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unter Anleitung von Dipl.-Biol. Sandra Reichler ausgeführt.

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Prüfer: apl. Prof. Dr. Thomas Braunbeck

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Eigenständigkeitserklärung

Ich erkläre hiermit, dass ich die vorliegende Bachelorarbeit selbstständig unter Anleitung verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

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2. Zusammenfassung

Die Populationen des Sumatra-Orang-Utans Pongo abelii sind, hauptsächlich verursacht durch Verlust ihres Lebensraumes, der Tropenwälder der indonesischen Insel Sumatra, im Lauf der letzten Jahrzehnte stark zurückgegangen. Die Art wird vom IUCN als vom Aussterben bedroht gelistet. Da damit zu rechnen ist, dass sich dieser Trend in den nächsten Jahren fortsetzen wird, spielt die Zucht in Zoos eine tragende Rolle bei der Arterhaltung.

Der Zoo Heidelberg nimmt seit langem am Europäischen Erhaltungszuchtprogramm (EEP) für Sumatra-Orang-Utans teil. Mit der aktuellen Gruppe war die Zucht jedoch bislang nicht erfolgreich, da eines der beiden Weibchen als unfruchtbar eingestuft wird und das andere Weibchen trotz seines potenziell ausreichenden Alters für die Geschlechtsreife hormonellen Analysen zufolge bisher noch keinen Menstruationszyklus aufweist.

Die vorliegende Arbeit gibt eine Einschätzung des Risikos, dass die aktuelle Zuchtsituation nicht ausschließlich dem physiologischen Status der Weibchen, sondern auch dem Sozialverhalten der Gruppe geschuldet ist. Da das Männchen in der Gruppe per Hand aufgezogen wurde und eine starke Bindung an Menschen zeigt, besteht der Verdacht, dass es kein Interesse an sexuellen Interaktionen mit den Weibchen zeigt.

Hierzu wurden die Gruppe im Zoo Heidelberg sowie die Sumatra-Orang-Utan-Gruppe des Neunkircher Zoos, welche als Vergleichsgruppe fungierte, während insgesamt ca. 180 Beobachtungsstunden beobachtet und das Verhalten mit Hilfe statistischer Vergleiche analysiert. Obwohl entscheidende Unterschiede im Sozialverhalten der beiden Gruppen, insbesondere im Sexualverhalten der Männchen, belegt werden konnten, gibt es keine Hinweise darauf, dass die Beziehungen der Gruppenmitglieder untereinander nicht den Erwartungen an das Verhalten von in Gefangenschaft gehaltenen Orang-Utans entsprechen. Es wird empfohlen, die hormonelle Entwicklung des jüngeren Weibchens weiter zu verfolgen und gegebenenfalls unterstützende Maßnahmen zu ergreifen oder eines der Weibchen gegen ein fertiles Weibchen auszutauschen und das Sozialverhalten innerhalb der Gruppe dann neu zu evaluieren.

Abstract

Populations of the Sumatran orangutan Pongo abelii have experienced a severe decline over the course of the last decades, mostly due to a loss of their rainforest habitat on the Indonesian island of Sumatra. The species is listed as critically endangered by the IUCN. Since it is expected that this trend continues in the next years, breeding in captivity plays a crucial role in the conservation of the species.

Heidelberg Zoo, Germany, has been a part of the European Endangered Species Programme for Sumatran orangutans for many years. With the current group, however, breeding has not yet been successful since one of the females is assessed as infertile and the other female, although potentially old enough for sexual maturity, does not yet have a menstrual cycle according to hormone analysis.

This study assesses the risk that the current breeding situation is not exclusively due to the physiological status of the females, but also to the social behaviour of the group. Since the male individual of the group has been hand-reared and strongly bonds with humans, it is suspected that it does not show interest in sexual interactions with the females.

For this, the group at Heidelberg Zoo as well as the group at Neunkirchen Zoo, which was used as a control group, were observed during about 180 hours in total and their behaviour analyzed through statistical comparisons. Even though essential differences in the social behaviour of the two groups, especially in the social behaviour of the males, could be documented, no evidence was found that relationships between the members of the group would not meet the expectation of the behaviour of orangutans kept in captivity. It is recommended to further follow the hormonal development of the younger female and apply supportive measures if required or to exchange one of the females for a fertile female and then re-evaluate the social behaviour of the group.

3. Introduction

3.1 Pongo abelii species description

3.1.1 Taxonomy

Pongo abelii, the Sumatran orangutan, is one of the two species of the genus Pongo which had historically been considered two subspecies of the same species, Pongo pygmaeus. However, for about a decade, the genus Pongo has been split into the two species of Pongo abelii and Pongo pygmaeus, the Bornean orangutan, which is divided in three different subspecies (Singleton et al., 2008). The two species differ in terms of genetics, physical appearance, diet, behaviour and life cycle rhythm (Delgado and van Schaik, 2000; Goossens et al., 2009; Noordwijk et al., 2009).

Phylum: Chordata
Class: Mammalia
Subclass: Eutheria
Order: Primates
Suborder: Haplorrhini (Dry-nosed primates)
Infraorder: Anthropoidea (Higher primates)
Parvorder: Catarrhini (Old world monkeys)
Superfamily: Hominiodea (Great and lesser apes)
Family: Hominidae (Great apes and humans)
Subfamily: Ponginae
Genus: Pongo
Species: Pongo abelii

(Singleton et al., 2008; Wehner and Gehring, 2013)

3.1.2 Range and lifestyle

Orangutans are the only Hominidae besides Homo sapiens which are found outside Africa and the biggest primarily arboreal primates (MacKinnon, 1988). Today, the habitat of the Sumatran orangutan are the lowland rainforests in the north of the Indonesian island of Sumatra while there are hints that the species' distribution had been far broader until the 1960s, extending further to the south of the island (Geissmann, 2003; Singleton et al., 2008). Permanent populations of Pongo abelii have only been found at altitudes of below 1000 m above sea level (MacKinnon, 1988; Singleton et al., 2008).

