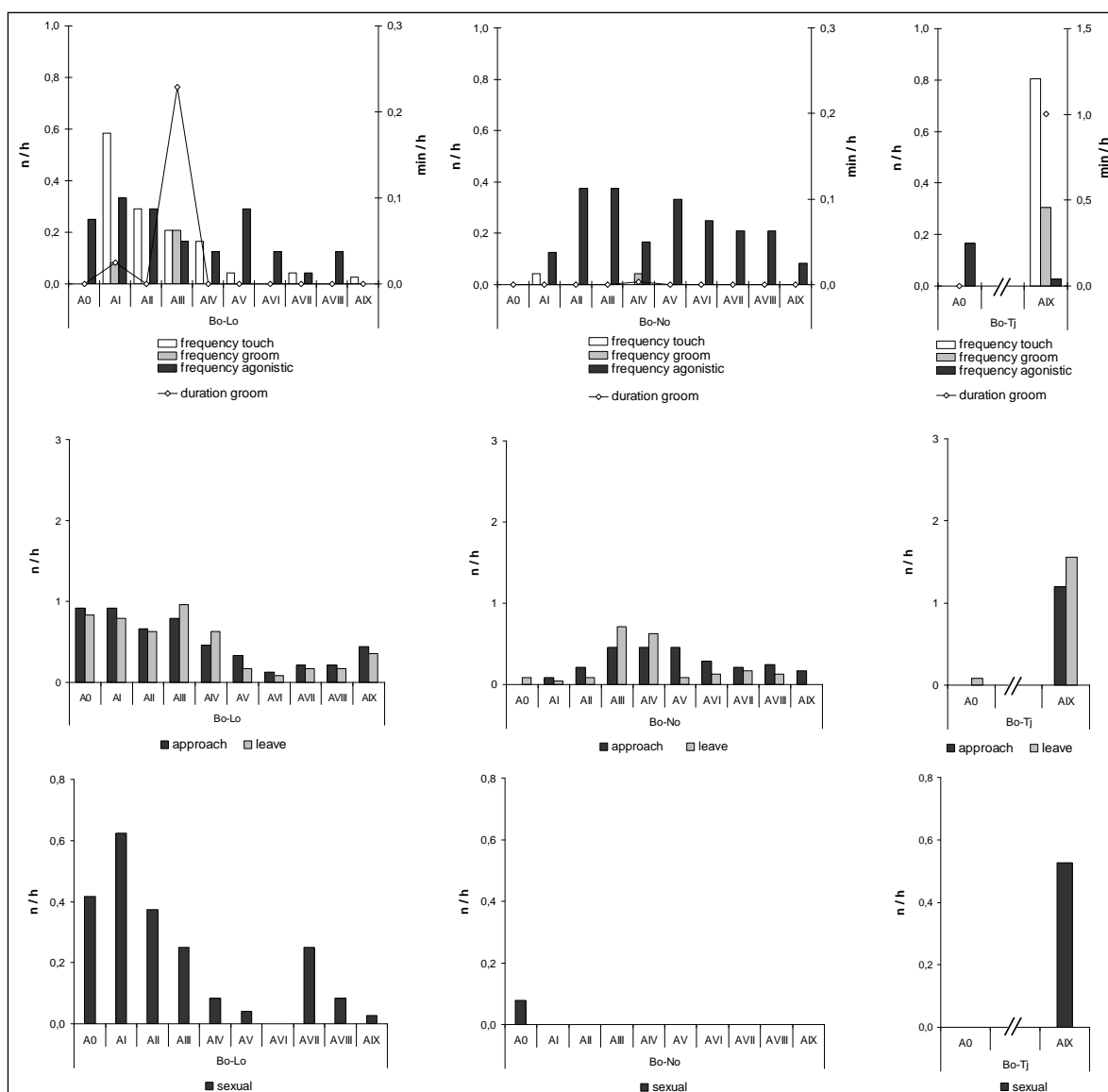


Fig. 3.17: Long-term series of interactions within male-female dyads

Mean frequencies of groom, touch, agonistic behaviours, approaches, leavings, and sexual interactions are shown per dyad and per observation period in which animals were kept in the same (sub-) group. The mean duration of grooming (min/h) is presented as open rhombus and line additionally.

Considering the dyad where partners were not kept together over the whole observation period (Bo-Tj; Fig. 3.17), frequency of *sociopositive* interactions, *approaches* and *leavings* were considerably higher and *agonistic* interactions were almost absent after subgroup-reassembly (AIX) compared to the period three years before (A0). During period AIX *sexual* interactions occurred.

Active-passive relations of *grooming*, *touching* and *agonistic* interactions within male-female dyads were stable regarding the different observation periods in all three dyads (Fig. 3.18). *Grooming* and *touching* were completely performed by the females towards the male (with the exception of touching in period AII in the dyad Bo-Lo). The male sent *dominant* behaviours just in some sessions, the females sent *submissive* behaviours in almost all sessions.

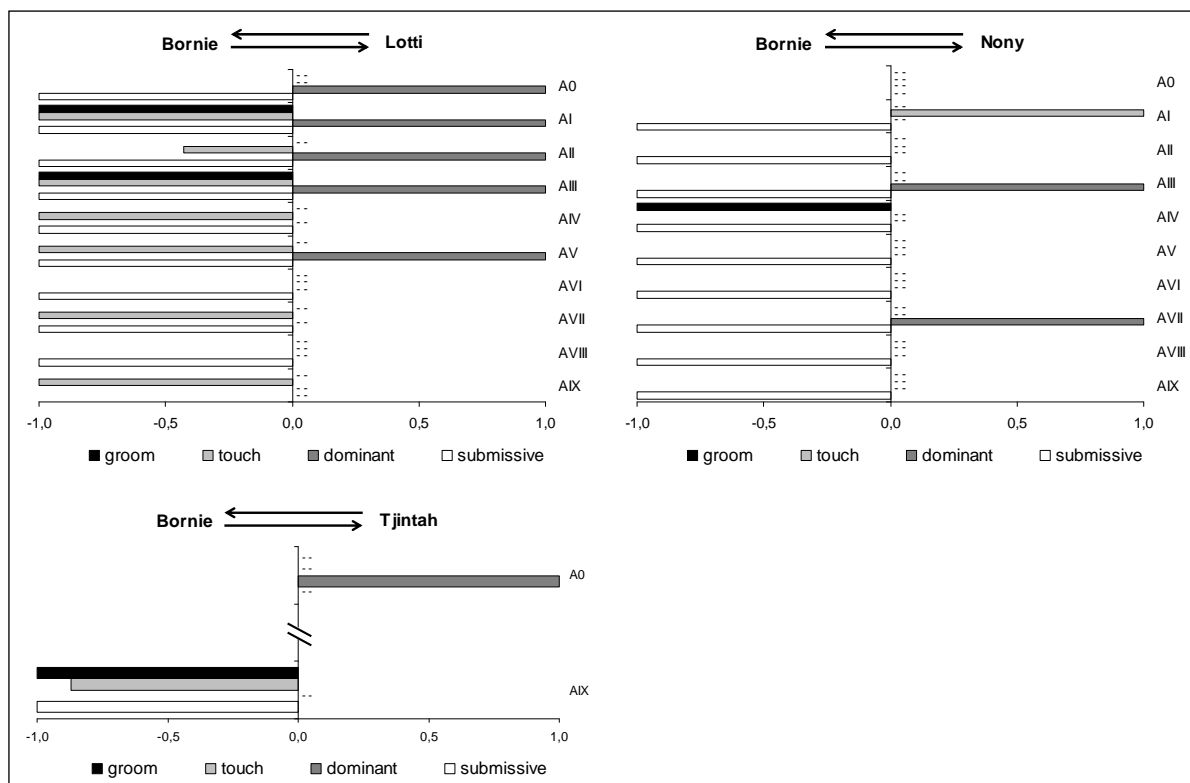


Fig. 3.18: Long-term observation of reciprocity within male-female dyads

Reciprocity indices of groom, touch, dominant and submissive interactions are shown per dyad and per observation period in which animals were kept in the same (sub-) group. Index value of 0 = both partners contributed equally to the behaviour; index value of -1 and 1 = the behaviour was completely performed one of the partners actively.

After the juvenile male was removed from one subgroup and introduced into the other one, the total frequency of interactions between the adult females did not differ much compared to periods before (Appendix, Fig. 8.36). Interactions between the adult male and the females decreased in frequency and duration. The adult male often interacted with the introduced juvenile male for an amount much higher than with the females (Appendix, Fig. 8.37).

3.3. SPATIAL BEHAVIOUR

The analyses of spatial behaviour were predominantly used to investigate fission-fusion tendencies. Basic traits can furthermore be used as complementary characteristics of social relationships. Based on the positions scans, interindividual distances were analysed. Aspects of the individuals' neighbourhood are presented. Per parameter analysed, data of the long-term observations at Cologne are also provided. Only data of sub-/adult individuals are considered. For reference, distances per dyad are given in the Appendix (Tab. 8.27).

3.3.1. Interindividual distances

Group average and sex-classes

In all groups, sub-/adult individuals often were located far away from each other (Fig. 3.19): averaged across all dyads, partners of a given dyad had a median distance of 10.7m.

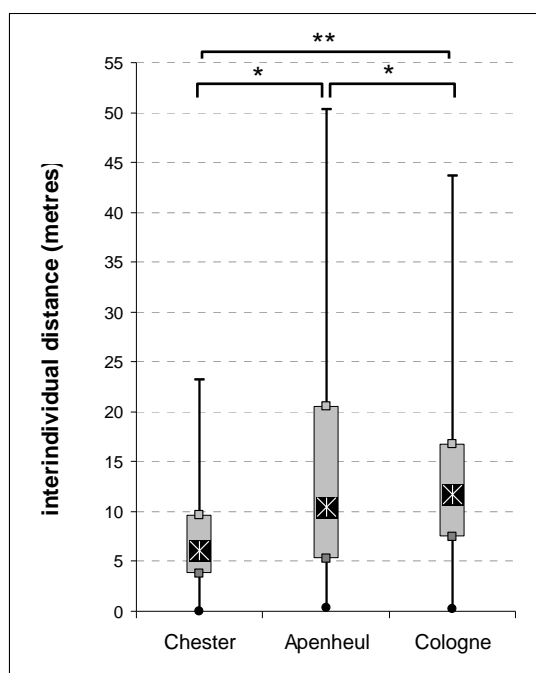


Fig. 3.19: Interindividual distances per group

Medians, quartiles, minimum and maximum distances are shown; values are averaged across all dyads of sub-/adult individuals per group. No. of dyads included: CE: 4; AH: 19; CN: 15. Mann-Whitney U : * $p < 0.05$, ** $p < 0.01$

Distances were highly variable in all groups (Fig. 3.19) ranging from body-contact up to a maximum of more than 23m (CE), 44m (CN), and 50m (AH). Comparing the zoos, average distances between animals at Apenheul and Cologne were significantly higher than distances at Chester, and at Cologne higher than at Apenheul (Mann-Whitney, CE vs AH: $U=12.500$; CE vs CN: $U=2.000$; AH vs CN: $U=72.000$; $p<0.05$).

Comparing the sexes between the groups (Fig. 3.20), distances between females and distances between males and females did not differ significantly (Kruskal-Wallis, F-F: $H=4.444$, Mann-Whitney, M-F: $U=11.000$; $p>0.05$). As a tendency, females at Apenheul and Cologne had up to 4m greater median distances to each other than females at Chester. Males and females at Cologne had about 3m greater distances to each other than those at Apenheul.

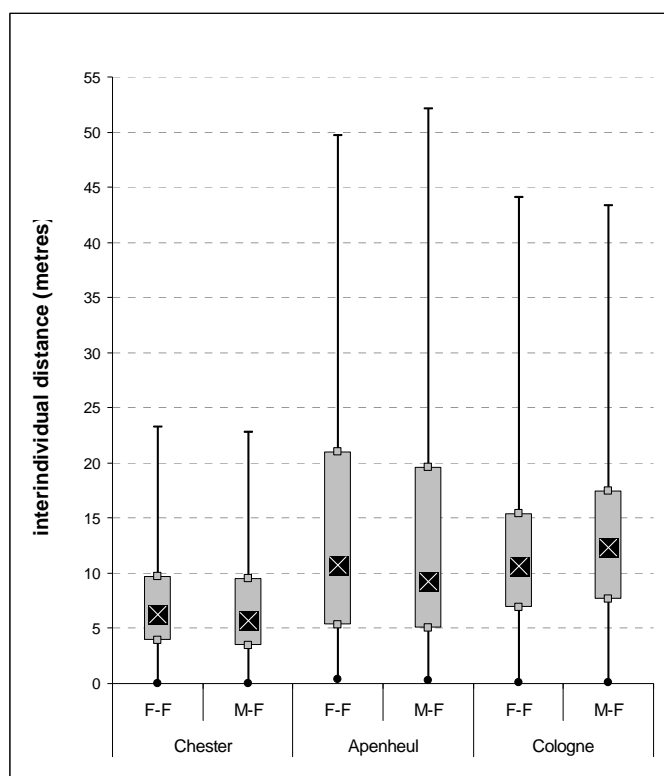


Fig. 3.20: Distances between sub-/adult individuals per group

Medians, quartiles, minimum and maximum distances between sub-/adult females and between sub-/adult females and sub-/adult males are shown. Number of dyads included: CE: F-F: 3, M-F: 1; AH: F-F: 13, M-F: 6; CN: F-F: 6, M-F: 8. Between-group comparison via Kruskal-Wallis test for F-F and Mann-Whitney U for M-F: $p>0.05$.

Within-group comparison revealed that average distances between the sexes also did not differ significantly (Fig. 3.20). At Apenheul, average distances between females were slightly higher than distances between the male and females (medians: F-F: 10.7m, M-F: 9.2m; Mann-Whitney, F-F vs. M-F $U=31.000$, $p>0.05$). At Cologne, females had slightly higher distances to males than among each other (medians: F-F: 10.7m, M-F: 12.3m, $U=22.000$, $p>0.05$).

However, there was a high variation within the class of sub-/adult females at Apenheul and Cologne (Appendix, Tab. 8.27) such that some dyads had distances of 6–8m smaller/larger than other dyads. Statistic testing however, revealed that at Cologne median distances between females did not differ significantly ($F=4.328$, $p=0.740$). At Apenheul, there was only one dyad for which the median distance differed significantly from those of four other dyads ($F=300.092$, $p=0.000$, post-hoc Dunn's test: Ra-Sa vs. Si-Jo: $Q=10.548$, Ra-Sa vs. Sa-Jo: $Q=9.855$, Ra-Sa vs. Ra-Ka: $Q=6.163$, Ra-Sa vs. Fi-Si: $Q=5.525$, all $p<0.05$). At Chester, median distances between dyads differed less than one metre.

Distances among male-female dyads were more consistent (Appendix, Tab. 8.27). There were no significant differences in the median distance between male-female dyads at Cologne ($F=12.609$, $p<0.05$, Dunn's test: Bo-Tj vs. Sa-Su: $Q=2.772$, $p>0.05$). At Apenheul, median distance significantly differed only between two dyads ($F=139.941$, $p=0.000$; Dunn's test: K-Ra vs. K-Fi: $Q=7.931$, $p<0.05$). At Cologne, the two sub-/adult males (period A0) had a median distance of 12.7m towards one another (Appendix, Tab. 8.27).

Long-term observations – Cologne

The analysis of the long-term dataset from Cologne revealed that the distances between adult individuals tended to be highest at periods when they were kept in one large group with more space available (Fig. 3.21). Average median distance between individuals was 13.5m in 2002, 6.3m in 2003-04, and 14.6m in 2005.

Between females, distances did not differ much between the periods of being kept in a large group. However, changes in distances between females were not testable due to sample-size. Distances between male-female dyads did not change significantly during the different periods (Friedman, M-F: $F=4.000$, $p>0.05$).

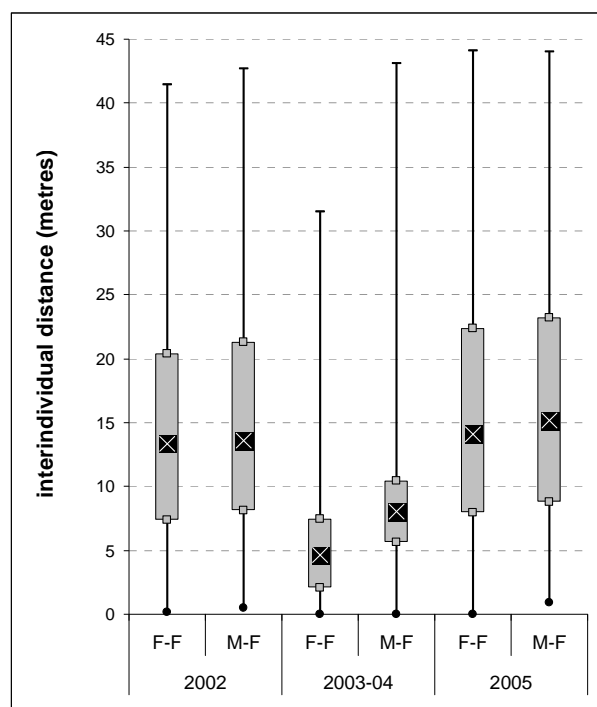


Fig. 3.21: Distances between sub-/adult individuals per observation period

Median, quartiles, minimum and maximum distances within female-female dyads and within male-female dyads are shown. Years represent the periods: 2002: A0, 2003-2004: AI-BVIII, 2005: AIX. No. of dyads included: 2002: F-F: 6, M-F: 8, 2003-04: F-F: 2, M-F: 2, 2005: F-F: 3, M-F: 3. Friedman test: M-F comparison, Mann-Whitney U test: F-F vs. M-F; all $p > 0.05$.

Comparing female-female and male-female dyads per observation periods (Fig. 3.21), their distances did not differ significantly from each other (Mann-Whitney, F-F vs. M-F: 2002: $U=1.470$, 2003/04: $U=3.365$, 2005: $U=1.127$; all $p > 0.05$).

Referring to the various dyads per each observations period (Fig. 3.22, Fig. 3.23), distances between the females and between females and the male were stable over time at periods kept in two subgroups (AI-BVIII). In contrast, at time-periods where individuals were kept in one large group (A0, AIX) distances between partners were 3-4 times higher. In female-female dyads (Fig. 3.22), distances between partners did not change much in the period following a change of subgroup composition (a juvenile male changed from one subgroup to the other one).

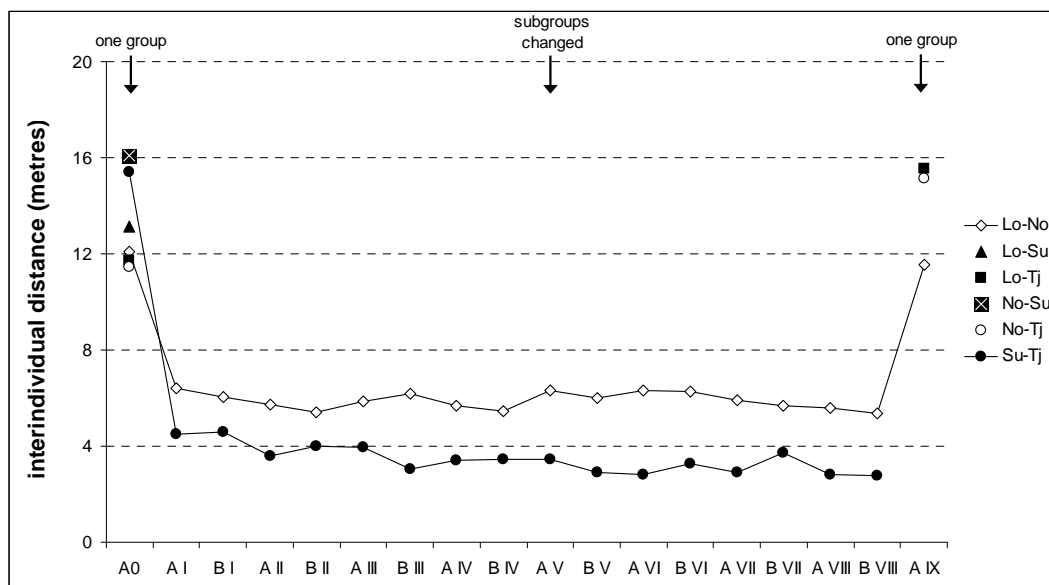


Fig. 3.22: Development distances between adult females

Median distances per dyad are shown for observation sessions between 2002 and 2005.

Within male-female dyads, distances between partners were stable as well (Fig. 3.23), with the exception that they increased within the first months after the juvenile male was introduced. Subsequently, distances decreased to the same level as before.