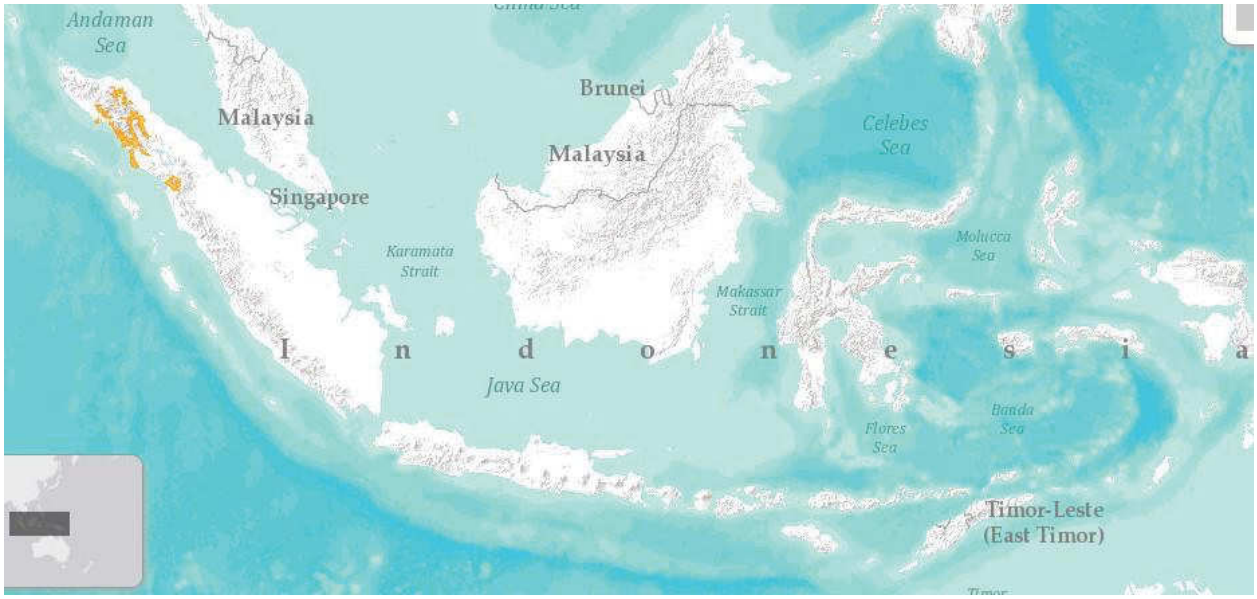


Fig. 1 Range of Pongo abelii on the Indonesian island of Sumatra (Singleton et al., 2008)

Pongo abelii tend to be more frugivorous than Pongo pygmaeus since their habitat overall is richer in fruit around the year due to different climatic conditions. This forces them less intensely to rely on leaves and the inner bark of trees during times of low fruit abundance as it is the case with Pongo pygmaeus (Schaik, 1999; Schuster et al., 2007). Figs, the fruit of several species of Ficus, are the most reliable and preferred fruit. They also occasionally feed on insects, birds' eggs and small vertebrates (Rijksen, 1978; Singleton et al., 2008). They build and use tools for numerous purposes such as using sticks to open fruit or dig for insects in tree bark, protecting their hands with leaves when handling thorny fruit or protecting themselves

with big leaves during tropical downpours (Rijksen, 1978; MacKinnon, 1988). Orangutans also have a vast botanical knowledge of the plants in their habitat which enables them to avoid toxic plants and use medical plants to fight symptoms of diverse illnesses such as headaches and ague (Schuster et al., 2007).

Fig. 2 Sexual dimorphism in Pongo abelii. Upper picture: adult male; lower picture: female. Heidelberg Zoo.

There is still a lack of precise information about the life cycle of both orangutan species due to their arboreal lifestyle and resulting low observability in a habitat that cannot easily be accessed (Rijksen, 1978). The sexual dimorphism they exhibit can readily be recognized in zoo animals (see fig. 2), with adult males reaching a height of up to 1.00 m and a weight of 80 to 90 kg. Females only reach around half that weight at a height of about 80 cm (MacKinnon, 1988; Geissmann, 2003). Important life events, on the other side, such as sexual maturity or the birth of the first infant, tend to be shifted to earlier points in the life span of zoo animals and therefore are difficult to assess for orangutans living in their natural habitat by means of research in zoos (Hosey et al., 2009).

Male orangutans exhibit bimaturism. They sexually mature between the age of 8 and 15 years. However, the development of secondary sexual characteristics such as cheek pads, throat pouches or long fur may then be arrested for several years until the age of 20. These subadult unflanged males resemble females in terms of outward appearance and apply a different mating strategy than their adult flanged counterparts. Since adult females prefer flanged males as mating partners, subadult males mostly force copulation (Rijksen, 1978; MacKinnon, 1988; Geissmann, 2003; Atmoko et al., 2009). This strategy has proven to be quite successful since subadult Sumatran orangutan males sire around 50% of infants (Atmoko et al., 2009). Adult males, on the other hand, occupy large home ranges of up to over 3000 ha which overlap with the home ranges of several females, which are comparatively smaller with a size up to 850 ha, while subadult males mostly are not able to establish an own home range and remain transient on their search for females while avoiding adult males (Geissmann, 2003; Singleton et al., 2008; Singleton et al., 2009). The adult males use long calls, which are an effective spacing mechanism in order to set territorial borders and avoid contact with other males. For females, the long call is also a directive towards the male both for mating purposes, but also to seek protection from harassment through subadult males in the proximity of a more dominant adult male (Fox, 2002; Kappeler, 2009; Setia et al., 2009). There is evidence that the long calls indicating the presence of an adult male play a role in suppressing the development of secondary sexual characteristics in subadult males. The transformation from subadult to adult male may be very rapid, taking not more than several weeks (Geissmann, 2003; Kappeler, 2009). Adult males show greatest interest in adult females on the fertile days of their ovulatory

cycle while both adult and subadult males prefer females with weaned infants as mating partners (Fox, 2002; Geissmann, 2003; Atmoko et al., 2009).

In the wild, the first ovulatory cycle in females, which during the entire life span depends on food availability and fat reserves, takes place between the age of 6 and 11 years. The length of a menstrual cycle ranges between 22 and 30 days. Neither a visible swelling of the outer genitals during the fertile days of the cycle nor a distinct bleeding takes place, making a more precise identification of these events for wild orangutans difficult (Rijksen, 1978; Graham, 1988; C. Knott, et al., 2009). Females mostly give birth to a sole infant for the first time at the age of 15 years after a gestation period of around 9 months (Singleton et al., 2008; Wich et al., 2009). During the first two years of its life, the infant is completely dependent on its mother who carries it while travelling while the male does not play a significant role in the upbringing. After that, the infant still maintains close contact with its mother and travels while holding hands with her or older siblings which is known as “buddy travel”. Juvenile orangutans spend gradually more time further away from their mother and are weaned gradually weaned until the age of around seven years. However, during adolescence until an age of about eight years young orangutans still stay close to their mother and might even still be around her or visit when she gives birth to the next infant, helping in its socialisation (MacKinnon, 1988; Noordwijk et al., 2009). This long period of association with the mother is necessary to obtain the skills needed for survival, ensuring low infant mortality (Noordwijk et al., 2009). As a result, the interbirth interval of Pongo abelii is between 8.2 to 9.3 years which is the longest among the great apes (Knott et al., 2009; Wich et al., 2009). The estimated longevity of Pongo abelii is over 50 years (Singleton et al., 2008).

3.2 Threats, conservation situation in situ and necessity of ex situ conservation

The most recent estimate of the population of Pongo abelii in the wild from the year 2007 is around 6,700 individuals ("How many orangutans are there?," 2007 - 2014), following a decade-long decline and thus has been listed as critically endangered by the IUCN since 2000 (Orangutan Population and Habitat Viability Assessment 2004; Singleton et al., 2008). The major threat is emanated through destruction of habitat through logging, both legal and illegal, unnatural wildfires and the conversion of forests to agricultural land, especially for oil palm

plantation, as well as habitat fragmentation due to the construction of roads. Pressure on habitats has increased over the last decade, following the facilitation of agricultural and logging investments made possible by a peace treaty ending a civil conflict and ensuring political stability in 2005 (Orangutan Population and Habitat Viability Assessment, 2004; Singleton et al., 2008). In some parts of their range, Sumatran orangutans are still hunted for food and are often killed by farmers and plantation owners as pests when raiding crops at the edge of the forest or within their former home range. About 20% of the population is located outside protected areas (Singleton et al., 2008). The long interbirth interval of females entail an offspring of no more than three or four infants during the whole lifespan of a female. Therefore, single populations are thought to be able to withstand an additional mortality of only 2% before they collapse in the long term (Marshall et al., 2009).

Pongo abelii is listed on Appendix I of CITES and is protected under Indonesian law. The Leuser Ecosystem conservation area, which is home to about 75% of the remaining wild Sumatran orangutan population, stresses sustainable management of the area. However, this does not exclude non-forest uses and the inclosed Gunung Leuser National Park only supports

for this species for many years. However, the current group has not yet successfully bred (Reichler, 2013, pers. comm.). While physiological reasons do play a major role in breeding success, the social behaviour within the group has to be considered as well since part of the problem might arise at the behavioural level.

4. Material and methods

4.1 Focus groups

In order to evaluate possible reasons for the current lack of success in the zoo's rearing efforts, the group at Heidelberg Zoo was observed as focus group of this work. The Sumatran orangutan group at Neunkirchen Zoo, Germany, was observed as a control group.

4.1.1 Heidelberg Zoo

The group at Heidelberg Zoo is kept in an inside enclosure with an area of around 66 m^2 and a height of about 6 m. In addition to this enclosure, animals have access to areas of retreat out of visitors' view with an area of around 30 m^2. When weather conditions are favourable, as it was the case during part of the observation period in the spring of 2014, animals are allowed access to an outside enclosure of around 85 m^2 and a height of around 4 m which can be accessed through a corridor connecting the inside and outside enclosure. The overall area of the enclosure is around 181 m^2 (see app. 7.1) (Reichler, 2014, pers. comm.).
The group at Heidelberg Zoo currently consists of three animals (see tab. 1).

Name	Sex	Date of birth	Place of birth	At Heidelberg Zoo since
Puan	♀	15th May, 1989	Heidelberg Zoo, Germany	Back since 18th February, 2004
Ujian	♂	25th June, 1994	Zurich Zoo, Switzerland	17th October, 2005
Sari	♀	14th October, 2003	Moscow Zoo, Russia	18th October, 2011

Tab. 1 Individuals at Heidelberg Zoo (according to Becker, 2014).

Via several excremental concentration measurements of pregnanediol-3-glucuronide, a progesterone metabolite, Puan, who is hand-reared, has been found to lack a menstrual cycle although no anomalies regarding her sexual organs could be detected. Since multiple attempts to induce her cycle with clomifene were unsuccessful, Sari will be the only female available for breeding in the current composition of the group (Reichler, 2013, pers. comm.; Stockklausner, 2014). Orangutans kept in captivity are known to reach puberty and adolescence earlier than wild animals (Hosey et al., 2009), meaning that Sari could be fertile at her age of 11 years. However, pregnanediol-3-glucuronide measurements have revealed that she does not yet have an ovulatory cycle either (Reichler, 2013, pers. comm.). Nevertheless, the current infertility of the female individuals may not be the sole reason for the lack of breeding success at Heidelberg Zoo. Ujian, who also is hand-reared, shows a strong general interest in humans including zoo visitors and so far has not shown much interest in sexual activity with the females of the group (Jakobs, 2013, pers. comm.; Reichler, 2013, pers. comm.). It is well possible that this apparent lack of interest is due to the present infertility of the female group members. Field observations and zoo research have shown that female orangutans are both more promiscuous and attractive to males during the fertile days of their cycle (Rijksen, 1978; Maple et al., 1979; Geissmann, 2003).