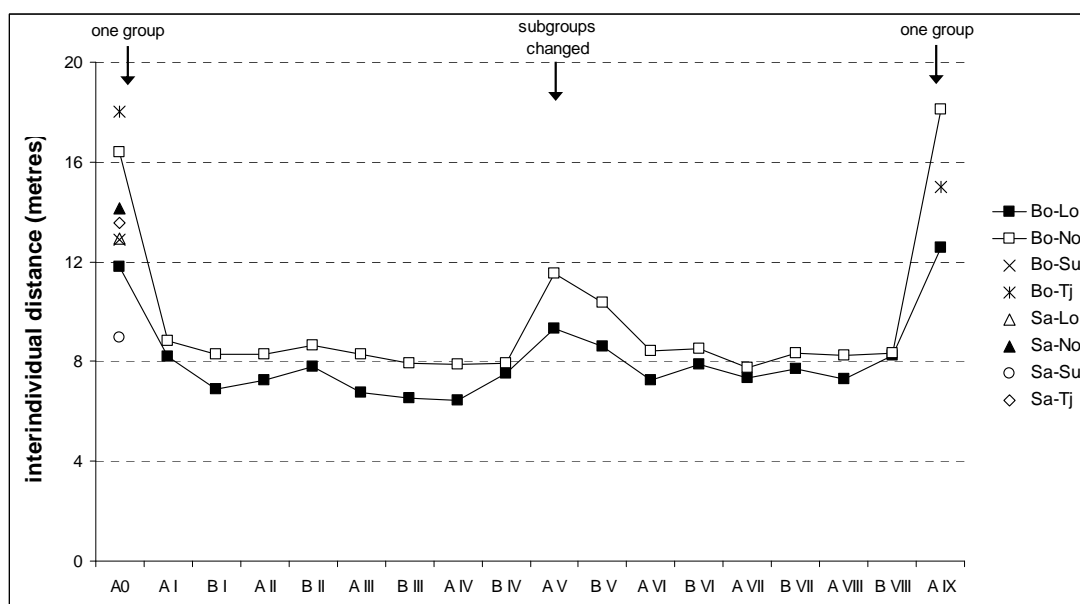


Fig. 3.23: Development distances between sub-/adult males and females

Median distances per dyad are shown for observation sessions between 2002 and 2005.

3.3.2. Patterns of neighbourhood

Main aspects of an individuals' nearest social surrounding were analysed referring to the parameters of nearest neighbour distance, frequency of proximity and changes of neighbours. For these parameters, the term 'spatial proximity' was used when two partners were found within a distance of 3m.

Nearest neighbour distance

The lowest distance to any sub-/adult of all possible partners at every scans' given point of time was analysed per individual. This is presented comparatively per group (Fig. 3.24) and per sex-class (Fig. 3.25).

Between-group comparisons showed that the groups did not differ significantly in their nearest neighbour median distance (Fig. 3.24). Averaged across animals, individuals had a neighbour in a median distance of 4.5m (Kruskal-Wallis: $H=1.160$, $p>0.05$).

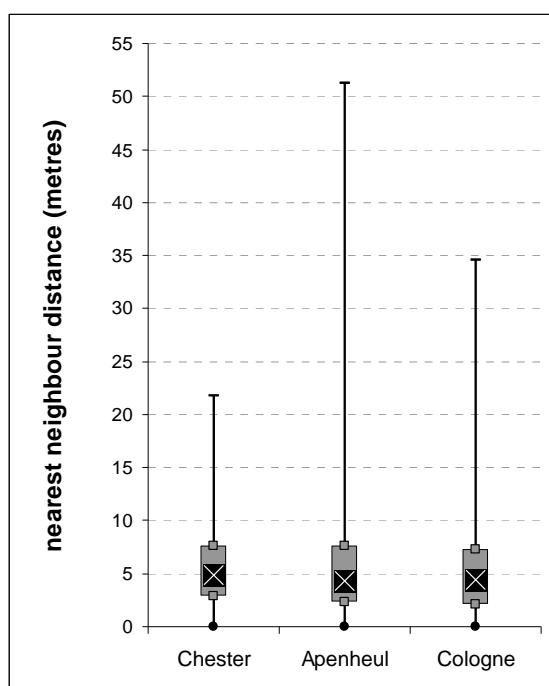


Fig. 3.24: Nearest neighbour distance per group.

Medians, quartiles, minimum and maximum distances to the nearest neighbour per sub-/adult individual are shown, averaged across animals per group. No. of individuals included: CE: 4; AH: 7; CN: 6. Kruskal-Wallis test: $p>0.05$.

Considering the range of neighbour distance, nearest partners were also often far away, i.e. in a distance larger than 7m. Sex-class comparison between the groups (Fig. 3.25) revealed that adult males and females did not differ in their nearest neighbour median distance. For females, neighbour distances did not differ significantly between the groups (Kruskal-Wallis: $H=1.295$, $p>0.05$). Between the males, distances did not differ either though statistical testing was not possible due to the small sample size of males per group. Within-group comparison revealed that nearest neighbours of females were about 1m closer than for males but differences were not significant (Mann-Whitney, AH: $U=0.000$, CN: $U=1.000$, $p>0.05$).

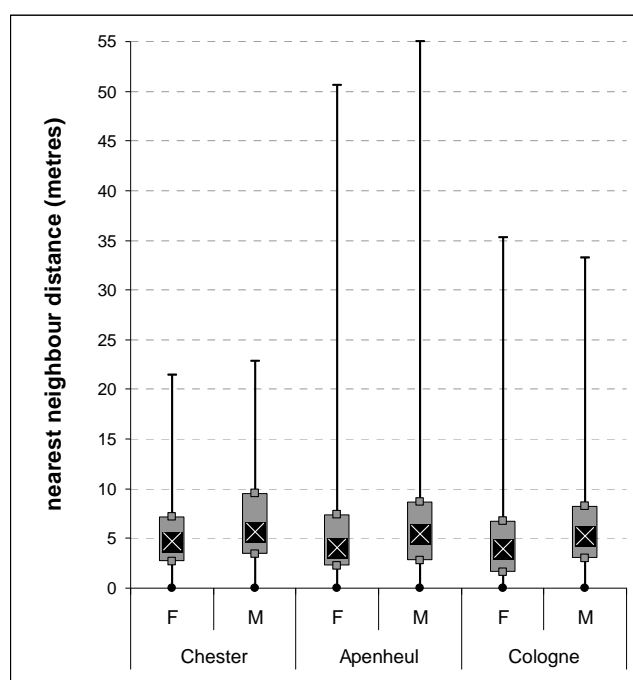


Fig. 3.25: Nearest neighbour distance in sub-/adult individuals per group.

Medians, quartiles, minimum and maximum distances to the nearest neighbour per female and male per group are shown. No. of individuals included: CE: F: 3, M: 1; AH: F: 6, M: 1; CN: F: 4, M: 2. Mann-Whitney U test, F vs. M within groups: all $p>0.05$.

For the Cologne colony the different observation periods are shown in Fig. 3.26. Comparing the periods, individuals had a nearest neighbour in smaller median distances (4.2m) when kept in two subgroups in 2003-04 (Friedman-test: $F=6.500$, $p<0.05$; Dunn's test: 2003-04 vs. 2005: $Q=2.475$, $p<0.05$; 2002 vs. 2003-04: $p>0.05$). In 2005, when kept in one group containing six individuals, nearest neighbours were found in greater median distances

(7.4m) than compared to 2002, when animals were kept in a group consisting of eight individuals (5.0m; Dunn's test 2002 vs. 2005: $Q=1.768$, $p>0.05$).

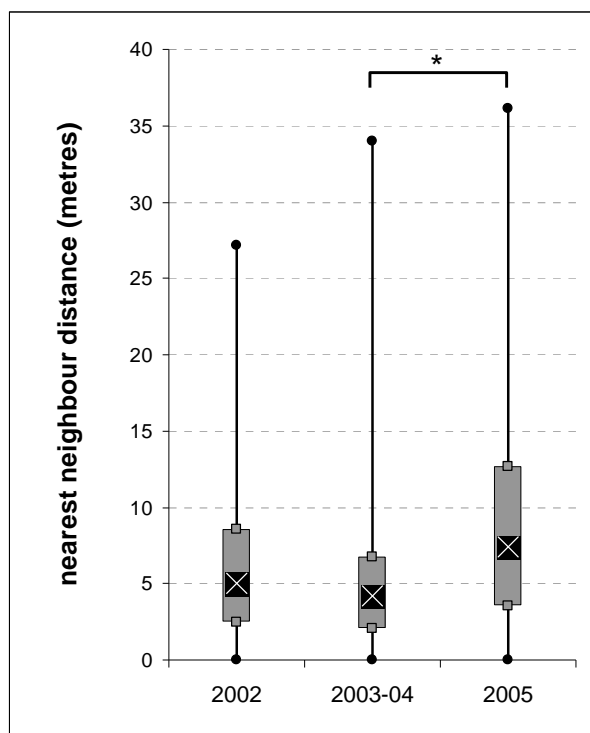


Fig. 3.26: Nearest neighbour distance per observation period at Cologne.

Medians, quartiles, minimum and maximum distances to the nearest neighbour per individual are shown, averaged across individuals at Cologne Zoo. Years represent the observation periods: 2002: A0, 2003-2004: AI-BVIII, 2005: AIX. No. of individuals included: 2002: 6, 2003-04: 5, 2005: 4. Friedman-test and Dunn's test: * $p<0.05$.

Proximity index

The analysis of the proximity index (see Chapter 2.2.3.) presented in the following paragraph refers to how often males and females were located spatially close to each other.

Though most sub-/adult partners had large median distances to each other, they also were in close proximity to a considerable amount of scan samples (Fig. 3.27), i.e. in 10-30% of scans in female-female dyads, and in 5-15% in male-female dyads. Averaged across all, proximity index for a given dyad was 0.13.

Comparing the groups in relation to their (sub-) group size (Fig. 3.27), there was a tendency that in smaller-sized (sub-) groups, proximity indices between individuals were higher than between individuals which were kept together with a higher number of conspecifics. However, between-group comparison showed that proximity indices between females and between males and females did not differ significantly between any of the groups (Kruskal-Wallis, F-F: $H=1.228$, Mann-Whitney M-F, $U=35.000$; $p>0.05$).

Within-group comparison for Apenheul and Cologne revealed that females were more often in proximity to each other than they were to a male but indices did not differ significantly (Mann-Whitney, F-F vs. M-F: AH: $U=33.500$, CN: $U=11.000$; all $p>0.05$).

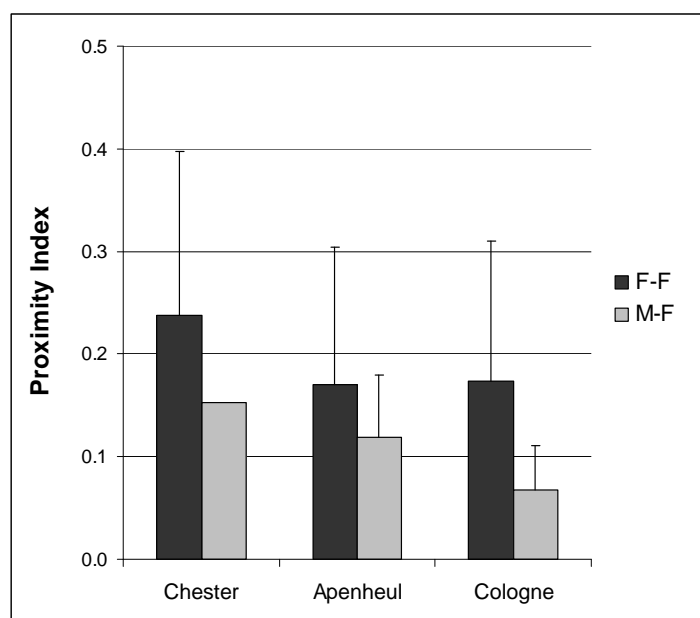


Fig. 3.27: Proximity index for female-female dyads and male-female dyads per group.

Proximity index: number of scans being within 3m distance in relation to total number of scans in sight. Mean values are given; error bars indicate the standard deviation. No. of dyads included: CE: F-F: 3, M-F: 1; AH: F-F: 13, M-F: 6; CN: F-F: 6, M-F: 8. Kruskal-Wallis: F-F and M-F between-group comparison: all $p>0.05$.

Comparing the observation periods at Cologne (Fig. 3.28), spatial proximity between females was less pronounced when the animals were kept in one large group than compared to the time-periods of smaller subgroups (2003-04). Data did not allow statistic tests due to sample sizes. At periods in which individuals were kept all together (2002, 2005), proximity between females did not change significantly (three dyads included; Wilcoxon, $Z=0.142$, $p>0.05$), either between males and females.

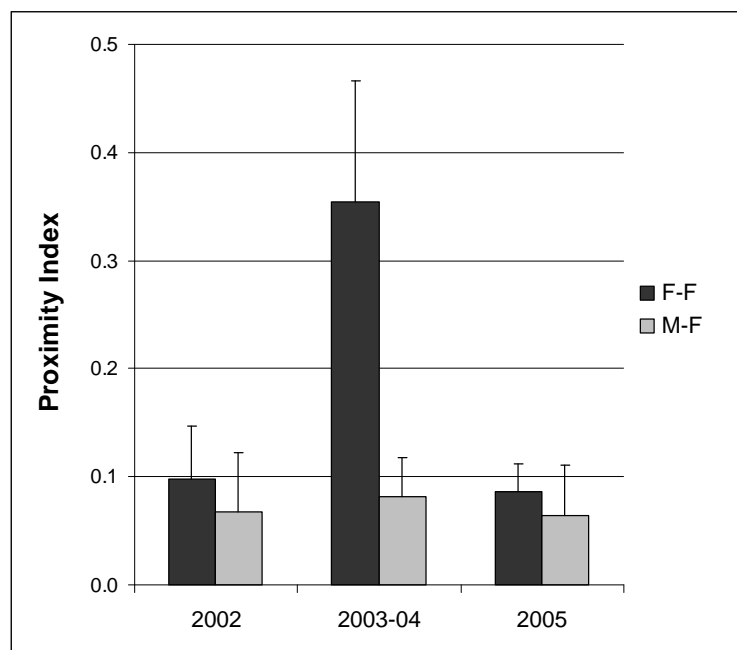


Fig. 3.28: Proximity index per observation period at Cologne

Mean proximity indices for female-female and male-female dyads are shown. Error bars indicate the standard deviation. Time periods (year) represent: 2002: A0, 2003-2004: AI-BVIII, 2005: AIX. No. of dyads included: 2002: F-F: 6, M-F: 8, 2003-04: F-F: 2, M-F: 2, 2005: F-F: 3, M-F: 3.

Sequence of neighbourhood

To investigate whether changes in neighbourhood were non-random, the short-term sequence going from one position scan at a given time-point to the next scan 10min later was examined.

This analysis of short-term sequences of a neighbours' presence and absence per group is shown in Fig. 3.29. In an average 54.2% of consecutive scan samples, an individual had no neighbour within a 3m radius at both points of time. In 32.0%, the presence and absence of a neighbour had alternated within a 10-min interval. Neighbours were present at both time-points in a smaller proportion (mean, 13.9%). The frequency of alternation in a neighbours' presence and absence did not differ between the groups (Kruskal-Wallis, $H=1.099$, $p>0.05$), nor did the frequency that a neighbour was absent at both time points ($H=0.285$, $p>0.05$). At Apenheul, neighbours were more often present at two consecutive scans than at Chester and Cologne but differences were not significant ($H=1.864$, $p>0.05$).

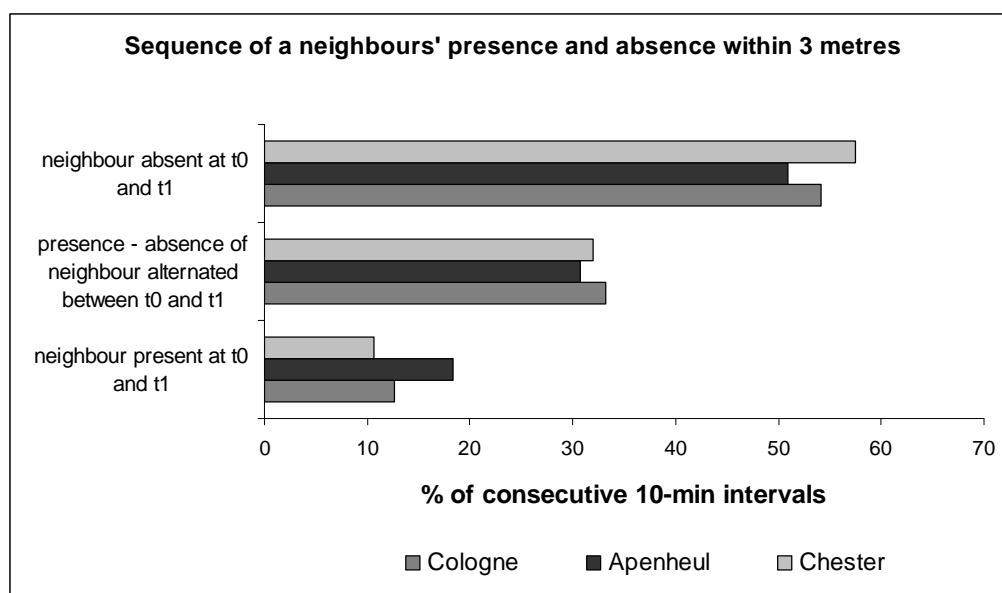


Fig. 3.29: Probability of a neighbours' presence and absence within 3m radius per group. Data are expressed as percentage of consecutive 10-min scans averaged across sub-/adult individuals per group. t_0 = time-point one (first scan), t_1 = next point of time (scan 10min later). Kruskal-Wallis test for the three possibilities of sequences: all $p > 0.05$.

3.4. LONG-TERM SAMPLING OF BEHAVIOURS

In addition to the dataset of 10-min units of focal animal sampling presented before, a second dataset was collected using 3-hrs units of focal sampling at the Cologne group additionally. The different observation methods are compared with reference to the proportion of time individuals spent on main activities. For social interactions, the behaviours *approach*, *groom*, *sit in contact* and *social play* per dyad are shown in more detail. The latency between two consecutive events of *grooming* within a 3-hrs unit, and *approaching* respectively, is presented subsequently.

Referring to activity profiles shown in Fig. 3.30, the mean proportion of time individuals spent on non-social and social behaviours did not differ significantly between the dataset of 10-min units (sessions AI-VIII) and the dataset collected via 3-hrs units (BI-VIII) with the exception of the time spent *within arm's reach* (paired-sampled t-test, *arms reach*: $t=3.378$, $p < 0.05$, all other behaviours $p > 0.05$). The proportion of the time spent on social interactions

varied less between individuals in the 3-hrs observation units though variance was still higher than in non-social activities (see standard deviation).

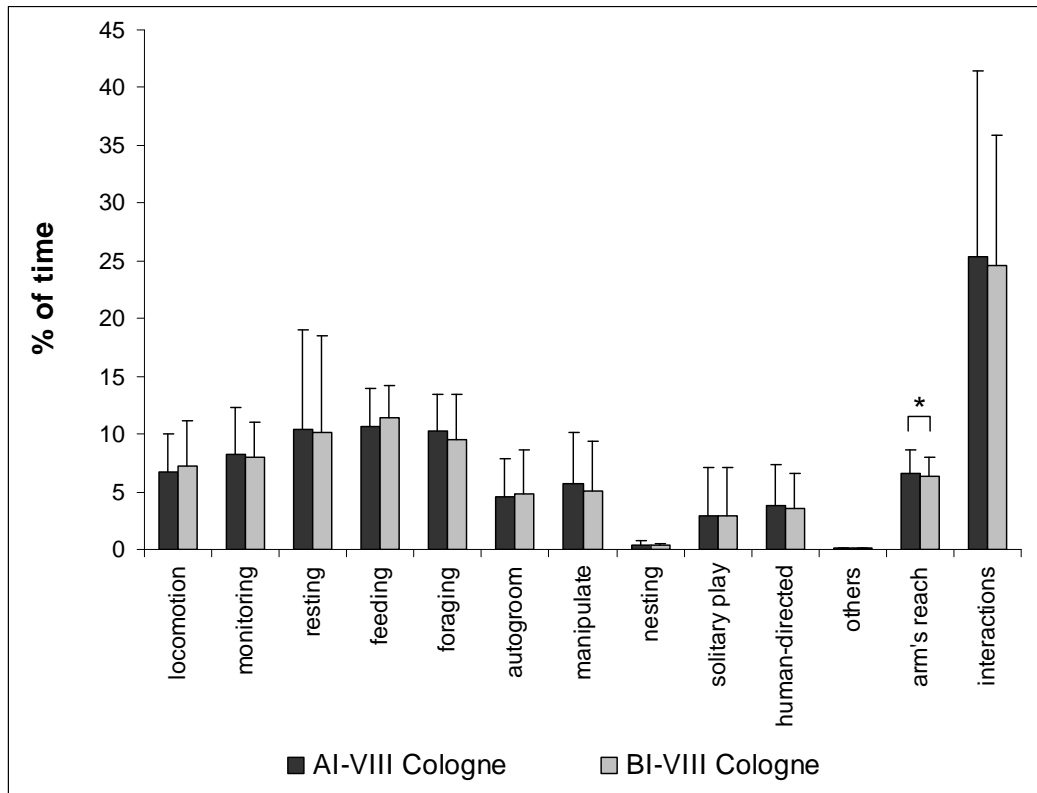


Fig. 3.30: Activity profile Cologne per observational method

Percentage of time individuals spent on non-social and social activities is shown, averaged across all individuals. Mean values are given; error bars indicate the standard deviation. Observation periods AI-VIII: focal animal time comprised 10-min units (total 96hrs/focal animal), BI-VIII were 3-hrs units (total 48hrs/focal animal). Paired-sampled t-test, * $p < 0.05$.