4.1.2 Neunkirchen Zoo

The group of Sumatran orangutans at Neunkirchen Zoo was chosen as control group for the Heidelberg group because group composition and keeping conditions are similar to those at Heidelberg Zoo.

While the exact measurements of the enclosures could not be obtained before the finalisation of this work, it is estimated that the inside enclosure the group is kept in is around half as high as the one at Heidelberg Zoo. The overall area is comparable. It has to be noted that the inside enclosure is separated by bars (see app. 7.2). The four small areas of retreat are mostly closed during the day and only used as sleeping areas at night or to separate one animal from the rest of the group, e.g. for training purposes. However, part of the inside enclosure is difficult or impossible to observe from the visitors' area due to the separation of the enclosure and the angle and position of the viewing windows, meaning the animals still have the opportunity to retreat out of visitors' view. When weather conditions are favourable, animals are allowed

access to an outside enclosure of around twice the volume of the one at Heidelberg Zoo which can be accessed through two short connecting corridors from the inside enclosure (see app. 7.2).

The group currently consists of five animals (see tab. 2).

Name	Sex	Date of birth	Place of birth	At Neunkirchen Zoo since
Noah	♀	8th December, 1983	Zoological Center Tel Aviv Ramat Gan, Israel	17th July, 2007
Masala	♂	21st January, 1991	Wilhelma Stuttgart, Germany	9th June, 1999
Struppi	♀	24th March, 2005	Hellabrunn Zoo Munich, Germany	17th July, 2007 (together with her mother Noah)
Rezeki	♀	6th August, 2007	Neunkirchen Zoo, Germany	Born about three weeks after the arrival of her mother Noah
Surya	♀	5th December, 2012	Neunkirchen Zoo, Germany	Infant of Masala and Struppi

Tab. 2 Individuals at Neunkirchen Zoo (according to Becker, 2014).

The birth of Rezeki shortly after the arrival of her mother Noah and sister Struppi at Neunkirchen Zoo in 2007 was surprising since it had not been known that Noah was pregnant when she was transferred from Munich to Neunkirchen. The stress of the transfer in combination with her advanced pregnancy may be one of the reasons why Noah was extremely aggressive against Masala, who then still was a subadult male with no secondary sexual characters, upon her arrival at Neunkirchen Zoo. Since she was superior in physical strength and induced a high stress level on him, they had to be separated. Even though it was tried to reintroduce them to each other a few years later after he had transformed into an adult male, it became very obvious that they had to be kept separated because now he showed high aggression against her, putting her in serious danger as he now was the stronger adversary. Thus, the inside enclosure remains separated by extra bars (see above; app. 7.2). Noah and Masala also can only be allowed access to the outside enclosure separately. The other females, however, can move freely through an opening in a sliding door in the bars which is small

enough for the two older individuals not to fit through (Ankner, 2014, pers. comm.; Fritsch, 2014, pers. comm.; Gregersen, 2014, pers. comm.).

Struppi, despite her very young age, takes good care of her infant Surya. She reached maturity at a very early age and soon showed interest in Masala. One factor that might have influenced this early sexual maturity might have been the fact that her younger sister Rezeki was born at an age at which juvenile orangutans typically are still dependent on their mother (Noordwijk et al., 2009). Masala had already sired an infant in 2003 while he was still a subadult with a female which is no longer a member of the group. He quickly became interested in Struppi as well (Ankner, 2014, pers. comm.; Fritsch, 2014, pers. comm.; Gregersen, 2014, pers. comm.). Hence, recording the behaviour and interactions of this group may reveal differences between the males of the two groups who were both hand-raised, but according to anecdotal information (Ankner, 2014, pers. comm.; Fritsch, 2014, pers. comm.; Gregersen, 2014, pers. comm.; Jakobs, 2013, pers. comm.; Reichler, 2013, pers. comm.;) have different social and sexual behaviour structures.

In the Neunkirchen group, Masala, Struppi and Rezeki were observed as focus animals. First and foremost, this approach considers the same number of individuals from each sex. Surya was not considered a focus animal as she is still too young to play a role in terms of sexual interactions. The same reason applies to Noah due to the overall highly agonistic relationship between her and Masala, which makes the separation of the two individuals necessary and has the overall effect of Noah not being of significance in terms of sexual interactions within the group either.

4.2 Observation

4.2.1 Ethogram

An ethogram is a catalogue of all behavioural patterns that form the behavioural repertoire of a species (Martin and Bateson, 2007). Ethograms have their limitations since rarely all members of a species behave in the same "species-typical" way (Martin and Bateson, 2007). Furthermore, they can never be complete as the complete scope of behavioural patterns of a species may be enormous. However, they provide a useful help when categorizing behavioural patterns.

The ethogram used in this study was composed both during preliminary observations in Heidelberg (7th – 13th November, 2013) and Neunkirchen (13th – 15th January, 2014) as well as during the actual observation periods since in both groups, behavioural patterns that had not been observed during preliminary observations were found over the course of observation.

4.2.2 Focal animal sampling

Focal animal sampling is the observation of one individual for a specified amount of time while recording all of its actions which occur during this period of time, including the length of the periods during which the individual is out of sight. When recording the social behaviour of the focus individual, it may be necessary to record aspects of other individuals' behaviour as well (Altmann, 1973; Martin and Bateson, 2007).