Concerning the mean frequency of interactions, there was a tendency that in most dyads values for the frequency of *grooming* were higher at 10-min observation units compared to the 3-hrs units (Tab. 3.24), and differences were almost significant (Wilcoxon: $Z=-1.923$, $p=0.055$). Frequencies of *approach*, *sit in contact* and *social play* were largely similar for the two types of observation methods.

		mean frequency n / h							
		approach		groom		contact		social play	
	dyad	10-min	3-hrs	10-min	3-hrs	10-min	3-hrs	10-min	3-hrs
F-F	Lo-No	1.9	2.2	1.7	1.2	0.4	0.4	0.02	
F-F	Su-Tj	5.0	5.3	0.9	0.9	1.0	1.1	0.05	0.02
M-F	Bo-Lo	0.4	0.3	0.04		0.01			
M-F	Bo-No	0.1	0.1	0.01					
F-J	Lo-Ba	2.1	2.1	0.1	0.2	0.6	0.8	2.6	2.4
F-J	Lo-Bu	0.7	1.0	0.03	0.1	0.1	0.2	0.4	0.6
F-J	No-Ba	7.1	6.4	1.7	1.1	3.0	2.1	3.7	2.6
F-J	No-Bu	3.4	4.3	0.1	0.2	0.1	0.2	3.2	4.5
F-J	Su-Bu	4.5	3.8	0.3	0.2	2.6	1.7	5.5	3.9
F-J	Bu-Tj	5.9	6.1	1.3	0.6	4.0	3.2	4.4	2.7
M-J	Ba-Bu	5.6	6.4	1.2	0.9	1.3	1.3	13.6	13.9
M-J	Bo-Ba	1.1	1.3	0.1	0.04	0.1	0.2	0.3	0.3
J-J	Bo-Bu	1.2	1.4	0.4	0.4	0.2	0.2	1.6	1.7
Wilcoxon Z		-1.293		-1.923		-0.510		-0.356	
p		0.196		0.055		0.610		0.722	

Tab. 3.24: Comparison of frequency of interactions per observational method

Mean frequency (n/h) of interactive events per dyad and per observational method are shown for approach, grooming, sit in contact and social play. 10-min units of focal time were used in period AI-VIII and 3-hrs units of focal time were used in periods BI-VIII. A blank cell indicates that the type of interaction did not occur within the dyad during the observation periods. Wilcoxon pair-wise comparison was applied for the four behavioural categories.

Referring to the mean duration of interactive bouts, in some dyads values for the duration of *grooming* bouts were higher at the 3-hrs observation units compared to the 10-min units (Tab. 3.25). In female-female dyads and in some female-juvenile dyads, the duration of *grooming* was 0.7-0.9min higher at the 3-hrs units than at the 10-min units. Differences between values, however, were not significant (Wilcoxon $Z=-1.689$, $p=0.091$). Duration of bouts of *sit in contact* and *social play* were similar for both observational methods and differed for the amount of seconds only.

	dyad	min / bout					
		groom		contact		social play	
		10-min	3-hrs	10-min	3-hrs	10-min	3-hrs
F-F	Lo-No	3.82	4.75	0.19	0.23	0.88	
F-F	Su-Tj	2.06	2.85	0.33	0.40	0.65	0.20
M-F	Bo-Lo	0.87		0.25			
M-F	Bo-No	0.08					
F-J	Lo-Ba	0.30	0.24	0.19	0.20	0.54	0.48
F-J	Lo-Bu	0.23	0.24	0.37	0.21	0.76	0.82
F-J	No-Ba	1.01	1.09	0.24	0.22	0.69	0.63
F-J	No-Bu	0.65	1.35	0.13	0.14	1.09	0.93
F-J	Su-Bu	0.33	0.30	0.21	0.23	0.73	1.01
F-J	Tj-Bu	0.86	1.66	0.25	0.29	0.79	0.83
M-J	Bo-Ba	0.27	0.27	0.01	0.16	1.00	0.87
M-J	Bo-Bu	0.37	0.35	0.26	0.16	0.80	0.96
J-J	Ba-Bu	0.45	0.46	0.18	0.18	1.17	1.15
Wilcoxon Z		-1.689		-0.711		-0.357	
p		n.s.		n.s.		n.s.	

Tab. 3.25: Comparison of duration of interactions per observational method

Mean duration (min/bout) of interactive bout per dyad and per observational method are shown for grooming, sit in contact and social play. 10-min units of focal time were used in period AI-VIII and 3-hrs units of focal time were used in periods BI-VIII. A blank cell indicates that the type of interaction did not occur within the dyad during the observation periods. Wilcoxon pair-wise comparison was applied for the three behavioural categories; n.s.: $p > 0.05$.

Referring to the time interval that partners of a given dyad *groomed* and *approached* each other, the number of 3-hrs units in which zero, one and at least two *grooming* events, and *approaches* respectively, occurred is shown in Fig. 3.31. In cases of more than one behavioural event, the latency between the end time and the start time of two consecutive events is given in Fig. 3.31 as well.

Partners of a given dyad did not *groom* during every 3-hrs unit. In 55.5% of units no *grooming* occurred. In 33.8% of units partners *groomed* each other at least two times. In contrast, partners of a given dyad *approached* each other during almost every 3-hrs unit, in 80% they *approached* at least two times (Wilcoxon, *groom* vs. *approach*: $Z = -2.847$, $p < 0.05$). At units in which partners did *groom* at least two times, average latency between two events was 19.6min. The average latency between two *approaches* was 9.0min. However, for both behaviours there was a high variance: latency ranged from seconds to above 90min and differences were not significant (Wilcoxon: $Z = -0.978$, $p = 0.328$).

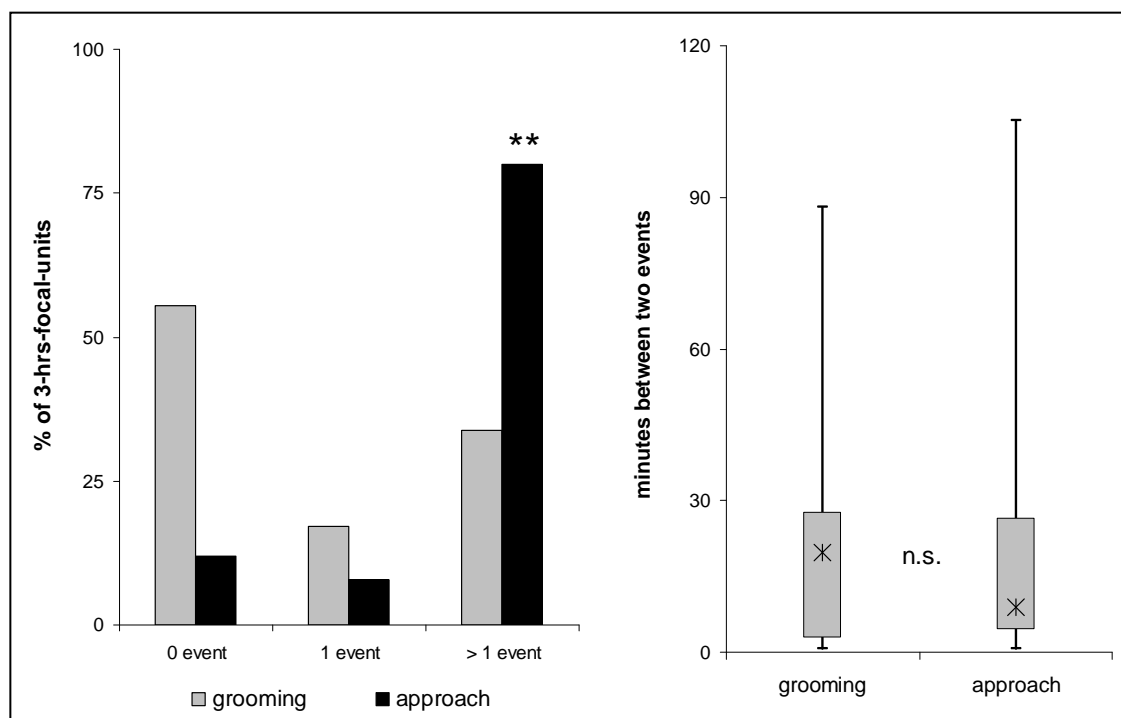


Fig. 3.31: Occurrence and time interval of grooming and approaching within 3-hrs units.

The percentage of 3-hrs focal units containing zero events, one event or at least two behavioural events is shown on the left hand. For 3-hrs focal units containing at least two events of grooming, and approaching resp., the time interval between two consecutive events is shown on the right hand given in minutes. Values are averaged across all dyads (median, quartiles, minimum, maximum). Wilcoxon pair-wise comparison: ** $p < 0.005$; n.s.: $p > 0.05$.

Concerning the age/sex class composition of dyads, in female-female dyads partners repeatedly *groomed* each other in about 50% of all 3-hrs units (Fig. 3.32). In the other half of observation units, however, they did not *groom* (21.9%, and 43.8%) or *groomed* only once during a 3-hrs unit.

In male-female dyads, *grooming* was observed not at all in any of the 3-hrs units. With the exception of mother-offspring dyads (No-Ba, Tj-Bu) and the juvenile-juvenile dyad (Ba-Bu), repeated *grooming* occurred in less than 50% of observation units in dyads containing a juvenile individual. In contrast to *grooming*, partner repeatedly *approached* each other in almost all observation units except male-female dyads (Fig. 3.32). In the latter, partners did not *approach* or *approached* only once during most 3-hrs units.

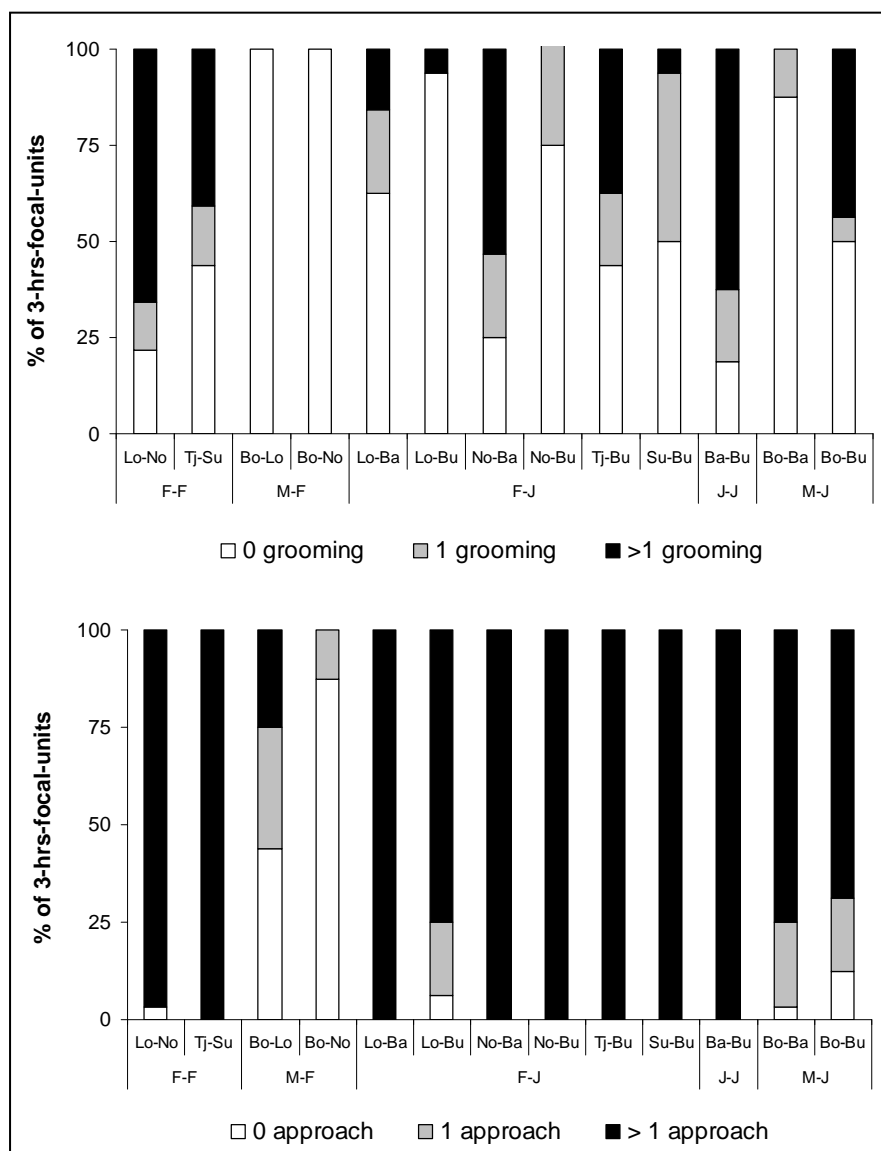


Fig. 3.32: Occurrence of grooming and approaching within 3-hrs units per dyad.

The mean percentage of 3-hrs focal units containing zero events, one event or at least two events of grooming, and approaching resp. is shown.

3.5. SUMMARY OF RESULTS

At Cologne and Apenheul, individuals spent about a fifth of their time on social interactions. At Chester, animals were engaged in social activities just for a small proportion of time, significantly less time compared to Cologne but not significantly less than at Apenheul. In the latter group, animals spent significantly more time *sitting within arm's reach* compared to Chester but not significantly more than at Cologne. At Chester, animals spent significantly more time on *social resting* and *social feeding* than individuals in the other

groups did. In all groups, the most frequent social activities were *approaching* and *leaving* a partner, followed by *sociopositive* interactions. *Agonistic* events occurred rarely; they were mainly *mild*.

Aberrant behaviours were observed most often at Cologne; however, they were generally rare in all groups and observed in few individuals only.

Adult individuals interacted a few times per hour; interactions lasted on average some seconds. A maximum of a few minutes was observed in a few dyads only. There were significant differences in the total frequency of interactions and duration neither between the groups nor between age/sex classes within groups. Nevertheless, there was a tendency that a sub-/adult female interacted more frequently with another adult female or with a juvenile partner than with a sub-/adult male. In all groups however, the amount of interactions highly varied between dyads of the same age/sex class.

Agonistic interactions between females occurred less often than in male-female dyads, and female-juvenile dyads respectively. Juveniles were often interactive partners for sub-/adults. Active-passive relations of *sociopositive* and *agonistic* interactions were unidirectional in most dyads. Senders of *grooming* mostly received *dominant* behaviours and/or were sender of *submissive* signals. However, *dominant/submissive* behaviours and/or *grooming* did not occur in all dyads. *Triadic* interactions were very rare.

Referring to the social relationships of the different age/sex classes, the female-female relationships tended to be affiliative with a varying amount of *sociopositive* interactions. *Touching* was the most common interaction. *Grooming* and *sit in contact* were most pronounced at Cologne. At Cologne, dyads did not differ significantly in their *grooming* rates. At Chester and Apenheul, there was only one dyad each in which partners *groomed* each other significantly more often than others. *Agonistic* interactions were not observed in all dyads. *Agonistic* behaviours were found mostly between the related females at Chester. The male-female relationships were marked by a scarcity of physical interactions. There were no statistic differences between dyads concerning *grooming* rates at Cologne. At Apenheul, higher *grooming* rates were only found in the related male-subadult daughter pair. Rates of *sexual* interactions did not differ between the dyads at Apenheul and Cologne. *Agonistic* interactions were observed in most of the dyads. The male and the subadult male at Cologne had a mild dominance relationship characterized by *submissive* signals by the subadult male. Sub-/adult-juvenile relationships both in female-juvenile and in male-juvenile dyads tended to be

friendly, varying in the amount of *sociopositive* interactions. Partners mainly *touched* each other and in some cases they exhibited extensive *social play*. *Agonistic* interactions were observed within most dyads. The juvenile-juvenile relationships were characterized by reciprocal and extensive *social play*, *touching* and a lack of *agonistic* interactions.

The long-term observations at the Cologne group revealed that the female-female relationships were stable regarding the frequency of interactions with a tendency of longer-lasting *grooming* bouts when partners were kept in smaller-sized subgroups. The male-female relationships were stable regarding the frequency of interactions as well. However, *grooming* was distributed inconstantly over time. The introduction of the juvenile male seemed to have an influence on the adult male's participation in interactions who was engaged in *social play* with the juvenile on occasion.

The patterns of spatial behaviour were characterized by large and highly variable interindividual distances, small nearest neighbour distances, and frequent changes of partners within the nearest surroundings. Median distances between individuals at Cologne and Apenheul were significantly higher than at Chester with distances being highest at Cologne. No other significant differences between the groups were found. At Cologne, individuals tended to be more widely dispersed under conditions of more available space. Concerning sex-class differences, females were in proximity to other females more often than to males. However, there were no significant differences between the sex-classes in any of the parameters analysed. Within sex-classes, distances between females at Chester and at Cologne did not differ significantly; at Apenheul only a few dyads differed significantly regarding their median distance. Distances between male-female dyads did not differ at Cologne; at Apenheul significant differences were found between two dyads only.

Data collected with the two different sampling methods at Cologne did not differ much from each other. For *grooming* there was a tendency that the 10-min sampling data resulted in higher frequencies and shorter durations of *grooming* bouts. Additionally, the 3-hrs sampling method provided information about the time-slots of *grooming* and *approaching*. In all age/sex classes partners *approached* each other on a more regular basis but *groomed* more irregularly. The latency between consecutive *grooming* events was higher than between two *approaches*.

4. DISCUSSION

This study aims to increase the understanding of the orangutans' social system, and sociality respectively, by investigating the social relationships in several groups of Bornean orangutans in captivity on a proximate level. The results of this study will be discussed with a special focus on the following aspects: (1) the individuals' sociability, (2) the structure of their social relationships, and (3) their fission-fusion tendencies.

4.1. SOCIABILITY

Although the orangutans of all groups spent most of their time on non-social activities, overall they showed higher levels of social activities compared to findings from free-ranging orangutans (Knott, 1999). The studied animals spent up to one sixth of their time on social resting and social feeding, and interacted also more frequently and with more physical contact than described for individuals in the wild (Rodman, 1973; Rijksen, 1978; Galdikas, 1984). In natural settings, orangutans sometimes spend a considerable amount of time with a conspecific (see Galdikas, 1985a; Sugardjito *et al.*, 1987; Mitani *et al.*, 1991; van Schaik, 1999). Quantitative direct comparisons are difficult however, as the orangutans' natural dispersal patterns differ considerably from the conditions in captivity. Nevertheless, the present finding of an overall high amount of social interactions compared to wild individuals is consistent with previous studies in captivity (Edwards and Snowdon, 1980; Poole, 1987; Zucker and Thibaut, 1995; Klein, 1999; Beaver, 2000). These authors explained their findings with regard to the greater availability of partners, higher density and abundance of food. Their results, however, were derived from only a small sample size and included a few hours of observation. In addition, the study by Poole (1987) was biased for selective day-time periods (periods of "high activity"). At Apenheul and Cologne – representing groups with a large number of partners – the overall high amount of social activities in relation to other daily activities may be further affected by the presence of juveniles and infants being an additional stimulating factor (see Wilson, 1982). Both factors were absent at Chester. On the dyadic level, individuals were engaged in social interactions for similar amounts in all groups.

The social relationships in the studied groups were mainly affiliative. Overall, *agonistic* interactions were rare, supporting the findings from previous zoo-studies (Edwards and Snowdon, 1980; Poole, 1987; Klein, 1999). Contrary, in free-ranging orangutans, the social relationships seem to be more variable (van Schaik and van Hooff, 1996). Although at some sites, some females encountered specific social partners preferentially (Singleton and van Schaik, 2002; Knott *et al.*, 2008), individuals are probably less familiar with each other due to the rare and short contacts.

The higher frequency of social activities found in the individuals studied may have been facilitated by limited spacing and avoidance possibilities in captive settings, and by their living together for many years, resulting in a great mutual knowledge (Zucker and Thibaut, 1995). For instance, at the Cologne group individuals knew each other since infancy, and showed the highest amount of *grooming*. Contrary, the Apenheul colony had been newly established, consisting of adult individuals that did not grow up together. In this group, *grooming* and prolonged *contact* occurred less often. In all groups, not only the mother-reared individuals but also the hand-reared ones displayed the social potential to cope with their conspecifics with a very low number of conflicts. This finding supports the hypothesis by Zucker and Ferrera (1990) which suggests that the rearing history might influence the individuals' social behaviour. An early (re-) integration of young animals thus facilitates not only the development of familiarity among partners but also the acquisition of social competence.

The local keeping conditions such as feeding routines and available space varied between the study groups and might have influenced the individuals' activity budget and amount of social activities. The results of this study reveal that the groups differed significantly in the time spent on *resting*, *monitoring*, *feeding* and *foraging* possibly related to differences in housing routines. Individuals at Chester and Apenheul for instance mainly received clumped feeding and their enclosures were less enriched. The results showed that, in contrast to the individuals at Cologne, they were more stationary and spent less time *foraging*. Under captive conditions, challenging situations such as complex food-processing and arboreal foraging patterns like in the wild habitat can hardly be provided. However, as mentioned by Perkins (1992) and Tripp (1985), the provision of spacious enclosures and many movable and edible objects may promote higher levels of activity. The higher level of mobility found at the Cologne group supports this assumption.

In addition, the results of this study indicate that the three groups differed in the proportion of time individuals spent on the total of social activities but scarcely differed in the proportion of various types of interactions. At Chester, the higher number of *agonistic* interactions might have been affected by the clumped feeding schedules and a smaller amount of usable space in one of the enclosures. Data about the influence of clumped feeding and/or spatial crowding are however, not available for captive orangutans. In captive bonobos, short-term spatial crowding was found to increase both grooming (Paoli *et al.*, 2007) and aggressiveness (Sannen *et al.*, 2004). In captive chimpanzees, Aureli and de Waal (1997) interpreted decreased rates of agonistic interactions under high-density conditions as an inhibition strategy to reduce opportunities for conflict. However, the researchers found increased social tension in terms of elevated rates of behavioural indicators of anxiety such as rough scratching and yawning.

Another factor which may affect an animals' behaviour in captivity is the presence of humans (Hosey and Druck, 1987; Chamove *et al.*, 1988). In the current study, *human-directed* behaviours were observed both in captive-born individuals (hand-reared and mother-reared) and in wild-born individuals. However, the behaviours made up only a small proportion of the animals' total activity. All groups were observed during phases of high visitor densities, and rates of *agonistic* interactions generally tended to be low. Nonetheless, cases of individuals breaking up distinct interactions with conspecifics (e.g. *grooming*, *playing*) due to the presence of e.g. 'permanent' visitors and care-givers were observed. Some individuals thus may be more responsive to the presence of humans than others. Previous studies about the effect of humans on the behaviour of orangutans (Birke, 2002; Breitkopf, 2006; Davey, 2007) support the present findings and also did not find an increase of agonistic behaviours in the presence of noisy (or 'active') human groups. However, the researchers observed higher levels of locomotory and foraging activities, as well as a higher amount of contact between mother-infant pairs and self-covering. In a study investigating the influence of visitors on stress hormones, Baumgartner (2010) did not find a positive correlation. In captive chimpanzees (Perret, 1994) and gorillas (Wells, 2005), however, higher levels of intra-group agonistic interactions were reported during high densities of visitors. It is thus possible that the presence of humans does not affect the level of *agonistic* interactions between the studied orangutans but may have at least a short-term effect on *sociopositive* behaviours.

Under captive conditions, there are multiple factors which may affect the development of aberrant behaviours, such as the local social set-up, low environmental stimuli, or an animals' rearing history (see Carlstead and Shepherdson, 2000). Under the aspect of animal welfare, these factors are regarded as potential stressors in zoo-environments. Living in a permanent group represents a stark contrast to the natural semi-solitary fission-fusion sociality of orangutans (Kaumanns *et al.*, 2004). The artificial group-keeping situation therefore may represent a factor influencing the development of atypical behaviours. In this study, aberrant behaviours were found in a few and mainly female individuals and with low rates of occurrence. Differences in the frequency of aberrant behaviours were found on the group-level with highest rates at the Cologne group. An individual responsiveness to the influence of social keeping conditions therefore can not be excluded. A few previous studies on captive orangutans reported the occurrence of atypical behaviours such as stereotypy and/or eating plastic (Beaver, 2000; Herbert and Bard, 2000). They support the speculation that permanent group-living may represent a potential stressor, at least for female Bornean orangutans (see also Weingrill and Heistermann, 2008).

Data of the current study were collected from different groups, including a larger sample size of (adult) individuals and considerably more hours of observation than compared to any other previous captive study investigating social aspects in orangutans. So far, relatively little is known about Bornean orangutans in captivity. Based on observations in natural settings, Delgado and van Schaik (2000) however suggested that differences in the sociability between Sumatran and Borneo orangutans might be explained in terms of habitat quality and population density. Since the individuals observed in the present study belonged to the Bornean species, their high degree of sociability thus provides evidence for the social potential of this species. These findings may also be relevant for the management in captivity.

The results of this study support the assumption that orangutans have the potential to engage in a high amount of social activities under permanent group-living conditions without many conflicts (e.g. Edwards, 1982; Klein, 1999). These findings are of special importance because they can not be demonstrated under natural conditions (see van Schaik *et al.*, 2009). Furthermore, the present findings indicate that the amount of potential social contact, e.g. the group-size, affects the total social activity but not the amount of interactions per dyad.

4.2. THE STRUCTURE OF SOCIAL RELATIONSHIPS

The analysis of the structure of social relationships in the three groups demonstrated in which way the orangutans managed a permanent group-living situation. The majority of social relationships tended to be affiliative, only a few were of an agonistic nature, while several were 'neutral' such that individuals *approached* and *left* but did not interact further. At Apenheul and Cologne, females tended to interact more often with other females or with juveniles than with a sub-/adult male. Interactions were mainly brief in all age/sex classes. *Triadic* interactions were rare. These basic findings support the predictions. Unexpectedly however, individual variation was higher than group-specific differences. Contrary, the different demographic conditions seemed to have not much influence on the structure of social relationships.

The high variation between dyads in the amount of interactions largely supports findings from field studies, which suggest 'individualised' or 'special' social relationships between adult individuals (Schürmann, 1982; Galdikas, 1984; Mitani, 1985a; van Schaik and van Hooft, 1996; Delgado and van Schaik, 2000). Comparable results to the present study have been reported from a small group of Bornean orangutans (Edwards and Snowdon, 1980) and from a large group of Sumatran orangutans by Klein (1999) in captivity. In the current study, there were no significant differences in the main categories of interactions in relation to the age/sex class composition of dyads. Similarly, Zucker and Thibaut (1995) who observed a group of Sumatran orangutans did not find differences in the mean duration of sociopositive interactions between different age and sex classes. Thus it can be assumed that the individual variation exceeds age/sex class related differences.

Although the frequency of interactions was relatively high in some dyads, the duration of bouts was relatively short in all dyads. Physical contact between sub-/adult individuals lasted on average some seconds only. Comparative, quantitative data from orangutans under natural conditions are not available. However, previous studies on captive groups of Sumatran orangutans showed mixed results. Klein (1999) for instance found longer and shorter bouts of physical contact between some adult individuals, while Zucker and Thibaut (1995) did not observe any contacts. Edwards and Snowdon (1980) and Poole (1987) did not measure the absolute duration of behaviours but used a scan sampling method. Quantitative data which could provide comparativeness for the frequency and duration of contacts thus are

limited. Concerning other primate species for which comparable captive data are available, a study on bonobos showed the duration of physical contact within female-female dyads to be five to six times higher (Kießling, 2008). Furthermore, females of a group of lion-tailed macaques (Groh, 2005) interacted twice as much than the female orangutans studied here. This inter-species comparison indicates that between the studied individuals, the social cohesion in terms of prolonged physical contact was rather low.

The finding of brief physical contact is supplemented by the result that *triadic* interactions were very rare. Similarly, triadic interactions (e.g. giving support in agonistic interactions) presumably do not occur between free-ranging orangutans (see van Schaik and van Hooff, 1996). For other apes, however, such interactions are described (e.g., chimpanzees: Baker and Smuts (1996) and Newton-Fisher (2006); bonobos: Badrian and Badrian (1984) and Vervaecke *et al.* (2000)). Most previous studies on captive groups of orangutans did not report the occurrence of triadic interactions. Anecdotal evidence on male intervention during female-female conflicts has been provided by a few studies (Edwards and Snowdon, 1980; Zucker, 1987; Klein, 1999). Recently, Tajima and Kurofori (2010) found non-aggressive interventions by third parties for settling conflicts. They suggested the orangutans to actively promote the peaceful coexistence of other individuals. In the current study, most *triadic* interactions were also without contact and non-aggressive. The males, however, seldom participated in *triadic* interactions probably because *agonistic* interactions between the females were rare per se.

Between the sub-/adult females of the study groups, some of the social relationships can be characterized as affiliative, marked by almost exclusively *sociopositive* interactions. In some others of the female-female relationships, dominance may have played a role since senders of *grooming* received *dominant* behaviours and/or were senders of *submissive* signals. This variability also occurred between females of the same age and similar reproductive status. For wild female orangutans, Galdikas (1984) discussed dominance relationships to be indicated best in relation to different age-classes and different reproductive status. Galdikas (*ibid.*) however also mentioned that peer groups might be more important for associations than genetic ties. The results of this study support all three aspects.

According to the grooming-model by Seyfarth (1977), the distribution of *grooming* and *agonistic* behaviours found between some of the females studied would indicate a so-called 'grooming up the hierarchy' at first. However, *dominant/submissive* signals and/or *groom-*

ing did not occur in all dyads. A potential service gained from grooming might be addressed to potential support in fights (Seyfarth, 1977) but this was almost absent in the studied groups. For free-ranging orangutans, rank differences have been discussed by van Schaik and van Hooff (1996) – although females rarely associate. In a captive Sumatran group, Klein (1999) assumed (undecided) dominance relationships among the four sub-/adult females. In the groups at Apenheul and at Cologne, most females were not related but there seemed to be no clear hierarchical structure among them. Additionally, there were almost no significant differences in *grooming* rates between dyads which would have indicated preferential affiliation among certain partners. At Chester, *sociopositive*, *dominant* and *submissive* signals between the related females were distributed in relation to age, and thus may indicate a dominance hierarchy. These results contrast to some findings for wild orangutans (see Singleton *et al.*, 2009) where preferential affiliation among female relatives and “not friendly relationships between females of different clusters” (Singleton *et al.*, 2009, p.212) were reported. For free-ranging Sumatran females, Utami *et al.* (1997) described hierarchical structures as an outcome of feeding competition and this might also be the case between the females at Chester affected by the clumped feeding schedules.

Overall, the female-female relationships could be characterized as tolerant and friendly. When *agonistic* interactions occurred, they were expressed via spatial avoidance or *mild dominant* behaviours. Serious conflicts were almost absent. Anecdotal cases of fights occurred unexpectedly without obvious preceding *agonistic* interactions. This finding is similar to observations in the field done by Rijksen (1978). He mentioned that “as a rule, attacks by females were explosive outbursts, not preceded by threatening signals” (Rijksen, 1978, p.279). In another previous study on captive individuals, Edwards and Snowdon (1980) speculated that at least female orangutans may have employed distinct means such as monitoring and spacing to keep agonistic-contact interactions at a subdued level.

Male-female relationships in this study consisted of low rates of physical contacts and can be characterized as ‘neutral’. This finding is largely compatible with observations from wild individuals where adult males are highly solitary apart from sexual contexts (MacKinnon, 1974; Galdikas, 1985b, c; Mitani *et al.*, 1991). Though occurring at low rates, brief events of *grooming* and *touching* between the males and some of the females were observed. These results are consistent with findings on other captive orangutans (Edwards and Snowdon, 1980; Zucker and Thibaut, 1995; Klein, 1999). Under captive conditions, adult males seem not to be that strictly solitary as described from the field, probably due to the greater famili-

arity between the group mates (Edwards and Snowdon, 1980; Poole, 1987). However, the present results did not indicate preferential affiliation in terms of *grooming* between specific pairs with one exception, the male-subadult daughter pair at Apenheul.

In the study groups, physical contact was also made during the *sexual* context. Few instances of *copulations* were observed at Apenheul and Cologne. At Cologne, some of the *copulations* were forced with two potentially non-receptive females. Such *rapes* by adult males also occur in the wild (Mitani, 1985b) and can not be attributed to the social living-conditions in captivity only.

The male-male relationship at Cologne can be characterized as a dominance relationship. The adult male tolerated the subadult male whereas the latter predominantly avoided closer proximity towards the elder. This behaviour is in accordance with findings from field studies (Galdikas, 1985b; van Schaik and van Hooff, 1996). Besides the cryptic life-style of subadult males in the presence of adult males, Utami and van Hooff (2004) and Maggioncalda *et al.* (2002) suggested that the arrest of secondary sexual development may be an adaptation allowing males to avoid aggression and associated stress. At Cologne, the subadult male had not developed secondary sexual characteristics, and was rarely involved in *sexual* interactions with the females. Probably the long-term mutual knowledge of the males further enabled the observed interactive pattern. Similarly, Poole (1987) reported amicable relationships between three fully adult males in captivity who had been reared together.

In the study groups at Apenheul and Cologne, the sub-/adults and juveniles often interacted with each other. Their relationships were basically friendly containing a small amount of *mild agonistic* elements. In their natural environment, Galdikas (1995) and van Schaik (1999) observed that non-consort associations between adolescents and adults are mostly initiated by the younger individuals. In previous captive studies on groups consisting of adults and juveniles, adolescents respectively (Poole, 1987; Zucker and Thibaut, 1995; Klein, 1999), the juveniles initiated contacts with older individuals more often than vice versa. However, direct comparisons are limited since the published data provide a few types of interactions only. The findings of the current study additionally indicate that a shared childhood including individuals of different age-classes might be advantageous concerning the aspect of acquisition of important social skills (such as raising offspring). In the wild, females with offspring sometimes associate in so-called 'nursery groups' in which offspring

can socialize (van Schaik, 1999). Also for independent immature animals, Meder (2007) assumed social contact to be still necessary for their further development.

The relationships between the mothers and their dependent offspring represented the strongest social relationships and are consistent with observations both in the wild (e.g. MacKinnon, 1974; Horr, 1975; Galdikas, 1984) and in captivity (Poole, 1987; Klein, 1999). The relationships between sub-/adult females and unrelated juveniles can be characterized as mainly friendly. The amount of mild *agonistic* elements did not differ from that in mother-offspring dyads. Findings from the field (Rijksen, 1978; Galdikas, 1984) and from captive studies (Edwards and Snowdon, 1980; Klein, 1999; Claßen, 2001) indicate that the quality of relationships between adult females and adolescents may vary more than found in the current study, ranging from friendly to agonistically coloured relationships.

The adult males at Apenheul and Cologne as well as the subadult male at Cologne were engaged in *social play* with the juveniles and behaved tolerant towards them. In the field, comparable opportunities for male-juvenile interactions presumably do not exist since females with mid-sized offspring are found to avoid associations with mature males (van Schaik, 1999). In captivity, adult males are reported to engage in social play with juveniles (Zucker and Thibaut, 1995; Klein, 1999). The authors suggest that the greater confidence of paternity in captivity contributes to the increased interactions by males with juveniles. In the present study groups, the juveniles were sired by the males and have grown up with them. The interactive pattern found may also be attributed to a form of paternal investment. In the field, females are suggested to employ paternity confusion behaviours as an anti-infanticide strategy (Utami *et al.*, 2002; Knott, 2010).

The juveniles at Apenheul and Cologne had mainly *playing* relationships among each other which is similar to findings both from the field (MacKinnon, 1974; Galdikas, 1985a; van Schaik, 1999) and from captivity (Edwards and Snowdon, 1980; Zucker and Thibaut, 1995). Based on her long-term observations in the wild, Galdikas (1984) mentioned that closer bonds established during adolescence presumably dissolve at adulthood.

The long-term observations from the Cologne group reveal that the quality of social relationships between adult individuals remained relatively stable over time, with a tendency of lower rates of tactile interactions when living together in a large group. This is the first study which investigates long-term patterns in this respect. Comparisons with reports from the field are hardly possible due to the rare encounters of defined pairs of individuals. There are only anecdotal reports that between some females repeated encounters are of the same

quality (Galdikas, 1984; Knott *et al.*, 2008). During the final observation session at Cologne, the amount of *sociopositive* and *sexual* interactions tended to increase between the male and one of the adult females. The altered interactive pattern, though representing an anecdotal case, may be attributed to the weaning of the female's offspring and a resulting receptivity. Correspondingly in the wild, the quality of encounters between males and females seems to – at least partly – vary depending on the females' reproductive status (Schürmann, 1982).

On the interactive level, this study demonstrates that the individuals were tolerant of each other, and that they had mainly affable social relationships with just a low number of conflicts under the conditions of “artificial” group-living. Considering the relatively low rates and short duration of physical contacts, and that the individuals had only a few or no significant preferences for specific partners to interact with, at least the adult individuals seemed to have established weak social bonds among each other. Furthermore, conspicuous greeting interactions which are assumed to function as a test of the quality of dyadic relationships (Kummer, 1968) were not observed. The network of social relationships seems to be loose as measured by the low number of *triadic* interactions. There has been no other previous captive study demonstrating these key results on the orangutans' sociality in a comparable way. For free-ranging orangutans, van Schaik and van Hooff (1996) suggest no active female bonding through affiliation, grooming or agonistic support. The present findings indicate that this may also apply for orangutans under the socio-ecological conditions in captivity.

4.3. FISSION-FUSION TENDENCIES

The interactive patterns described beforehand were embedded into the scope of spatial behaviour found in the study groups. The individuals were located several metres away from each other again soon after an “encounter”. The presence and absence of a partner nearby often alternated. At grouping situations with many partners and more space available these tendencies were more pronounced than between partners in small permanent (sub-) groups. At Apenheul, where husbandry schedules stimulated a fission-fusion situation, corresponding tendencies were less pronounced in the spatial behaviour of the individuals as compared to Cologne.

Quantitative comparisons of fission-fusion tendencies between zoo-living and free-ranging orangutans are difficult due to the spatial restrictions in captivity resulting in a lack of opportunities to substantially separate from partners. Furthermore, the spatial definition of a social group used by field studies includes a radius of 50m distance (e.g. Knott *et al.*, 2008) which would be the maximum possible distance in some of the groups of the current study. However, as mentioned by Romero and Aureli (2007) underlying processes of fission events may be functionally similar in captivity (see also Aureli and Schaffner, 2005). On a qualitative level, the spatial patterns found in the present study reflect traits of fission-fusion structures in all groups. This study is the first one providing detailed data about the spatial patterns and referring to fission-fusion structures in captivity. Furthermore, no previous study has been carried out on a group of orangutans under flexible social keeping schedules like the one at Apenheul.

The finding that partners sought and tolerated each others proximity regularly is in accordance with results found by Klein (1999) in a captive group of Sumatran orangutans. A comparison of proximity indices with other captive groups of orangutans however, can not be done due to the lack of studies referring to this parameter. Compared to other primates living in highly flexible societies such as bonobos, the proximity indices found in the studied orangutans were similar to those described for bonobos in captivity (Stevens *et al.*, 2006) and in the wild (Furuichi and Ihobe, 1994). This comparison shows that the studied orangutans displayed a similar level of attraction and tolerance, at least short-termed.

In all groups of the current study, there were small distances between nearest neighbours and – in contrast – large median interindividual distances. Average distances between individuals at Cologne were significantly greater than those between individuals at Apenheul and Chester. In a small captive group of orangutans, Zucker and Ferrera (1990) found slightly smaller mean distances but also a great variability among observation sessions. In a study on semi-free adolescent and juvenile Bornean orangutans, Bolhassan (2001) found interindividual distances comparable to the results presented. Other comparable quantitative data of interindividual and nearest neighbour distances are not available for other captive groups of orangutans, for free-ranging orangutans either. Regarding chimpanzees and bonobos, which are also organised in fission-fusion societies, and for which comparable data of nearest neighbour distances are available, values just slightly differ from what was found in this study. White and Chapman (1994) found mean nearest neighbour distances of 4.1m and 5.5m in free-ranging chimpanzees, and bonobos respectively. Newton-Fisher (2002) re-

ported a mean distance of 1m between nearest adult male chimpanzees within a party. Referring to the possible maximum distances for the studied groups of orangutans compared to the unlimited space in the wild and distance found at least in chimpanzees and bonobos, the results indicate that the spatial cohesion between the individuals was low.