For this study, a sampling period of ten minutes for one individual before changing to the next one was selected during preliminary observations. Sample session length varied between 2 and 4.5 hours in Heidelberg, but was between 3 and 4 hours most of the time. Observation was carried out at variable times between 10.15 and 17.15. In Neunkirchen, sample session length was around 5 hours most of the time during a variable time frame between 9.50 and 16.45, although most observation days started at about 11.00 due to a longer way to the zoo for the observer. The comparatively shorter session length in Heidelberg as well as the greater variability was mostly due to more difficult observation conditions in Heidelberg. The orangutans kept at Heidelberg Zoo are able to retreat into areas of retreat within the enclosure at almost any given time which cannot be observed from the visitors' area where the observer was located (see 4.1.1; app. 7.1). At Neunkirchen Zoo, on the other hand, the comparatively small areas of retreat are not accessible for the animals most of the time (see 4.1.2; app. 7.2). Hence, the only times when focus individuals could not be observed at Neunkirchen Zoo were the periods when they were located in areas of the enclosure that are difficult to view from the visitors' area. In Heidelberg, however, animals make ample use of the opportunity to retreat out of visitors' view, especially before noon and in other periods of the day that are usually spent resting and therefore were sometimes out of sight for longer periods of time (up to one hour and longer) which were therefore discarded from further analysis.

At Heidelberg Zoo, the overall observation period was separated into two parts. The first observation period took place between 15th November, 2013, and 21st December, 2013, on 15

observation days. After observation was terminated at Neunkirchen Zoo, the second period of observation at Heidelberg Zoo was recorded between 24th February, 2014, and 21st March, 2014, on 17 observation days. On 11 of these days during the second period, animals had access to the outside enclosure. Overall observation time pooled from both observation periods was 35 hours for Ujian, 35.67 hours for Sari and 35.58 hours for Puan.

At Neunkirchen Zoo, observation took place between 18th January, 2014, and 13th February, 2014, on 19 observation days. During this period, the female focus animals had access to the outside enclosure on five observation days. Masala had access to the outside enclosure on only three of these days (see 4.1.2). Overall observation time for all three focus individuals was 25 hours.

4.2.3 Ad libitum sampling

Ad libitum sampling is the recording of behaviour with no systematic constraints. The observer records what is most readily observable, whatever seems most relevant at the given sampling time or whatever else falls into his or her often unconscious recording decision (Altmann, 1973; Martin and Bateson, 2007). For obvious reasons, this sampling method entails a bias in sampling and therefore results are less reliable and comparable than those of other sampling methods (Altmann, 1973). However, ad libitum sampling can be used to record rare but important events (Martin and Bateson, 2007) which was done here.

In this work behavioural patterns corresponding to the supercategory of sexual behaviour as well as to the category of socionegative behaviour were recorded ad libitum during the above-mentioned observation periods, regardless if they were performed by the focal animal that was observed during the time of occurrence or by one of the other focal individuals.

4.3 Statistical analysis

4.3.1 Qualitative analysis

The behavioural patterns listed in the ethogram were categorized, incoherently based on existing behavioural profiles (Jantschke, 1972; Rijksen, 1978; Maple, 1980), but also refined specifically to the focus group and the overall question of the study. In general, the activities

which are performed alone were categorized rather approximately whereas social interactions in general and sexual behaviour, which does not play a significant role in terms of quantitative analysis, in particular, were categorized more in detail than in other studies since they are of particular interest in the frame of this work.

4.3.2 Quantitative analysis - focal animal sampling

4.3.2.1 Comparison of percentages

The percentage of behavioural patterns over the total observation time among the different focus individuals were compared.

4.3.2.2 Indices of association

The index of association expresses the extent to which two individuals are observed associating with each other (Martin and Bateson, 2007). It was calculated for each possible dyad of focus animals in both focus groups using the formula below and comprising data from the following categories:

- Matings (forced and consensual)
- Possible and definite sexual interest
- Social play
- Other sociopositive interactions
- Observing others, in case the observation took place for at least two consecutive minutes without interruption
- Interactions with infants (both own offspring and infants of others)
- All categories described in the supercategory "interactions with members of other species".

$$\text{Index of association} = \frac{N(GH)}{N(G)+N(H)+N(GH)},$$

with N(GH) representing the number of occasions individual G associates with individual H, N(G) being the number of occasions individual G is observed without individual H and N(H) indicating the number of occasions individual H is observed without individual G.

The results are presented in the form of a sociogram with the thickness of lines connecting the individuals representing the extent of their associations (Martin and Bateson, 2007) (see 5.2.3). As not all of the individuals mentioned in the sociogram were observed as focus animals and as also human interaction partners are included, N(H) was not available for these interaction partners. Therefore, for the dyads involving individuals that are not focus animals, the value for N(GH) was used to estimate the strength of the associations with them.

4.3.3 Quantitative analysis - ad libitum sampling

4.3.3.1 Dominance indices

The dominance index expresses the position within the overall ranking order of a given individual within a group. It was calculated for each individual using the formula below and then ranked for both focus groups.

$$\text{Index of dominance} = \frac{N(d)}{N(s)},$$

with N(d) representing the number of conflict situations an individual was dominant over another and N(s) indicating the number of conflict situations the same individual was submissive to another (Jantschke, 1972).

4.3.3.2 Frequency of sexual interactions

The frequency per hour of all behavioural patterns described in the supercategory of sexual interactions were compared for both focus groups.

4.3.3.3 Maintenance of sexual proximity

In this study, the extent to which the occurrence of sexual behaviour is owing to the responsibility of one or the other member of the dyad is of utmost interest. The responsibility of individual M for initiating such an interaction can be calculated using the formula below and data from the categories of mating (both forced and consensual) and sexual interest (both definite and possible).