The spatial and social behavioural patterns found in the studied orangutans matched: usually not more than two individuals *approached* and *left* each other again; partners interacted *sociopositively* but just briefly. This patterning resembles what is described as fission-fusion sociality in wild orangutans (van Schaik, 1999). The analysis of the 3-hrs unit dataset from Cologne supports and supplements these findings as individuals *approached* within short time-slots, and *groomed* inconsistently within larger time-slots. The sampling rule of longer focal units has not been used in any other previous study of captive orangutans. The comparison of the activity profiles revealed that the data of both methods were valid. The differences concerning the duration of *grooming* bouts may represent a true difference, they might be however also caused by the smaller sample size of 3-hrs units. Apart from that, the findings show that also for captive studies longer focal units provide the opportunity to analyse behavioural sequences, giving supplementary information about the temporal patterns of “encounters”.

4.4. GENERAL CONCLUSIONS

This is the first study which investigates aspects concerning the social system and sociality in captive Bornean orangutans including several groups, a larger number of individuals, and long-term observations. A large and detailed dataset is provided not only about the interactive behaviour but also about spatial patterns for the first time.

The socio-ecological conditions for an animal in captivity often deviate from the wild. Some resulting effects however, might be expressed and detected at an accelerated pace within a limited and manageable artificial environment. As one possible effect, both intensified sociopositive contact and conflicts may occur frequently due to the permanent high density of social partners. However, the findings of this study do not indicate this. The present study shows that the individuals dealt with the artificial group-living situation with a low level of conflicts. At the same time, they had social relationships characterized by weak social bonds between adult partners in terms of low physical affinity, short contact, and only little prefer-

ence for specific partners to interact with. *Following* behaviour to keep proximity was rare and individuals did not maintain stable distances to each other, both indicating a low level of spatial (and temporal) cohesion. The “minimized” form of fission-fusion structures found in the study groups occurred although potential social contact was available *ad libitum*. Additionally, the feeding conditions in captivity would permit a more cohesive group-living when following the assumption that high(er) gregariousness is too costly in free-ranging orangutans due to high feeding competition (see Mitani *et al.*, 1991). Referring to the theoretical concept by Aureli *et al.* (2008), one could classify orangutans as a species with high fission-fusion dynamics including short-term associations, less differentiated social relationships, and more cohesive societies if ecological conditions permit. The findings of the current study would support this hypothesis by providing the first proximate data, which had been missing so far. Moreover, this study suggests that orangutans have the ability to cope with a longer-termed group-living situation along with exhibiting the observed fission-fusion structures at the same time.

Suggestively, the affable living-together of the orangutans may be facilitated by an intrinsic motivation to separate from and congregate with partners regularly. Especially the results from the Cologne group support this hypothesis. Assuming a general motivation to exhibit fission-fusion propensities and to interact occasionally might also help to explain the elevated degree of sociability under captive conditions compared to the wild. Furthermore, such a motivation may constrain the development of strong social bonds. In the study groups, the spacious enclosures allowed exhibiting fission-fusion tendencies. More restricted conditions might pose conflicts to occur more frequently. The recent issue of the European studbook (Becker, 2009) points into the same direction as the results of this study indicate, recommending spacious enclosures and more flexible housing schedules.

Mechanisms regulating the social relationships in orangutans might be found in enhanced cognitive skills, presumably associated with the social complexity in fission-fusion societies (Aureli *et al.*, 2008). The low level of conflicts found in this study (and in previous studies) may be attributed to enhanced inhibitory skills which Amici *et al.* (2008) proposed to be positively associated with fission-fusion dynamics. Under captive conditions, partners are familiar with and permanently available to each other. Additionally, food is constantly available. Thus, another explanation for the low amount of physical contact as well as low rates of conflicts may be that the individuals were tolerant of each other and had no need to interact a lot (Edwards and Snowdon, 1980; Goodall, 1986). However, anecdotal

observations of serious conflicts also indicate that skills for conflict resolution (e.g. reconciliation) and its tension-reduction function as found in other apes and monkeys (see Aureli *et al.*, 2002) possibly are not determined in the orangutans' interactive repertoire. Conflicts seem to be managed rather by spatial avoidance. In captivity, this should be facilitated by husbandry schedules.

4.5. FUTURE WORK

As mentioned by Which *et al.* (2009) the management of zoo-living orangutans has increased their survival rate. The European population, however, still faces low breeding success and includes many hand-reared individuals (Kaumanns *et al.*, 2004; Becker, 2009). The results of the current study do not indicate obvious problems for the individuals to deal with the (social) keeping conditions, such as an intolerance of social closeness. But there are hints for an individual responsiveness which indicates at least a subtle incompatibility as in a few dyads observed.

Flexible keeping schedules such as the one at Apenheul provide a variety of opportunities and may help to avoid serious conflicts and resulting potential long-term stressors. In this context, future studies might assess whether the behaviour of forced copulations observed in the present study might be influenced by keeping conditions, the males' rearing-history, and/or by an individual idiosyncrasy. Even though, or perhaps precisely because the males of the study groups were engaged in interactions with the females only occasionally, keeping conditions should enable males and females to separate from each other.

Comparative studies on individuals under different keeping conditions may help to assess the effects of housing situations on the animals' activity and possible correlations with atypical behaviours. A combined research project, carried out on several differently kept groups, analysing hormonal stress levels and interactive and non-interactive behaviours would be advantageous.

This study points out that Bornean orangutans have the potential to cope with an artificial permanent group-living. Whether Sumatran orangutans may show an even greater degree of sociability under captive conditions should be investigated by comparative studies. With regard to the structure of social relationships in orangutans, further studies should verify the findings of the present one, ideally including many different groups. The main focus should be laid on social bonds, investigating their type and strength.

This study comprises a long-term dataset of one group, however, there were hints (such as the development of male-female relationships) that the quality of relationships in orangutans may change over an even larger period of time than covered by this study, stressing the need for further long-term studies.

This is the first study pointing out that fission-fusion tendencies comparable to the wild also seem to exist in orangutans in captivity. It would be of great interest to evaluate a possibly underlying intrinsic motivation of the animals by investigating this phenomenon on many different groups. Additionally, the effects of a particular keeping strategy on the degree of fission-fusion tendencies should be investigated in greater detail. This could be done by comparing the same set of individuals under different social keeping conditions (i.e., stable versus flexible). Such studies might help not only optimising the captive management of orangutans but also can be useful for further testing theoretical concepts (e.g. Aureli *et al.*, 2008) of a species' sociality.

5. ABSTRACT

This study investigates the social relationships in captive groups of Bornean orangutans (*Pongo pygmaeus*) concerning their social system and sociality. Wild orangutans are supposed to live in fission-fusion societies with a high flexibility in spatial and social structures. Zoo-living orangutans however are usually housed in stable groups. It is unclear whether a permanent group-living under the spatial restrictions of captivity over longer periods of time corresponds to the orangutans' social potential. The orangutans' social system is still not well understood. Proximate data referring to mechanisms regulating the social relationships, including a sufficient sample size of individuals, are largely missing so far.

This study examines the structure of social relationships, the persistence and form of fission-fusion tendencies, and how the individuals deal with the group-living conditions. Three sets of orangutans were comparatively studied. Two groups were housed under constant group-keeping conditions; one group was kept under flexible conditions. The analyses focused on the patterns of the interactive and spatial behaviour. Additionally, long-term observations were carried out on one of the groups, and a second sampling method was implemented allowing a sequence analysis of behaviours.

The results of this study support the assumption that orangutans have the potential to engage in a higher amount of social activities compared to the wild without many conflicts. To evaluate this social potential under natural conditions is hardly possible. The structure of social relationships between the studied animals was largely compatible to what is described for free-ranging orangutans, though the relationships tended to be generally friendlier. The different keeping conditions seem to have little influence on the social patterns. The socio-spatial patterns were characterized by frequent encounters and leavings; interactions were mainly sociopositive but brief. On the structural level, this pattern is in accordance with the fission-fusion sociality described for wild orangutans. Orangutans may possibly have an intrinsic motivation to merge and split regularly and to establish only weak social bonds. Future work should refer to this, both under the conditions in the wild and under human care. The findings of this study can contribute to the further development of new concepts on fission-fusion dynamics in primates. This work points out that a detailed analysis of the interactive and spatiotemporal patterns under the conditions in captivity provides important and supplemental clues about the sociality of orangutans. This may account also for the management of this endangered species in zoos and fragmented areas in the wild.

6. ZUSAMMENFASSUNG

Die vorliegende Studie untersucht die sozialen Beziehungen bei Borneo Orangutans (*Pongo pygmaeus*) in menschlicher Obhut bezüglich ihres Sozialsystems und ihres Zusammenlebens. Im Freiland leben Orangutans nach bisherigem Kenntnisstand in „fission-fusion“ Sozietäten, die sich durch große räumliche und soziale Offenheit auszeichnen. In Zoos werden Orangutans allerdings meist in konstanten Gruppen gehalten. Es ist bislang nicht klar, ob ein langfristiges und permanentes Gruppenleben unter den räumlich begrenzten Bedingungen in Gefangenschaft dem sozialen Potential von Orangutans entspricht. Das Sozialsystem von Orangutans ist bislang nicht vollständig geklärt. Es ist bisher kaum an einer adäquaten Anzahl an Tieren untersucht worden, wie die sozialen Beziehungen auf proximaler Ebene funktionieren.

Diese Arbeit untersucht die Struktur der sozialen Beziehungen, die Ausprägung möglicher fission-fusion Tendenzen, und wie die Individuen mit dem künstlich induzierten Gruppenleben zurechtkommen. Dies wurde an den Orangutan-Gruppen dreier Zoos vergleichend erforscht. In zwei Zoos wurden die Tiere in konstanten Gruppen, und in einem unter flexiblen Bedingungen gehalten. Der Schwerpunkt der Analysen lag auf den interaktiven und räumlichen Verhaltensmustern der Tiere. Bei einer der Gruppen wurden zusätzlich Langzeitbeobachtungen durchgeführt, sowie eine weitere Beobachtungsmethode zur Sequenzanalyse von Verhaltensabläufen angewendet.

Die Ergebnisse dieser Studie bestätigen die Annahme, dass Orangutans das Potential haben, sich unter den sozialen und ökologischen Bedingungen in menschlicher Obhut mehr mit sozialen Aktivitäten zu beschäftigen als es bei wildlebenden Tieren beobachtet wurde. Dieses Potential ist unter Freilandbedingungen nur schwer zu untersuchen. Auf struktureller Ebene ähnelten die sozialen Beziehungen zwischen den Tieren dem, was bei Zusammentreffen von wildlebenden Orangutans gefunden wurde, wobei die Beziehungen zwischen den hier untersuchten Tieren generell freundlicher erschienen. Die unterschiedlichen Haltungsbedingungen hatten dabei keinen großen Einfluss auf die Beziehungsmuster. Die gefundenen sozialen und räumlichen Muster entsprachen einer fission-fusion Organisation insofern, dass sich die Individuen häufig voneinander entfernten und wieder trafen; die Interaktionen waren meist soziopositiv aber nur kurz. Möglicherweise haben Orangutans eine intrinsische Motivation, soziale und räumliche Nähe zu Partnern immer wieder aufzusuchen und zu verlassen, und dabei nur schwache Bindungen mit diesen aufzubauen. Zukünftige Studien soll-

ten sich darauf sowohl unter den Bedingungen im Freiland als auch unter denen in menschlicher Obhut beziehen. Die Befunde dieser Studie können zur Weiterentwicklung neuer Konzepte zur Dynamik von fission-fusion Strukturen bei Primaten beitragen. Diese Arbeit verdeutlicht, dass eine detaillierte Analyse der interaktiven und räumlich-zeitlichen Muster unter Zoobedingungen wichtige und ergänzende Hinweise über das soziale Zusammenleben von Orangutans liefern kann. Diese können auch hilfreich für das Management dieser bedrohten Art in Zoos und bei fragmentierten Gebieten im Freiland sein.

7. REFERENCES

- Amici, F., Aureli, F., and Call, J. (2008). Fission-fusion dynamics, behavioral flexibility, and inhibitory control in primates. *Current Biology* 18: 1415-1419.
- Ancrenaz, M., Marshall, A., Goossens, B., van Schaik, C.P., Sugardjito, J., Gumal, M., and Wich, S. (2008). Pongo pygmaeus. *IUCN 2009. IUCN Red List of Threatened Species*.
- Aureli, F., and de Waal, F.B.M. (1997). Inhibition of social behavior in chimpanzees under high-density conditions. *American Journal of Primatology* 41 (3): 213-228.
- Aureli, F., Cords, C.M., and van Schaik, C.P. (2002). Conflict resolution following aggression in gregarious animals: a predictive framework. *Animal Behaviour* 64: 325-343.
- Aureli, F., and Schaffner, C.M. (2002). Relationship assessment through emotional mediation. *Behaviour* 139: 393-420.
- Aureli, F., and Schaffner, C.M. (2005). Fission-fusion dynamics complicate the regulation of social relationships. *Primate Eye* 86: 6.
- Aureli, F., Schaffner, C., Boesch, C., Bearder, S.K., Call, J., Chapman, C.A., Connor, R., di Fiore, A., Dunbar, R.I.M., Henzi, S.P., Holekamp, K., Korstjens, A.H., Layton, R., Lee, P., Lehmann, J., Manson, J.H., Ramos-Fernández, G., Strier, K.B., and van Schaik, C.P. (2008). Fission-Fusion Dynamics. New Research Frameworks. *Current Anthropology* 49 (4): 627-654.
- Badrian, A., and Badrian, N. (1984). Social organization of Pan paniscus in the Lomako Forest, Zaire. In Susman, R.L. (ed.), *The Pygmy Chimpanzee: Evolutionary Biology and Behavior*. Plenum Press, New York, pp. 325-346.
- Baker, K.C. and Smuts, B.B. (1996). Social relationships of female chimpanzees: Diversity between captive groups, *Chimpanzees Cultures*. pp. 227-242.
- Baumgartner, G. (2010). Hormonhaushalt von Orang Utans bei Gehegewechsel und Vergesellschaftung mit zwei neuen Weibchen. Master thesis. University Vienna, Vienna.
- Beaver, G.M. (2000). The effects of the social habitat implemented by zoos on the behavior of the naturally semi-solitary orangutan (*Pongo pygmaeus pygmaeus*). *American Journal of Primatology* 51 (S1): 42.
- Becker, C. (2009). EEP for Orangutans. Studbook for Europe XXVII/2009. Zoo Karlsruhe, Karlsruhe.
- Bergman, T.J. (2010). Experimental evidence for limited vocal recognition in a wild primate: implications for the social complexity hypothesis. *Proceedings of The Royal Society B: Biological Sciences* 277 (1696): 3045-3053.
- Birke, L. (2002). Effects of browse, human visitors and noise on the behaviour of captive Orang Utans. *Animal Welfare* 11 (2): 189-202.

- te Boekhorst, I.J.A., Schürmann, C.L., and Sugardjito, J. (1990). Residential status and seasonal movements of wild orangutans in the Gunung Leuser Reserve (Sumatra, Indonesia). *Animal Behaviour* 39: 1098-1109.
- Bolhassan, G. (2001). Interaction between adolescent and juvenile orangutans undergoing rehabilitation at Matang Wildlife Centre, Malaysia. *Hornbill* 5.
- Breitkopf, J. (2006). Der Einfluss von Zoobesuchern auf das Verhalten von Orang-Utans (*Pongo pygmaeus*). Final thesis. Universität zu Köln, Köln.
- Bygott, J.D. (1979). Agonistic behaviour, dominance, and social structure in wild chimpanzees of the Gombe National Park. In Hamburg, D.A. and McCown, E.R. (eds.), *The great apes*. Benjamin/Cummings, Menlo Park, pp. 405-427.
- Caldecott, J., and Miles, L. (2005). *World Atlas of Great Apes and their Conservation. Prepared at the UNEP World Conservation Monitoring Centre*. University of California Press, Berkley, USA.
- Carlstead, K., and Shepherdson, D. (2000). Alleviating Stress in zoo animals with environmental enrichment. In Moberg, G.P. and Mench, J.A. (eds.), *The Biology of Animal Stress. Basic principles and implications for animal welfare*. CABI Publishing, New York, pp. 337-354.
- Chamove, A.S., Hosey, G.R., and Schaezel, P. (1988). Visitors excite primates in Zoos. *Zoo Biology* 7 (4): 359-369.
- Claßen, D. (2001). Gehegenutzung und soziale Strukturen bei Orang Utans (*Pongo pygmaeus*) in menschlicher Obhut. Diploma Thesis. Universität zu Köln, Köln.
- Crook, J.H. (1970). Social organization and the environment: aspects of contemporary social ethology. *Animal Behaviour* 18 (2): 197-209.
- Davey, G. (2007). Visitors' effects on the welfare of animals in the zoo: a review. *Journal of Applied Animal Welfare Science* 10 (2): 169-183.
- Delgado, R.A., and van Schaik, C.P. (2000). The behavioural ecology and conservation of the orangutan (*Pongo pygmaeus*): A tale of two islands. *Evolutionary Anthropology* 9 (5): 201-218.
- Dunbar, R.I.M. (1988). *Primate social systems*. Cornwell University Press, Ithaca, New York.
- Edwards, S.D., and Snowdon, C.T. (1980). Social behaviour of captive, group-living orangutans. *International Journal of Primatology* 1 (1): 39-62.
- Edwards, S.D. (1982). Social potential expressed in captive, group-living orangutans. In de Boer, L.E.M. (ed.), *The orangutan: its biology and conservation*. Dr. W. Junk Publishers, The Hague, pp. 249-255.
- van Elsacker, L., Vervaecke, H., and Verheyen, R.F. (1995). A review of terminology on aggregation patterns in bonobos (*Pan paniscus*). *International Journal of Primatology* 16 (1): 37-52.

- Fox, E. A., Sitompul, A.F., and van Schaik, C.P. (1999). Intelligent tool use in wild Sumatran orangutans. In Parker, S.T., Miles, H.L., and Mitchell, R.W. (eds.), *The Mentality of Gorillas and Orangutans*. Cambridge University Press, Cambridge, pp. 99-116.
- Furuichi, T., and Ihobe, H. (1994). Variation in male relationships in bonobos and chimpanzees. *Behaviour* 130 (3-4): 211-228.
- Galdikas, B.M.F. (1979). Orangutan adaptation at Tanjung Puting Reserve: mating and ecology. In Hamburg, D.A. and McCown, E.R. (eds.), *The Great Apes*. Benjamin/Cummings, Menlo Park, California, pp. 195-233.
- Galdikas, B.M.F. (1983). The orangutan long call and snag crashing at Tanjung Puting Reserve. *Primates* 24 (3): 371-384.
- Galdikas, B.M.F. (1984). Adult female sociality among wild orangutans at Tanjung Puting Reserve. In Small, M. (ed.), *Female Primates: Studies by Women Primatologists*. Liss, New York, pp. 217-235.
- Galdikas, B.M.F. (1985a). Orangutan Sociality at Tanjung Puting. *American Journal of Primatology* 9: 101-119.
- Galdikas, B.M.F. (1985b). Adult male sociality and reproductive tactics among orangutans at Tanjung Puting. *Folia Primatologica* 45: 9-24.
- Galdikas, B.M.F. (1985c). Subadult male orangutan sociality and reproductive behavior at Tanjung Puting. *American Journal of Primatology* 8 (2): 87-99.
- Galdikas, B.M.F. (1988). Orangutan diet, range, and activity at Tanjung Puting, Central Borneo. *International Journal of Primatology* 9 (1): 1-35.
- Galdikas, B.M.F. (1995). Social and reproductive behaviour of wild adolescent female orangutans. In Nadler, R.D., Galdikas, B.M.F., Sheehan, L., and Rosen, N. (eds.), *The neglected Ape*. Plenum Press, New York, pp. 163-181.
- Goodall, J. (1986). *The chimpanzees of Gombe, Patterns of Behaviour*. The Belknap Press of Harvard University Press, Cambridge, England.
- Goossens, B., Setchell, J.M., James, S.S., Funk, S.M., Chikhi, L., Abulani, A., Ancrenaz, M., Lackman-Ancrenaz, I., and Bruford, M.W. (2006). Philopatry and reproductive success in Bornean orang-utans (*Pongo pygmaeus*). *Molecular Ecology* 15 (9): 2577-2588.
- Goossens, B., Chikhi, L., Jalil, M.F., James, S., Ancrenaz, M., Lackman-Ancrenaz, I., and Bruford, M.W. (2009). Taxonomy, geographic variation and population genetics of Bornean and Sumatran orangutans. In Wich, S.A., Utami-Atmoko, S.S., Setia, T.M., and van Schaik, C.P. (eds.), *Orangutans: Geographic variation in behavioral ecology and conservation*. Oxford University Press, New York, pp. 1-14.
- Groh, C. (2005). Die Entwicklung sozialer Beziehungen bei zoolebenden Bartaffen (*Macaca silenus*). Diploma Thesis. Universität zu Köln, Köln.
- Groves, C.P. (1989). *A theory of human and primate evolution*. Oxford University Press, Oxford.

- Groves, C.P. (2001). *Primate Taxonomy*. Smithsonian Institution Press, Washington.
- Harcourt, A.H. (1979). Social relationships among adult female mountain gorillas. *Animal Behaviour* 27: 251-264.
- Harcourt, A.H., and Stewart, K.J. (1983). Interactions, relationships and social structures: the great apes. In Hinde, R.A. (ed.), *Primate social relationships: an integrated approach*. Blackwell Scientific Publications, Oxford, pp. 307-314.
- Herbert, P.L., and Bard, K. (2000). Orangutan use of space in an innovative habitat. *Zoo Biology* 19: 239-251.
- Hinde, R.A. (1975). Interactions, relationships and social structure in nonhuman primates. In Kawamura, S. (ed.), *Proceedings from the Symposia of the fifth Congress of the International Primatological Society*. Japan Science Press, Tokyo, pp. 13-24.
- Hinde, R.A. (1979). *Towards understanding relationships*. Academic Press, London.
- van Hooff, J.A.R.A.M. (1995). The orangutan: a social outsider. In Nadler, R.D., Galdikas, B.M.F., Sheehan, L., and Rosen, N. (eds.), *The neglected Ape*. Plenum Press, New York, pp. 153-162.
- Horr, D.A. (1975). The Borneo orang-utan: Population structure and dynamics in relationship to ecology and reproductive strategy. In Rosenblum, L. (ed.), *Primate Behavior. Developments in Field and Laboratory Research*. Academic Press, New York, pp. 307-323.
- Hosey, G.R., and Druck, P.L. (1987). The influence of zoo visitors on the behaviour of captive primates. *Applied Animal Behaviour Science* 18 (1): 19-29.
- Husson, S.J., Wich, S.A., Marshall, A.J., Dennis, R.D., Ancrenaz, M., Brassey, R., Gumal, M., Hearn, A.J., Meijaard, E., Simorangkir, T., and Singleton, I. (2009). Orangutan distribution, density, abundance and impacts of disturbance. In Wich, S.A., Utami-Atmoko, S.S., Setia, T.M., and van Schaik, C.P. (eds.), *Orangutans: Geographic variation in behavioral ecology and conservation*. Oxford University Press, New York, pp. 77-96.
- Jolly, A. (1966). Lemur social behaviour and primate intelligence - step from prosimian to monkey intelligence probably took place in a social context. *Science* 153: 501-508.
- Kaplan, G., and Rogers, L.J. (2000). *The orangutans. Their evolution, behavior, and future*. Perseus, Cambridge, Mass.
- Kappeler, P.M. (1999). Convergence and divergence in primate social systems. In Fleagle, J.G., Janson, C.H., and Reed, K.E. (eds.), *Primate Communities*. Cambridge University Press, Cambridge, pp. 158-170.
- Kappeler, P.M., and van Schaik, C.P. (2002). Evolution of primate social systems. *International Journal of Primatology* 23 (4): 707-740.
- Kaumanns, W., Krebs, E., and Nogge, G. (2004). Menschenaffen in Menschenhand. Langzeitentwicklung europäischer Menschenaffenpopulationen. *Der Zoologische Garten* 74 (4-5): 217-228.

- Kießling, S. (2008). Social relationships in zoo-living bonobos, *Pan paniscus*. PhD thesis. Universität Ulm, Ulm.
- MacKinnon, K. (1974). The behaviour and ecology of wild orang-utans (*Pongo pygmaeus*). *Animal Behaviour* 22: 3-74.
- Klein, S. (1999). Die sozialen Strukturen dreier Menschenaffenarten (*Gorilla g. gorilla*, *Pan troglodytes verus*, *Pongo abelii*) im Zoo. Diploma thesis. Westfälische Wilhelms-Universität Münster, Münster.
- Knott, C.D. (1998a). Changes in orangutan diet, caloric intake and ketones in response to fluctuating fruit availability. *International Journal of Primatology* 19 (6): 1051-1079.
- Knott, C.D. (1998b). Social system dynamics, ranging patterns and male and female strategies in wild Bornean orangutans. *American Journal of Physical Anthropology* 105 (S26): 140.
- Knott, C.D. (1999). Orangutan behavior and ecology. In Dolhinow, P., and Fuentes, A. (eds.), *The nonhuman primates*. Mountain View: Mayfield Publishing, pp. 50-57.
- Knott, C.D., Beaudrot, L., Snaith, T., White, S., Tschauer, H., and Planansky, G. (2008). Female-female competition in Bornean orangutans. *International Journal of Primatology* 29: 975-997.
- Knott, C.D. (2010). Female reproductive strategies in orangutans, evidence for female choice and counterstrategies to infanticide in a species with frequent sexual coercion. *Proceedings of The Royal Society B: Biological Sciences* 277 (1678): 105-113.
- Kummer, H. (1968). *Social organization of hamadryas baboons. A field study*. University of Chicago Press.
- Kummer, H. (1971). *Primate societies*. Aldine-Atherton, Chicago.
- Kummer, H. (1978). On the value of social relationships to nonhuman primates: A heuristic scheme. *Biology and Social life* 17 (4/5): 687-705.
- Liebal, K., Pika, S., and Tomasello, M. (2006). Gestural communication of orangutans (*Pongo pygmaeus*). *Gesture* 6 (1): 1-38.
- MacKinnon, K. (1974). The behaviour and ecology of wild orang-utans (*Pongo pygmaeus*). *Animal Behaviour* 22: 3-74.
- Maggioncalda, A.N., Czekala, N.M., and Sapolsky, R.M. (2002). Male orangutan subadulthood: A new twist on the relationship between chronic stress and developmental arrest. *American Journal of Physical Anthropology* 118 (1): 25-32.
- Maple, T.L. (1982). Orang utan behaviour and its management in captivity. In de Boer, L.E.M. (ed.), *The Orang Utan: its biology and conservation*. Dr. W. Junk Publishers, The Hague, pp. 257-268.
- Marshall, A.J., Salas, L.A., Stephens, S., Nardiyono, Engström, L., Meijaard, E., and Stanley, S.A. (2007). Use of limestone karst forests by Bornean orangutans (*Pongo pygmaeus*

- morio*) in the Sangkulirang peninsula, east Kalimantan, Indonesia. *American Journal of Primatology* 69: 1-8.
- Martin, P., and Bateson, P. (1986). *Measuring behaviour. An introductory guide*. Cambridge University Press, Cambridge.
- Meder, A. (2007). Great ape social systems. In Henke, W. and Tattersall, I. (eds.), *Handbook of Paleoanthropology*. Springer Verlag, Berlin Heidelberg, pp. 1235-1271.
- Mitani, J.C. (1985a). Sexual selection and adult male orangutan long calls. *Animal Behaviour* 33: 272-283.
- Mitani, J.C. (1985b). Mating behaviour of male orangutans in the Kutai Game Reserve, Indonesia. *Animal Behaviour* 33: 392-402.
- Mitani, J.C. (1990). Experimental field studies of Asian ape social systems. *International Journal of Primatology* 11 (2): 103-126.
- Mitani, J.C., Grether, G.F., Rodman, P.S., and Priatna, D. (1991). Associations among wild orang-utans: sociality, passive aggregations or chance? *Animal Behaviour* 42: 33-46.
- Mitra Setia, T., Delgado, R.A., Utami-Atmoko, S.S., Singleton, I., and van Schaik, C.P. (2009). Social organization and male-female relationships. In Wich, S.A., Utami-Atmoko, S. S., Setia, T.M., and van Schaik, C.P. (eds.), *Orangutans: Geographic variation in behavioral ecology and conservation*. Oxford University Press, New York, pp. 245-255.
- Morrogh-Bernard, H.C., Husson, S.J., Knott, C.D., Wich, S.A., van Schaik, C.P., van Noordwijk, M.A., Lackman-Ancrenaz, I., Marshall, A.J., Kanamori, T., Kuze, N., and bin Sankong, R. (2009). Orangutan activity budgets and diet: a comparison between species, populations and habitats. In Wich, S.A., Utami-Atmoko, S.S., Setia, T.M., and van Schaik, C.P. (eds.), *Orangutans: Geographic variation in behavioral ecology and conservation*. Oxford University Press, New York, pp. 119-133.
- Munn, C., and Fernandez, M. (1997). Infant development. In Sodara, C. (ed.), *Orangutan species survival plan husbandry manual*. Chicago, pp. 59-66.
- Nellemann, C., Miles, L., Kaltenborn, B.P., Virtue, M., and Ahlenius, H. (2007). *The last stand of the orangutan – State of emergency: Illegal logging, fire and palm oil in Indonesia's national parks*. Norway.
- Newton-Fisher, N.E. (2002). Relationships of male chimpanzees in the Budongo Forest, Uganda. In Boesch, C., Hohmann, G., and Marchandt, L.F. (eds.), *Behavioural diversity in Chimpanzees and Bonobos*. Cambridge University Press, Cambridge, pp. 125-137.
- Newton-Fisher, N.E. (2006). Female coalitions against male aggression in wild chimpanzees of the Budongo Forest. *International Journal of Primatology* 27 (6): 1589-1599.
- Nishida, T. (1968). The social group of wild chimpanzees in the Mahali Mountains. *Primates* 9: 167-224.

- van Noordwijk, M.A., and van Schaik, C.P. (2009). Intersexual food transfer among orangutans: do females test males for coercive tendency? *Behavioral Ecology and Sociobiology* 63 (6): 883-890.
- Paoli, T., Tacconi, G., Tarli, S.M.B., and Palagi, E. (2007). Influence of feeding and short-term crowding on the sexual repertoire of captive bonobos (*Pan paniscus*). *Annual Zoological Fennici* 44.
- Perkins, L.A. (1992). Variables that influence the activity of captive orangutans. *Zoo Biology* 11: 177-186.
- Perret, K. (1994). Einfluß von Zoobesuchern auf das Verhalten von Schimpansen (*Pan troglodytes*). Diploma thesis. Ruhr-Universität Bochum, Bochum.
- Poole, T.B. (1987). Social behaviour of a group of orangutans (*Pongo pygmaeus*) on an artificial island in Singapore Zoological Gardens. *Zoo Biology* 6: 315-330.
- Riedler, B., Millesi, E., and Pratje, P.H. (2010). Adaptation to forest life during the reintroduction process of immature *Pongo abelii*. *International Journal of Primatology* 31: 647-663.
- Rijksen, H.D. (1978). *A field study on Sumatran Orang-Utans (Pongo pygmaeus abelii, lesson 1827): Ecology, Behaviour, and Conservation*. Veenman, H. and B.V. Zonene, Wageningen.
- Rodman, P.S. (1973). Population composition and adaptive organization among orangutans of the Kutai Reserve. In Crook, J.H. and Michael, R.P. (eds.), *Comparative Ecology and Behaviour of Primates*. Academic Press, London, pp. 171-209.
- Rodman, P.S. (1979). Individual activity patterns and the solitary nature of orangutans. In Hamburg, D.A. and McCown, E.R. (eds.), *The Great Apes*. Benjamin/Cummings, Menlo Park, California, pp. 235-255.
- Rodman, P.S., and Mitani, J.C. (1987). Orangutans: sexual dimorphism in a solitary species. In Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.M., and Struhsaker, T.T. (eds.), *Primate Societies*. University of Chicago Press, Chicago, pp. 146-154.
- Rodman, P.S. (1988). Diversity and consistency in ecology and behaviour. In Schwartz, J.H. (ed.), *Orang-Utan biology*. Oxford University Press, New York, pp. 31-51.
- Romero, T., and Aureli, F. (2007). Spatial association and social behaviour in zoo-living female ring-tailed coatis (*Nasua nasua*). *Behaviour* 144: 179-193.
- Rowe, N. (1996). *The pictorial guide to the living primates*. Pogonias Press, New York.
- Russon, A.E. (2002). Return to the native: cognition and site-specific expertise in orangutan rehabilitation. *International Journal of Primatology* 23 (3): 461-478.
- Russon, A.E., and Begun, D.R. (2004). Evolutionary origins of great ape intelligence: an integrated view. In Russon, A.E. and Begun, D.R. (eds.), *The evolution of Great Ape Intelligence*. Cambridge University Press, Cambridge, UK, pp. 353-368.

- Sannen, A., van Elsacker, L., and Eens, M. (2004). Effect of spatial crowding on aggressive behaviour in a bonobo colony. *Zoo Biology* 23 (5): 383-395.
- van Schaik, C.P., and van Hooff, J.A.R.A.M. (1983). On the ultimate causes of primate social systems. *Behaviour* 85: 91-117.
- van Schaik, C.P., van Noordwijk, M.A., de Boer, L.E.M., and den Tonkelaar, I. (1983). The effects of group size on time budgets and social behaviour in wild long-tailed macaques (*Macaca fascicularis*). *Behavioral Ecology and Sociobiology* 13: 173-181.
- van Schaik, C.P. (1989). The ecology of social relationships amongst female primates. In Standen, V. and Foley, R.A. (eds.), *Comparative socioecology. The behavioural ecology of humans and other mammals*. Blackwell, Oxford, pp. 195-218.
- van Schaik, C.P., and van Hooff, J.A.R.A.M. (1996). Towards an understanding of the orangutan's social system. In McCrew, W.C., Marchant, C.F., and Nishida, T. (eds.), *Great Apes Societies*. Cambridge University Press, Cambridge, pp. 3-15.
- van Schaik, C.P. (1999). The socioecology of fission-fusion sociality in orangutans. *Primates* 40 (1): 69-86.
- van Schaik, C.P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C.D., Singleton, I., Suzuki, A., Utami, S.S., and Merrill, M. (2003). Orangutan cultures and the evolution of material culture. *Science* 299 (5603): 102-105.
- van Schaik, C.P., Preuschoft, S., and Watts, D.P. (2004). Great ape social systems. In Russon, A.E. and Begun, D.R. (eds.), *The evolution of thought: evolutionary origins of great ape intelligence*. Cambridge University Press, pp. 190-209.
- van Schaik, C.P., Wich, S.A., Utami, S.S., and Odom, K. (2005). A simple alternative to line transects of nests for estimating orangutan densities. *Primates* 46 (4): 249-254.
- van Schaik, C.P., Ancrenaz, M., Djojoasmoro, R., Knott, C.D., Morrogh-Bernard, H., Odom, K., Nuzuar, s.n., Utami-Atmoko, S.S., and van Noordwijk, M.A. (2009). Orangutan cultures revisited. In Wich, S.A., Utami-Atmoko, S.S., Setia, T.M., and van Schaik, C.P. (eds.), *Orangutans: geographic variation in behavioral ecology and conservation*. Oxford University Press, New York, pp. 299-309.
- van Schaik, C.P., Marshall, A.J., and Wich, S.A. (2009). Geographic variation in orangutan behavior and biology. Its functional interpretation and its mechanistic basis. In Wich, S.A., Utami-Atmoko, S.S., Setia, T.M., and van Schaik, C.P. (eds.), *Orangutans: Geographic variation in behavioral ecology and conservation*. Oxford University Press, New York, pp. 351-361.
- Schürmann, C.L. (1982). Mating behaviour of wild orangutans. In de Boer, L.E.M. (ed.), *The Orang Utan: its biology and conservation*. Junk, The Hague, pp. 269-284.
- Schürmann, C.L., and van Hooff, J.A.R.A.M. (1986). Reproductive strategies of the orangutan: new data and a reconsideration of the existing socio-ecological models. *International Journal of Primatology* 7: 265-287.
- Seyfarth, R.M. (1977). A model of social grooming among adult female monkeys. *Journal of Theoretical Biology* 65: 671-698.

- Siegel, S. (1988). *Nonparametric statistics for the behavioural science*. McGraw Hill, New York.
- Silk, J.B. (2002). Using the 'F' word in primatology. *Behaviour* 139 (2-3): 421-446.
- Silk, J.B., Alberts, S.C., and Altmann, J. (2006). Social relationships among adult female baboons (*Papio cynocephalus*) II. Variation in the quality and stability of social bonds. *Behavioral Ecology and Sociobiology* 61: 197-204.
- Singleton, I., and van Schaik, C.P. (2001). Orangutan home range size and its determinants in a Sumatran swamp forest. *International Journal of Primatology* 22 (6): 877-911.
- Singleton, I., and van Schaik, C.P. (2002). The social organisation of a population of Sumatran orangutans. *Folia Primatologica* 73: 1-20.
- Singleton, I., Wich, S.A., and Griffiths, M. (2008). *Pongo abelii*. *IUCN 2009. IUCN Red List of Threatened Species*.
- Singleton, I., Knott, C.D., Morrogh-Bernard, H.C., Wich, S.A., and van Schaik, C.P. (2009). Ranging behaviour of orangutan females and social organization. In Wich, S.A., Utami-Atmoko, S.S., Setia, T.M., and van Schaik, C.P. (eds.), *Orangutans: Geographic variation in behavioral ecology and conservation*. Oxford University Press, New York, pp. 205-213.
- Sterck, E.H., Watts, D.P., and van Schaik, C.P. (1997). The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology* 41 (5): 291-309.
- Stevens, J.M.G., Vervaecke, H., de Vries, H., and van Elsacker, L. (2006). Social structures in *Pan paniscus*: testing the female bonding hypothesis. *Primates* 47: 210-217.
- Struhsaker, T.T. (1969). Correlates of ecology and social organisation among African cercopithecines. *Folia Primatologica* 11 (1): 80-118.
- Sugardjito, J., te Boekhorst, I.J.A., and van Hooff, J.A.R.A.M. (1987). Ecological constraints of the grouping of wild orang-utans (*Pongo pygmaeus*) in the Gunung Leuser National Park, Sumatra, Indonesia. *International Journal of Primatology* 8 (1): 17-41.
- Symington, M.M. (1990). Fission-fusion social organization in *Ateles* and *Pan*. *International Journal of Primatology* 11 (1): 47-61.
- Tajima, T., and Kurofori, H. (2010). Non-aggressive interventions by third parties in conflicts among captive Bornean orangutans (*Ponpo pygmaeus*). *Primates* 51 (2): 179-182.
- Tobach, E., Greenberg, G., Radell, P., and McCarthy, T. (1989). Social behavior in a group of orang-utans (*Pongo pygmaeus abelii*) in a zoo setting. *Applied Animal Behaviour Science* 23 (1-2): 141-154.
- Tobach, E., and Porto, N. (2006). Note on social behavior of long-term captive female orangutans (*Pongo pygmaeus abelii*). *Psychology Report* 98 (1): 177-183.
- Tripp, J.K. (1985). Increasing activity in captive orangutans: provision of manipulable and edible materials. *Zoo Biology* 4 (3): 225-234.