M's responsibility for sex. interactions = $\frac{I(M)}{I(M)+I(O)} - \frac{T(M)}{T(M)+T(O)}$,

with I(M) representing the number of occasions on which the interaction was initiated by individual M and I(O) the number of occasions on which the interaction was initiated by individual O. Respectively, T(M) indicates the number of occasions on which the interaction was terminated by M and T(O) the number of occasions on which the interaction was terminated by O (Martin and Bateson, 2007).

Since the behavioural patterns described in the category of possible sexual interest carry a risk of being non-sexually motivated sociopositive interactions, they were treated separately from other sexual interactions.

5. Results

5.1 Qualitative analysis

The qualitative analysis of the complete scope of behavioural patterns observed yielded the following categorisation of behaviours:

5.1.1 Invisibility

This category is used to describe the occasions during observation periods on which the focus animal is either completely out of sight or cannot be observed precisely enough to obtain reliable data. This is the case while the animal is either positioned in parts of the enclosure that cannot be observed from the visitors' area or in some other position that makes precise observation impossible. Examples for this are sitting behind a rock or with its back turned towards the observer while focussing on small-scale activities such as feeding or autogrooming. Other situations that are categorized as invisible are the occasions on which the observer has to change or adjust her own position in order to keep track of the focus animal, for example during position changes from routside to inside enclosure, or when a larger group of zoo visitors temporarily blocks the view on the animals.

5.1.2 Behavioural patterns performed alone

Resting

This category lists all activities which aim at reposing and conserving energy, such as

- sleeping
- dosing
- lying
- sitting or hanging at the enclosure's bars.

They may, but do not necessarily have to, be accompanied by time-filling activities and a general observation of the individual's surroundings, but cannot be carried out at the same time as any activity demanding a greater amount of attention and energy such as locomotion or the directed observation of visitors.

Fig. 3 Rezeki resting in a hammock, Neunkirchen Zoo.

General observation

On many occasions, it is obvious that the animal is paying close attention to its surroundings while or despite resting, but without focussing on anything in particular. For example, at Heidelberg Zoo, with the animal looking out of the window towards the visitors' area, it is sometimes impossible to differentiate whether it is observing one visitor in particular, a group of visitors, the observer, the free-range animals in the great ape house or the visitors' area as a whole.

Fig. 4 Masala observing his surroundings, Neunkirchen Zoo.

Locomotion

Different ways for orangutans to move from one position to another include

- walking
- climbing
- swinging at ropes etc.
- brachiation.

Fig. 5 Ujian (left) brachiating through the upper part of the enclosure, Heidelberg Zoo.

Feeding

This category describes all behavioural patterns related to food intake. Besides feeding and drinking itself, obtaining food is the most important activity and can be done either by simple collection from the floor, platforms or the bars above the enclosure where the food is usually placed or given directly by the zookeeper at Heidelberg Zoo. More complex methods of obtaining food include searching the floor, corners or cracks for food, getting food out of containers or other enrichment elements or using tools such as sticks to collect food which otherwise would be out of reach.

Fig. 6 Sari collecting herbs outside the enclosure, Heidelberg Zoo.

Autogrooming and comfort behaviour

Since orangutans spend a great amount of their time on their own, social grooming is less common than with the other great apes. Hence, they are mostly self-dependant for grooming their coat, although this behavioural pattern seems to be more common in zoo animals (Rijksen, 1978). It may include

- grooming of coat and skin with fingers, fingernails, lips, teeth or tongue
- scratching
- cleaning hands, feet, hair etc. from dirt and dust
- cleaning the nose
- rubbing eyes.

For facility reasons, the behavioural patterns of urination and defecation were also included in this category, as well as several behaviours that can be interpreted as pain relief, such as holding the head with one hand in case of headache or inspecting minor scratch and bite marks after a fight.

Fig. 7 Ujian autogrooming, Heidelberg Zoo.

Play

Play and exploratory behaviour, which are virtually impossible to distinguish, can be observed to a much greater extend in infants and adolescent individuals than in adults and is often separated into object play and motion play (Brown, 2009). For both types of play behaviour, the only restrictions are the availability of objects and anatomical constraints which is why not all possible behavioural patterns will be listed. Behavioural patterns such as searching the floor, cracks, holes, containers or other enrichment elements can rather be interpreted as exploratory behaviour.

With adult individuals, these behaviours are often replaced with time-filling activities which may be performed while observing or resting, although to a lesser extent, these can be observed in younger individuals as well. They include behavioural patterns such as thumb-sucking or chewing objects.

Fig. 8 Sari playing with a piece of cardboard, Heidelberg Zoo.

Building

Besides nest-building behaviour, this category also includes the production and use of tools and the manipulation of complex structures, e.g. trying to unscrew a bolt of the enclosure. Orangutans are both intelligent and patient and thus capable of dismantling very solid enclosures and objects, if necessary with the help of self-produced tools (Jantschke, 1972; MacKinnon, 1988; Jakobs, 2013, pers. comm.). It was thus deemed necessary to create a category which points out the differences to the regular play and exploratory behaviour.

Fig. 9 Sari using a stick to reach for an object outside of her reach on the other side of the bars, Heidelberg Zoo.

5.1.3 Interactions involving members of other species

Interactions with other animals

Showing interest in or interacting with animals belonging to a different species may include the observation of animals such as other zoo animals nearby, visitors' dogs or birds flying by, as well as chasing after animals of a different species such as mice or insects within the enclosure.

Fig. 10 Noah, Rezeki, Surya and Struppi (left to right) observing the snow leopards Panthera uncia in the enclosure next to theirs, Neunkirchen Zoo.

Interactions with zookeepers

The zookeepers responsible for the keep of the great apes and other monkeys are the most significant human beings in the orangutans' social structure in both zoos (Fritsch, 2014, pers. comm.).