- Utami, S.S., Wich, S.A., Sterck, E.H.M., and van Hooff, J.A.R.A.M. (1997). Food competition between wild orangutans in large fig trees. *International Journal of Primatology* 18 (6): 909-927.
- Utami, S.S., Goossens, B., Bruford, M.W., de Ruiter, J.R., and van Hooff, J.A.R.A.M. (2002). Male bimaturism and reproductive success in Sumatran orang-utans. *Behavioral Ecology* 13 (5): 643-652.
- Utami, S.S., and van Hooff, J.A.R.A.M. (2004). Alternative male reproductive strategies: male bimaturism in orangutans. In Kappeler, P.M. and van Schaik, C.P. (eds.), *Sexual selection in primates: New and comparative perspectives*. Cambridge University Press, Cambridge, pp. 196-207.
- Utami-Atmoko, S.S., Singleton, I., van Noordwijk, M.A., van Schaik, C.P., and Setia, T.M. (2009). Male-male relationships in orangutans. In Wich, S.A., Utami-Atmoko, S.S., Setia, T.M., and van Schaik, C.P. (eds.), *Orangutans: geographic variation in behavioral ecology and conservation*. Oxford University Press, New York, pp. 225-234.
- Vervaecke, H., de Vries, H., and van Elsacker, L. (2000). Function and distribution of coalitions in captive bonobos (*Pan paniscus*). *Primates* 41 (3): 249-265.
- Vogel, C. (1975). Soziale Organisationsformen bei catarrhinen Primaten. In Kurth, G. (ed.), *Hominisation und Verhalten*. Gustav-Fischer Verlag, Eibl-Eibesfeldt, Stuttgart, pp. 159-200.
- Walters, J.R., and Seyfarth, R.M. (1986). Conflict and cooperation. In Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W., and Struhsaker, T.T. (eds.), *Primate Societies*. University of Chicago Press, Chicago, pp. 306-317.
- Weingrill, T., and Heistermann, M. (2008). Factors associated with faecal glucocorticoid levels in zoo orangutans. *Folia Primatologica* 79 (5): 397-398.
- Wells, D.L. (2005). A note on the influence of visitors on the behaviour and welfare of zoo-housed gorillas. *Applied Animal Behaviour Science* 93 (1-2): 13-17.
- Which, S.A., Shumaker, R.W., Perkins, L., and de Vries, H. (2009). Captive and wild orangutan (*Pongo* sp.) survivorship: a comparison and the influence of management. *American Journal of Primatology* 71 (8): 680-686.
- White, F.J., and Chapman, C.A. (1994). Contrasting chimpanzees and bonobos: nearest neighbour distances and choices. *Folia Primatologica* 63: 181-191.
- Wich, S.A., and van Schaik, C.P. (2000). The impact of El Niño on mast fruiting in Sumatra and elsewhere in Malesia. *Journal of Tropical Ecology* 16: 563-577.
- Wich, S.A., Utami-Atmoko, S.S., Setia, T.M., Rijksen, H.D., Schürmann, C.L., van Hooff, J.A.R.A.M., and van Schaik, C.P. (2004). Life history of wild Sumatran orangutans (*Pongo abelii*). *Journal of Human Evolution* 47: 385-398.
- Wich, S.A., Geurts, M.L., Setia, T.M., and Utami-Atmoko, S.S. (2006). Influence of fruit availability on Sumatran orangutan sociality and reproduction. In Hohmann, G., Robbins, M.M., and Boesch, C. (eds.), *Feeding ecology in apes and other primates. Ecological, physical and behavioral aspects*. Cambridge University Press, pp. 335-356.

- Wich, S.A., Meijaard, E., Marshall, A.J., Husson, S.J., Ancrenaz, M., Lacy, R.C., van Schaik, C.P., Sugardjito, J., Simorangkir, T., Traylor-Holzer, K., Doughty, M., Supriatna, J., Dennis, R.D., Gumal, M., Knott, C.D., and Singleton, I. (2008). Distribution and conservation status of the orang-utan (*Pongo* spp.) on Borneo and Sumatra: how many remain? *Fauna and Flora International, Oryx* 42 (3): 329–339.
- Wich, S.A., Utami-Atmoko, S.S., Setia, T.M., and van Schaik, C.P. (2009). *Orangutans: Geographic variation in behavioral ecology and conservation*. Oxford University Press, New York.
- Wilson, S.F. (1982). Environmental influences on the activity of captive apes. *Zoo Biology* 1: 201-209.
- Wrangham, R.W. (1979). On the evolution of ape social systems. *Social Science Information* 18: 335-368.
- Wrangham, R.W. (1980). An ecological model of female-bonded primate groups. *Behaviour* 75: 262-300.
- Zucker, E.L., Dennon, M.B., Puleo, S.G., and Maple, T.L. (1986). Play profiles of captive adult orangutans: a developmental perspective. *Developmental Psychobiology* 19 (4): 315-326.
- Zucker, E.L. (1987). Control of intragroup aggression by a captive male orangutan. *Zoo Biology* 6: 219-223.
- Zucker, E.L., and Ferrera, P.S. (1990). Sociospatial relationships during gestation in captive lowland gorilla and orangutan groups. *Deutscher Zoologischer Garten N.F.* 60 (5): 253-262.
- Zucker, E.L., and Thibaut, S.C. (1995). Proximity, contact, and play interactions of zoo-living juvenile and adult orangutans, with focus on the adult male. In Nadler, R.D., Galdikas, B.M.F., Sheehan, L., and Rosen, N. (eds.), *The neglected Ape*. Plenum Press, New York, pp. 239-249.

8. APPENDIX

Ethogram – definition of behaviours

*: duration was recorded; ^a: every movement was recorded as one single bout; ^b: behaviour was not recorded as such when performed within a sequence of social play

Social activities:

(A: animal A, B: animal B)

approach

A moves in direction towards B and stops in a distance within arm's reach (divergence 5° max.)

advance

A moves in direction towards B and stops in a distance from B smaller than 3m but greater than arm's reach

leave / withdrawal

A leaves the radius of arm's reach to B at a normal, smooth pace

pass by

A moves in direction towards B and continues past B nearby (within arm's reach)

follow*

A moves behind B in a distance of 5m max. into the same direction; A starts moving within 10s max. after B has left the radius of arm's reach in the same direction (divergence 5° max.)

proximity*

A is stationary within arm's reach to B but not in physical contact and without exhibiting any other behaviour

social monitoring

A observes B from a distance greater than arm's reach for at least 5s *

hold out hand

A extends its arm in direction of B whilst turning ventrally towards B within a distance < 2 arm's reach and maintains the position for some time

graze

A passes nearby B while touching B lightly with parts of its torso (excl. hand, foot, mouth)

touch^a

A taps at part of B's body with its hand, finger, foot, or mouth without force (excl. mouth to face contact)

kiss^a

A makes short-term physical contact with its mouth to the face of B

make contact

A initiates physical contact to B with some part of its torso

contact*

A and B are stationary and in physical contact for at least 5s without exhibiting any other behaviour

„lean arm on“^a

A places one arm slightly around the shoulder/neck of B while sitting/standing at B's side without ventral contact with B

embrace

A places one or both arms around the upper part of B's body while having ventral contact with B and being stationary

tandem

A holds on B's hair or hangs on to B's body with hands or is clinging with ventral contact whilst walking

allogroom*

A runs its fingers or the back of his hand through the hair of B (against the direction of growth) and exposes a small area of skin, from which it may remove small particles with its fingers or the extended under-lip

social play contact*

A and B are gnaw wrestling, usually accompanied by open-mouthed play face shown by both participants, and A and B are engaged simultaneously and reciprocally; objects/substrate can be included by the participants during playing; a playing sequence is regularly interrupted by pauses during which the partners stay nearby one another; a sequence stops if none of the participants initiated playing again after 5s max.

social play no-contact*

A and B are playfully chasing and fleeing one another reciprocally without physical contact; a playing sequence is regularly interrupted by pauses during which the partners stay nearby one another; a sequence stops if none of the participants initiated playing again after a pause of 5s max.

play invitation

A walks towards or sits nearby or is hanging above B performing exaggerated slouched movements

maternal behaviour

behavioural elements occurring between mother-infant exclusively (carry, cling, hold, rest in clinging-contact, collect, shove, nipple-contact)

interaction with newborn

A touches, fondles, plays, or invites to play with a newborn which is not its own

beg contact

A looks intently at B's chewing mouth and/or looks alternately at B's mouth and B's hand holding food, and A cups its hand around the underside of B's muzzle or holds his hand around the back of B's head and presses its slightly opened mouth on to that of B; A grasps B's hand holding food and draws it to itself

beg no-contact/peer

A looks intently at B's mouth holding the face very close to that of B and/or looks alternately at B's mouth and B's hand holding food

give / share food contact

A gives chewed food to B through mouth-mouth contact (smacking sound is often audible)

share food no-contact

A drops food onto the protruding underlip, or in the hand of B; A allows B to eat simultaneously from the same food item which it is holding and/or A allows B to take food item out of its hand/foot (A doesn't hold the food item tightly)

take away food^a

A grasps food item which B is holding tightly and draws the food to itself in a rapid movement

take away object^a

A grasps object/substrate which B is holding tightly and draws the object/substrate to itself in a rapid movement

take food/object intention

A tries to grasp food item/object which B is holding tightly but fails

hair tease^{a, b}

A grasps a bunch B's hair and pulls or rattles at it

pelt^{a, b}

A throws object/substrate directed to B

scuffle

A tries to release B grip of its hand/foot by grasping or gently pushing the muzzle against the hand or foot of B which held it's own, and then A and B both grasp the hand or foot of the partner and try to release the other's grip; includes alternately and rapid movements without much force but not in playful manner

grasp

A firmly grips B by a limb and holds on

draw

A drags B towards its body or along for some distance while holding B on a limb

shrink back / flinch from s.o.^a

A performs an abrupt retreat movement by ducking the head and upper part of the body directed backwards to B

give precedence to s.o.

A and B move towards same target (e.g. food item) whilst coming from different directions; shortly before reaching the target A stops moving but is still looking towards the target, and B reaches the target

displace

sequence of: A moves in direction to B, B leaves its location and moves away as soon as A reaches out arm's reach, and A takes place at B's previous position

retreat from s.o.

A moves in a direction away from B at smooth speed as soon as B reached out a distance of 3-5m but not arm's reach; often: A moves reversely and/or looks back at B while moving away

retreat without approach

A moves in a direction away from B at smooth speed before B reached out a distance of 3-5m, and A looks back at B while moving away

fleeing

A moves away from B at great speed as soon as B reached out a distance of 3-5m, or after a preceding agonistic interaction between A and B

fleeing without approach

A moves away from B at great speed before B reached out a distance of 3-5m and/or without a preceding agonistic interaction between A and B occurring

push back-no contact^a

A performs a rapid and 'sweeping away' movement with its hand/arm towards B without touching B

push back-contact^a

A shoves away B emphatically with its hand/foot/shoulder and with physical contact

threaten/bite intention

A performs a fierce brusque opening of its mouth exposing the teeth while the head is jerked in the direction of B; includes bite-intentional movement directed to some part of B's body

bite

A closes its jaws abruptly and with force onto some part of B's body

hit^a

A slaps B forcefully with the extended hand, brought downwards from above and landing on the head or on the shoulder of B (the stroke is not playful but is unrestrained and accurately aimed)

chase (brusque charge)

A rushes towards B in a straight line and at fast pace

present (proceptive behaviour)

A hangs, stands, or lies on its back (with its legs wide apart) in such a position that its genital region is clearly exposed and close to B (regularly performed by females directed to males)

positioning / orientate s.o. *

A holds B on the lower part of its torso or legs and places and/or attempts to place B's genital region exposed to its own genital region

genital inspection contact*

A holds its face close to the genital region of B and touches that region with a finger or the extended underlip; A sniffs the place of contact on their finger after a brief touch

genital inspection no-contact *

A holds its face close to the genital region of B and sniffs directly at the genital region

genital rubbing *

A rubs its genital region at some part of B's body (often including vertical movements of the pelvis); includes also in males: A holds on B's finger, hand, foot, or head and rubs it along its own erect penis

copulation *

A copulates with B un-forcefully including a sequences of intromission, thrusting and ejaculation

rape *

copulation is performed forcefully including struggling, hitting

copulation-trial *

A attempts to insert its penis into B's vagina but does not perform a complete copulation

urine drinking

A drinks the urine which B has excreted

positioning between B and C / intervene

A postures spatially between B and C which are in proximity or engaged in any other interaction, then B or C leaves the radius of their arm's reach

approach to give support

A approaches B interacting with C which receives agonistic acts, and A remains nearby C and is orientated towards B; sequences can be accompanied by threatening behaviour or chasing away B

displace from s.o.

sequence of: A moves into direction to B and C which are sitting within each others arm's reach, B moves away from C as soon as A reached out arm's reach, and A takes place at B's previous position

Non-social activities (outside arm's reach to another group mate)**locomotion ***

move above or at ground level (bipedal and quadrupedal walking, climbing, brachiation, swinging), object¹ or substrate² can be carried along (excl. food)

forage *

any of: swap, shove, blow aside substrate while scanning the ground for food (sporadic pick ups of single food left-over can occur); gather bunch of grass; process food item by the aid of hands/feet/mouth; angle for food with hands or object/substrate as tool outside the enclosure's boundary; shake grains out of the tube; pick with branch into a food-tube

hidden forage*

head is covered with object/substrate while foraging

carry food

hold food item(s) with any part of the body whilst moving

feed / drink

any of: bit off/chew/gulp down (part of) food item; pick up grains continuously; lap/suck up grains; lick off food from branch/blade of straw/hand; drink water

hidden feed

head and/or neck is covered with object/substrate while feeding

regurgitate ^a

vomit/retch food

lap pap

lick off regurgitated food-pap; chew and gulp down retched food-pap

rest*

lie, sit inactively for at least 15s while eyes open or closed (no attentively scanning of the surroundings)

hidden rest*

head and/or neck is covered with object/substrate while resting

nest*

draw near substrate/object(s) and spread it around the body often while plucking the material to pieces and fixing/pushing it on the ground sometimes accompanied by bending and interlacing the material

manipulate, tool use*

examine and altering object/substrate/physical furnishings using hands/feet/mouth/teeth or a second object/substrate as a tool (excl. tool use in the context of foraging and autogroom)

¹ gunnysack, paper, cardboard roll, plastic, football, wooden-log, plastic tube; Chester: firehose

² straw, wood-wool, branch, soil

solitary / object play*

making vigorous and exaggerated movements often accompanied by open-mouthed play face (e.g. somersaulting, pirouetting, twisting at a rope); move playfully with an object/substrate without intending to alter the object

autogroom*

any of: pick through and/or slowly brush aside fur with hand(s), inspect small irregularities; scratching movement during which the fingertips are drawn across the fur or skin; touch including wiping eyes, pick mouth, clean teeth; object/substrate can be used as tool

biting of hair*

slowly brush aside fur with hand(s) and lips, then hold fast the hair with lips and bit off or pull out; when the act of bit off/pull out could not be observed reliably it was recorded as 'biting off presumed'

masturbate, self-inspection *

any of: examine and/or manipulate one's genitals with hand/foot, rub the genitals against object/substrate, put penis into a hole, tube etc. while moving pelvis vertically up and down

urinate, defecate

excretion of faeces or urine

human-directed behaviour*

any of: approach viewing window (border of the moat) up to at least 1.5m; watch human from max. 1.5m; sit down in front of window, stand up at window, knock at window, throw substrate/object and/or spit, and hold out hand towards human; behaviour was recorded as one bout until the front side of the animal's body was turned away from the human for at least 5s and/or a switch to a behaviour of another category

monitoring *

non-social: sit, lie, stand immobile for at least 5s while scanning the surroundings attentively (if monitoring off-show cages, bonobos or chimpanzees it was be noticed)

visitor: sit, lie, stand immobile for at least 5s while observing human in a distance > 1.5m

stereotypy*

movement pattern that is performed in a repetitive fashion and out of its original context and seems to serve no useful purpose (e.g. cage-circling)

coprophagy

play with and/or eat faeces

patrolling *

walking systematically around the island/boundary of enclosure stopping at intervals to scan the surroundings (intervals shorter than 5s)

display *

shake vigorously at furnishings and/or move furnishings in a way that they are slapping against other structures

call *

performance of a loud and prolonged vocalisation (includes 'long call' and 'lork call')

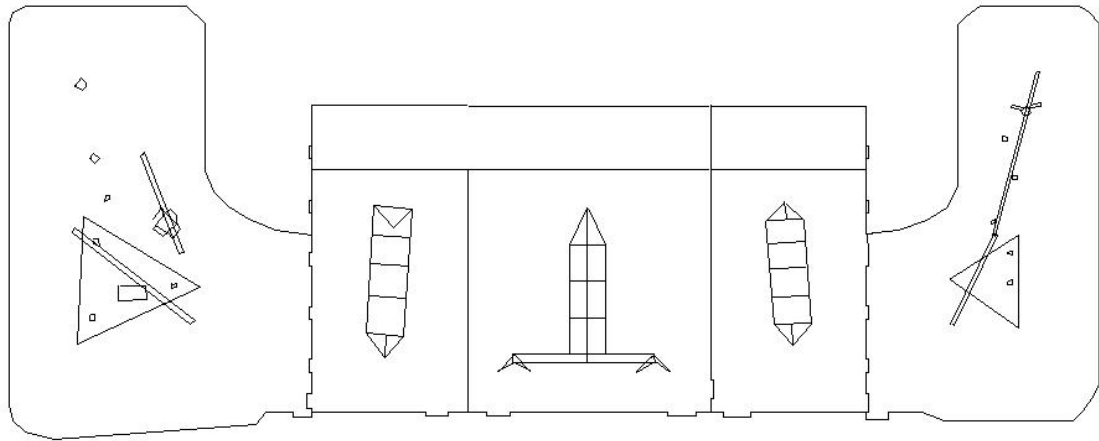


Fig. 8.33: Facilities Chester Zoo

Enclosure-sizes: indoors: end-sided enclosures: 115.8m² each, middle enclosure: 171.77m²; outdoor islands: left-handed: 391.29m², right-handed: 282.42m² (9.5m height-trees). All three indoor enclosures were furnished with a T-shaped metal climbing apparatus each of about 8m height. Fire hoses served as ropes/vines on the frames. Both outdoor islands were equipped with a metal climbing frame, vertical tree-trunks and ropes.

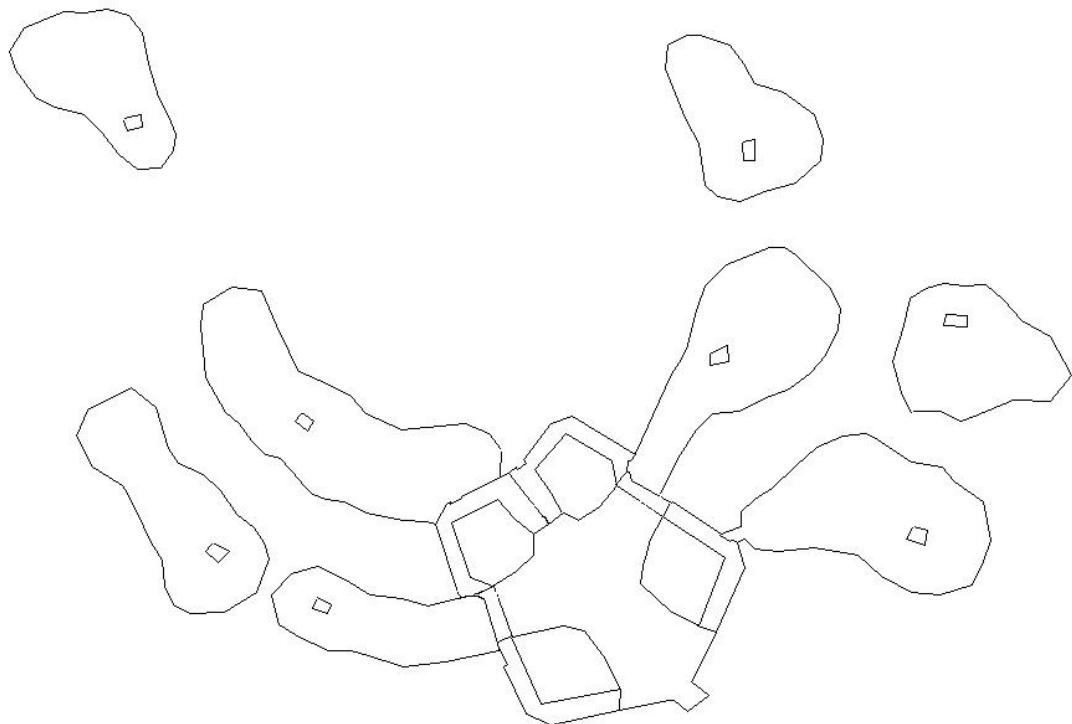


Fig. 8.34: Facilities Stichting Apenheul

Enclosure-sizes: indoors 233m² total, outdoors 1124.4m² total. The indoor enclosures had a balcony at 3.5m. The indoor enclosures were equipped with wooden climbing apparatus, platforms, and ropes (7.3m max. height). The outdoor islands were equipped with chestnut trees (up to 10-15m height), ropes and wooden platforms.