Interacting or trying to interact with them is possible through behaviours such as

- observation of the person
- making and holding eye contact
- contact through vocalisation
- contact through gestures
- approaching the bars when a zookeeper approaches
- performing social behaviours such as begging, social play or impressing (see below) towards the keeper
- cooperating with the zookeeper, for example by approaching when being called by name.

But also the increased interest in areas only zoo staff can access, indicated by behavioural patterns such as observing these areas for longer than a few seconds or reacting to the zookeepers' familiar sounds by turning the head and looking into the respective direction, reveal the importance of the zookeepers' role for captive orangutans.

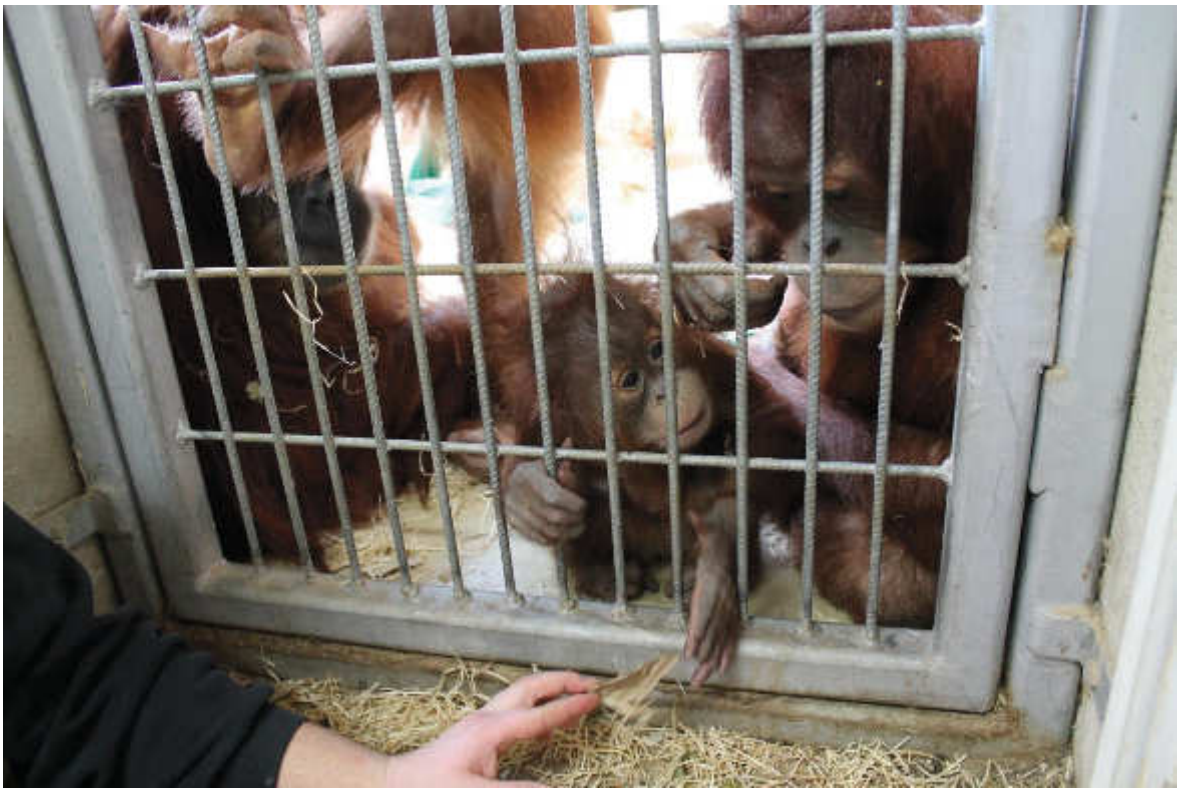


Fig. 11 Surya and Struppi interacting with a zookeeper, Neunkirchen Zoo.

Interaction with other familiar persons

Other familiar persons are persons that are not involved in the keeping of the orangutans and do not get into direct contact with them, but who are around the enclosure on a more or less regular basis and therefore are recognized by the animals. These may include other zoo staff such as gardeners or workmen, zoo rangers/guides, visitors who visit the zoo regularly and often spend a lot of time at the ape house during their visit, or the observer herself.
Interacting or trying to interact with them is possible through
- observation
- making and holding eye contact
- contact through vocalisation
- contact through gestures
- approaching the visitor observation facilities when the respective persons approach
- performing social behaviours such as begging, social play or impressing (see below) towards them.