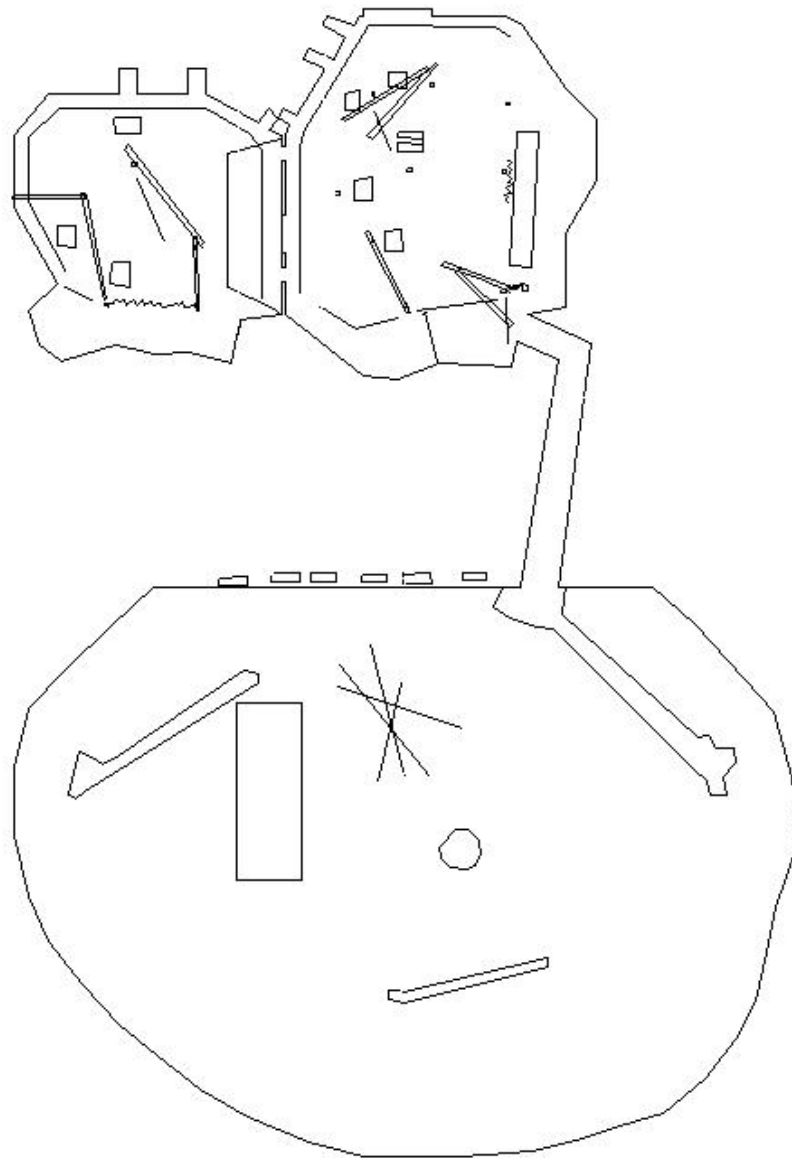


Fig. 8.35: Facilities Cologne Zoo

Enclosure-sizes: indoors: 100m² (left-handed enclosure) + 145m² (right-handed enclosure), 6.5m max. height; outdoors: 485m². The indoor enclosure was glass-fronted with a metal-barred ceiling. It was equipped with ropes, hammocks, horizontal and vertical natural tree-trunks and ladder systems. The outdoor was equipped with natural tree-trunks and two wooden climbing structures with ropes connected to the metal-barred gable-side (11m height). Mesh and bushes served as barriers to the visitors' walkway, with three large windows at intervals.

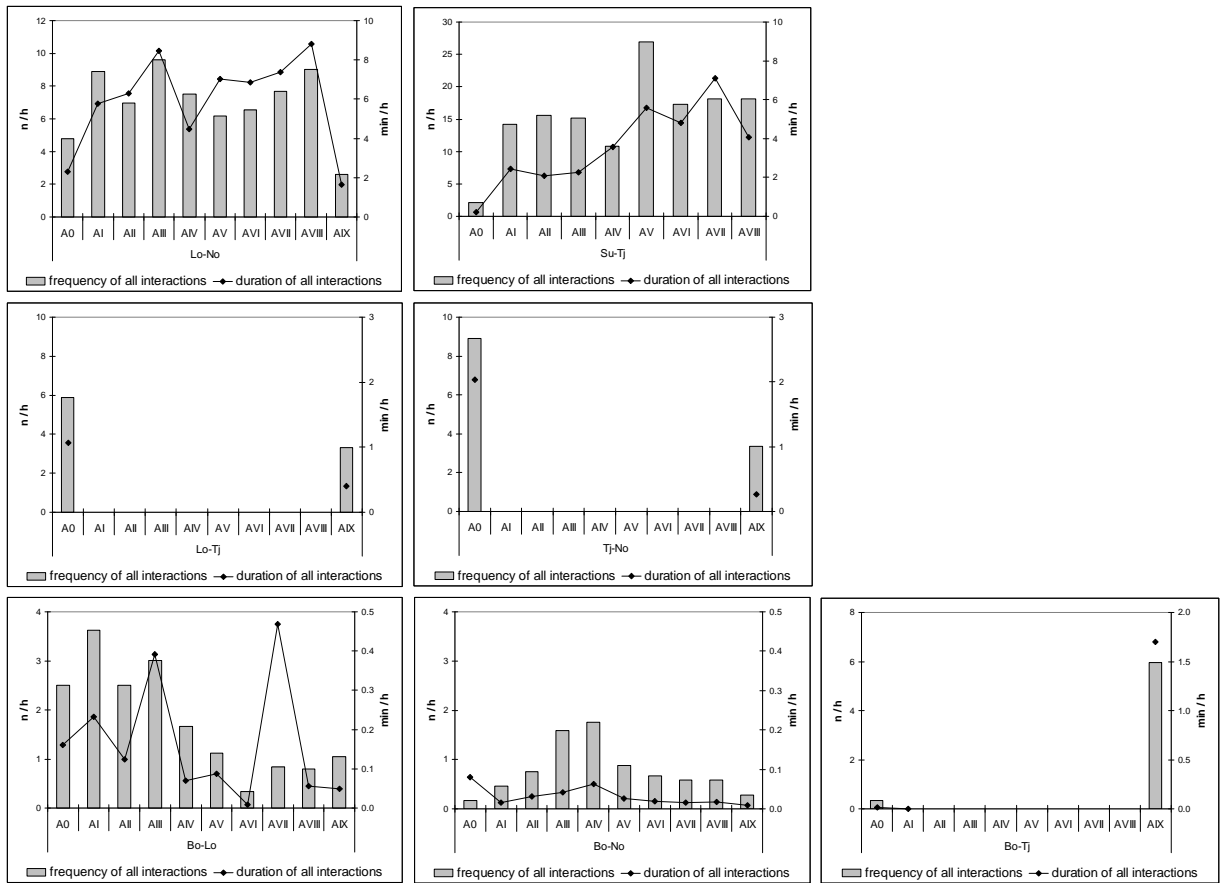


Fig. 8.36: Long-term observations of dyadic interactions–adult individuals

Mean frequency (bars) and mean duration in min/h (lines) of all interaction per dyad and per observation session is shown. A lack of data indicates that partners of a given dyad were not kept together in the same subgroup.

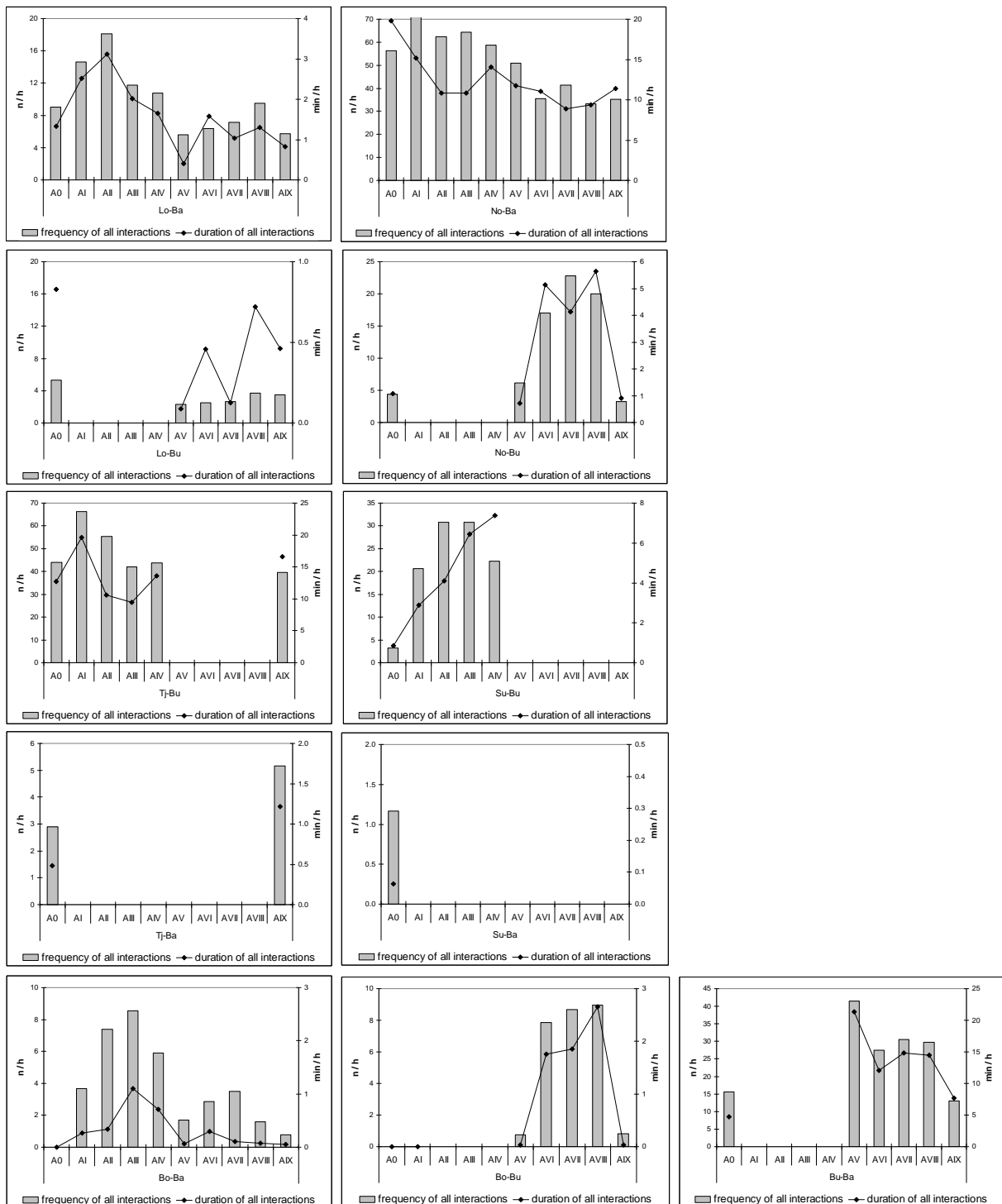


Fig. 8.37: Long-term observations of dyadic interactions—adult and juvenile individuals
 Mean frequency (bars) and mean duration in min/h (lines) of all interaction per dyad and per observation session is shown. A lack of data indicates that partners of a given dyad were not kept together in the same subgroup.

	dyad	groom	touch	dominant	submissive
Chester	Mar-Sar		-0,3	1,0	-1,0
	Mar-Lei	-0,8	-0,1	1,0	-1,0
	Sa-Lei	-1,0	-0,4	0,6	-1,0
	Mat-Pu	0,3	-0,2	-1,0	1,0
Apentheul	K-Rad		0,0		-1,0
	K-Kat	0,6	-0,6	1,0	-1,0
	K-San		-1,0	1,0	-1,0
	K-Fin		-1,0	1,0	-1,0
	K-Sil		-1,0		-1,0
	K-Jos	-1,0	-1,0	1,0	-1,0
	Rad-Kat	-0,7	-0,3	1,0	-1,0
	Rad-San		0,0		-1,0
	Rad-Fin			1,0	-1,0
	Rad-Jos				-1,0
	Kat-San	-0,2	0,3	-0,3	1,0
	Kat-Fin				1,0
	Kat-Jo				
	San-Fin		0,9	0,0	
	San-Sil		0,0		
	San-Jos	-1,0	-0,2	0,7	
	Fin-Sil	-1,0	-1,0	0,0	1,0
	Fin-Jos		-0,3	1,0	
	Sil-Jos	0,7	0,4	1,0	
	Rad-Wi	-0,6	-0,8	0,7	
Rad-Bin		1,0		-1,0	
Kat-Wi	0,0	-0,4	0,3		
Kat-Bin	1,0	1,0	0,5	-1,0	
Wi-Fin		0,3	1,0		
Bin-Fin		0,3			
Wi-Jos		0,4	-1,0		
Wi-San	0,6	0,2	-0,7	1,0	
San-Bin	-0,9	-0,5	1,0	-1,0	
Bin-Sil			-1,0	1,0	
Bin-Jos		-0,3	1,0		
K-Wi		-1,0	-1,0	-1,0	
K-Bin		-1,0		-1,0	
Wi-Bin	0,2	0,7			
Cologne	Lo-No	-0,6	-0,6	0,7	
	Lo-Su		0,3		
	Lo-Tj	-0,7	-0,1	1,0	
	No-Tj	0,1	0,6	-1,0	1,0
	No-Su			1,0	-1,0
	Su-Tj	-1,0	-0,7	0,5	1,0
	Bo-Lo	-1,0	-0,9	1,0	-1,0
	Bo-No	-1,0	1,0	1,0	-1,0
	Bo-Tj	-1,0	-0,9	1,0	-1,0
	Bo-Su		-1,0		
	San-Lo				1,0
	San-Non		0,3	-1,0	1,0
	Sa-Tj		-0,5		
	San-Su	-1,0	-0,3		
	Bo-San				-1,0
	Lo-Ba	1,0	0,1	1,0	
	Lo-Bu	0,6	0,4	1,0	
	No-Ba	1,0	-0,5	1,0	-1,0
	No-Bu	1,0	-0,2	1,0	-1,0
	Tj-Ba	-1,0	0,4		
	Tj-Bu	0,7	-0,6	0,9	-1,0
	Su-Ba		-1,0		
	Su-Bu	0,6	-0,6	1,0	-1,0
	Bo-Ba	-0,8	-1,0	1,0	-1,0
Bo-Bu	-1,0	-0,5	1,0	-1,0	
San-Ba		-1,0			
San-Bu		-0,3			
Ba-Bu	0,7	0,3	-0,8		

Tab. 8.26: Reciprocity indices per dyad

Chester				
dyad	Ma-Sr	Ma-Le	Sr-Le	Pu-Mt
min	0.0	0.0	0.0	0.0
quartile 25	4.4	3.2	4.1	3.4
median	6.8	5.4	6.4	5.7
quartile 75	10.2	8.9	10.0	9.5
max	22.5	23.1	24.3	22.8

Apenheul																			
dyad	Ra-Ka	Ra-Sa	Ra-Fi	Ra-Jo	Ka-Sa	Ka-Fi	Ka-Jo	Sa-Fi	Sa-Si	Sa-Jo	Fi-Si	Fi-Jo	Si-Jo	K-Ra	K-Ka	K-Sa	K-Fi	K-Si	K-Jo
min	0.0	0.0	0.4	2.6	0.0	0.2	1.4	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.3	0.3	0.0	0.7
quartile 25	3.8	5.9	5.1	12.2	5.3	5.5	14.9	4.4	1.9	1.0	3.4	4.5	1.4	7.0	5.0	6.0	4.7	3.5	6.0
median	6.1	11.6	8.4	25.6	9.6	9.3	28.9	8.3	7.2	3.3	6.4	10.3	4.1	12.6	11.2	12.2	6.8	6.8	9.2
quartile 75	11.9	20.8	16.1	36.1	21.3	21.2	36.3	27.5	24.6	7.9	15.7	26.7	7.0	18.5	19.8	27.7	12.1	13.3	25.2
max	51.3	52.7	51.3	42.1	55.0	52.3	44.2	55.3	40.2	48.5	53.6	52.4	47.4	47.9	52.8	53.6	44.6	55.0	54.6

Cologne															
dyad	Lo-No	Lo-Su	Lo-Tj	No-Su	No-Tj	Su-Tj	Bo-Lo	Bo-No	Bo-Su	Bo-Tj	Sa-Lo	Sa-No	Sa-Su	Sa-Tj	Bo-Sa
min	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.9	0.0	0.1	0.0	0.0	0.0	2.0
quartile 25	3.3	10.7	8.5	9.9	7.9	1.2	5.3	6.4	10.4	8.8	8.3	9.6	4.6	8.2	9.3
median	6.5	13.1	13.6	16.1	13.3	4.2	8.0	9.5	12.9	16.2	13.4	14.9	9.4	14.0	13.2
quartile 75	9.2	16.2	22.5	21.9	21.9	6.2	10.8	11.8	16.7	23.7	19.6	20.3	16.0	20.9	20.0
max	44.4	44.6	43.8	42.1	44.3	42.7	43.2	44.3	44.5	44.5	44.1	42.4	42.0	41.6	43.4

Tab. 8.27: Interindividual distances per dyad

Medians, quartiles, minimum and maximum distances per dyad are shown, given in metres.

9. DANKSAGUNG

Mein besonderer Dank gilt Herrn PD Dr. Thomas Ziegler für die Übernahme des Erstgutachtens und Herrn Prof. Dr. Ansgar Büschges für das Zweitgutachten. Bei Herrn Prof. Dr. Gunther Nogge möchte ich für die initiale Vergabe und Ermöglichung dieser Arbeit am Zoologischen Garten Köln bedanken.

Ein sehr großes Dankeschön von mir geht an Herrn Dr. Werner Kaumanns für die jahrelange Hilfsbereitschaft, Kritik, und anregenden Diskussionen.

Den Direktoren, Kuratoren, und wissenschaftlichen Mitarbeitern aller beteiligten zoologischen Einrichtungen möchte ich für die Ermöglichung der praktischen Durchführung dieser Arbeit, und für die Bereitstellung der Unterkunft in Chester und Apenheul danken. Stellvertretend seien hier Dr. Stephanie Wehnelt, Dr. Frank Rietkerk und Warner Jens erwähnt.

Ganz herzlich möchte ich mich bei allen Tierpflegern der drei Zoos für ihre Zeit, Hintergrundinformationen, die Pausengespräche, und ihr Vertrauen bedanken.

Ein großes Dankeschön gilt Simone, Steffi, Dré und Melanie für das Korrekturlesen sowie den Kolleginnen und Kollegen der wissenschaftlichen Arbeitsgruppen des Kölner Zoos für den interdisziplinären Austausch und ihr offenes Ohr bei diversen Problemchen. Rainer und Lars seien für das Programmieren von „Animal Tracker“ und „Monkey Business“ lobend zu erwähnen, die das Bewältigen der Datenmenge um ein Vielfaches erleichtert haben.

Bedanken möchte ich mich ebenfalls ganz besonders bei meiner Mutter sowie meinen Freunden, und insbesondere Lars für ihr immerwährendes Interesse an meiner Arbeit, Hilfe bei Computerfragen, und ihr Verständnis für die Einschränkungen bei manch zwischenmenschlichen sozialen Aktivitäten.

Zu guter Letzt gilt mein „geistiges“ Dankeschön meinen Studienobjekten, den Orangutans, die durch ihre persönlichen Eigenheiten und ihr Wesen mich immer wieder aufs Neue beeindruckt und begeistert haben, und so zum Durchhalten, Weiterführen und Beenden dieser Arbeit beigetragen haben.

10. ERKLÄRUNG

Ich versichere, dass ich die von mir vorgelegte Dissertation selbständig angefertigt, die benutzten Quellen und Hilfsmittel vollständig angegeben und die Stellen der Arbeit – einschließlich Tabellen, Karten und Abbildungen –, die anderen Werken im Wortlaut oder dem Sinn nach entnommen sind, in jedem Einzelfall als Entlehnung kenntlich gemacht habe; dass diese Dissertation noch keiner anderen Fakultät oder Universität zur Prüfung vorgelegen hat; dass sie – abgesehen von unten gegebenen Teilpublikationen – noch nicht veröffentlicht worden ist sowie, dass ich eine solche Veröffentlichung vor Abschluss des Promotionsverfahrens nicht vornehmen werde. Die Bestimmungen der Promotionsordnung sind mir bekannt. Die von mir vorgelegte Dissertation ist von Herrn PD Dr. Thomas Ziegler betreut worden.

Teile meiner Arbeit sind wie folgt publiziert:

Kongressbeiträge (Vortrag):

11th Meeting of the Gesellschaft für Primatologie (Hannover, Germany):

Classen, D. and Kaumanns, W. (2009). Fission-fusion species under human care: The example of orangutans. Abstract. Conference contributions, GfP 2009: 48.

Kongressbeiträge (Poster):

1st Congress of the European Federation for Primatology / 9. Tagung der Gesellschaft für Primatologie (Göttingen, Germany):

Classen, D., Kaumanns, W., and Kiessling, S. (2005). Social relationships in zoo-living Bornean orangutans (*Pongo pygmaeus*). Abstract. Primate Report 72: 24.

6th International Zoo and Wildlife Research Conference on Behaviour, Physiology and Genetics (Berlin, Germany):

Classen, D., Kiessling, S., and Kaumanns, W. (2007). Every once in a while—patterns of spatial behaviour in two captive groups of Bornean orangutans. Abstract. Conference contributions, IZW: 61.

Köln, den 08.05.2011