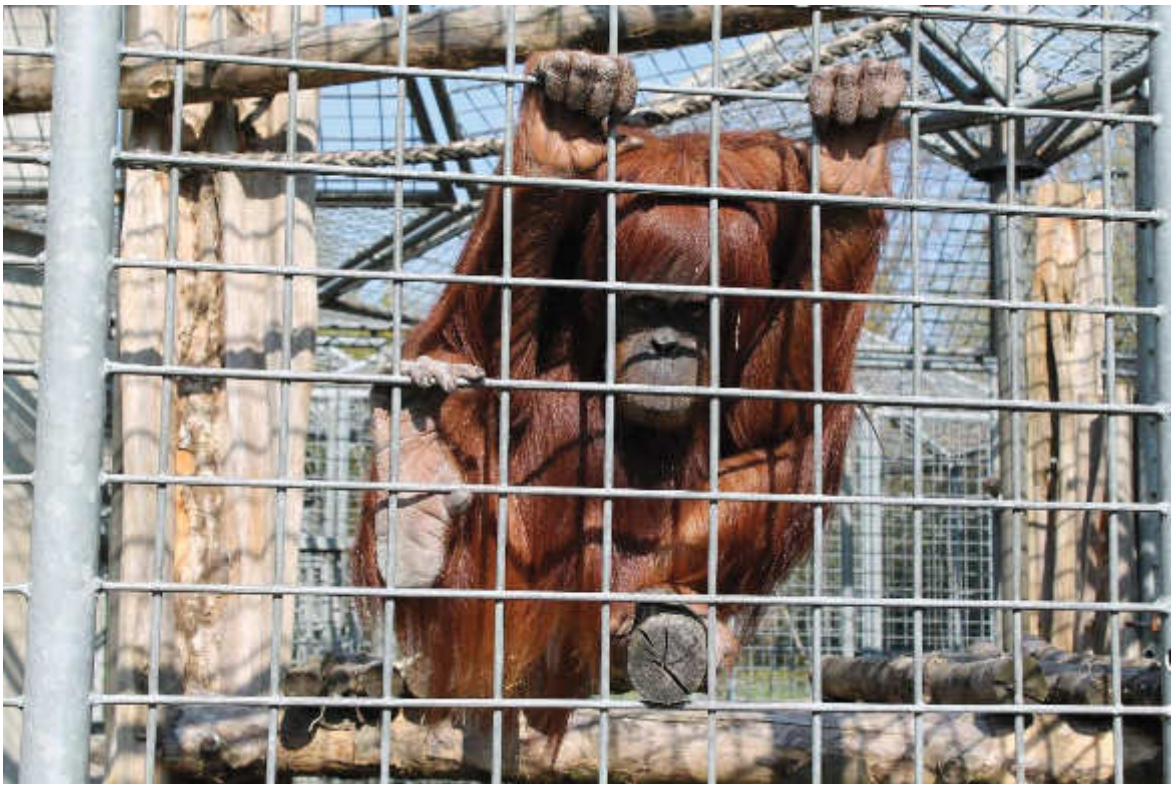


Fig. 12 Puan observing the observer, Heidelberg Zoo.

Interaction with visitors

This category comprises all behavioural patterns described for interactions with other familiar persons. The only difference is that they are directed at one or several regular zoo visitors who do not visit the zoo on a regular basis. It has to be noted that a portion of the orangutans' interest in zoo visitors seems to be due to food the visitors bring along, however this factor is often hard to differentiate from real interest in the person.

5.1.4 Social interactions

Sociopositive interactions

Sociopositive behaviour may also be described as affiliative behaviour (Rijksen, 1978). In the orangutans observed, it may be displayed through rather subtle behavioural patterns like making and keeping eye contact for longer than several seconds without any socionegative behaviour following. However, most expressions of empathy are easy to recognize since they mostly require close physical contact. This may involve huddling together and is often expanded to allogrooming with one individual grooming the other's hair. Also, the receiver allowing the initiator of the behaviour to perform it without resistance or avoidance can be interpreted as a sociopositive interaction. The strongest sociopositive interaction observed, hinting at a strong bond between two individuals, is the defence against another individual. Several of the following categories describe sociopositive interactions as well, but are treated separately.

Fig. 13 Puan (left) grooming Sari (right), Heidelberg Zoo.

Social play

This category of sociopositive interaction between two or more individuals is treated separately for it reveals important differences between different age groups.

Social play includes all behavioural patterns described in sole play when performed together with others. However, the greatest portion of social play includes activities that cannot be performed alone. Important social plays are

- chasing each other
- pulling at another individual's hair or limbs
- playful fighting, wrestling or gnaw-wrestling (Rijksen, 1978).

Sometimes, these behavioural patterns are accompanied by a play face. The receiver of such activities may either chose to allow them or join in or to ignore them, fend them off or move away.

Fig. 14 Rezeki (left) and Struppi (right) wrestling playfully with Surya climbing above them, Neunkirchen Zoo.

Begging and sharing

This category comprises all interactions between two individuals that center around one or several objects. In most cases this object is food, but it may also be nest-building material or an object one of the two partners is playing with. Included in this category are

- begging for food or other items (with/without success)
- sharing food or other items
- stealing food or other items without any socionegative behaviour from the partner following.

While the sharing of food or other items may easily be counted as a sociopositive interaction, all the other behaviours listed are fitting less clearly into other categories, making a separate categorization necessary.

Fig. 15 Rezeki begging Masala for food, Neunkirchen Zoo.

Socionegative interactions

This category lists all agonistic behavioural patterns, ranging from dominant and submissive behaviour to open aggression.

Behaviours which are used to clarify the rank within the social order may include

- avoiding an individual higher in rank
- supplanting an individual lower in rank from food, preferred resting places etc.
- forcibly taking another animal's food or other items it is just occupying itself with, including forcing the other animal to open its mouth and taking out the food it is eating.

The individual lower in rank may also try to fend off the attack or contact of the more dominant individual or try to defend the items about to be stolen, especially food, through carrying them away, hiding them, trying to collect food faster than the other animal or by leaving a small part of its share for the persecutor in order to distract him and be able to move away.

The individual higher in rank, on the other hand, may either just ignore the other one's action or either fend them off or avoid them by moving out of the other animal's range.

Aggressive behaviour includes chasing or punching the other animal or holding it in place while it shows intentions to move away. This may be accompanied by aggressive facial expressions and sounds, such as bared teeth or screaming. During the complete observation period, only very few openly aggressive situations which were directed at Sari by Puan could be observed while no serious fight including aggressive facial expression was recorded.

Observation of others

This behavioural pattern shows interest in another member of the group without directly interacting with it. The individual in question may observe only one other group member or several individuals at the same time, as well as their interactions with each other.

Fig. 16 Ujian (left) and Sari (center) observe Puan who is trying to get food out of a barrel above the enclosure, Heidelberg Zoo.

Mother-infant interactions

Interactions from this category are usually sociopositive. They are treated separately from other sociopositive behavioural patterns because they are based on a much stronger bond between the individuals. Also, they were only observed at Neunkirchen Zoo since there is currently no infant in the Heidelberg group.

Interactions between mothers and infants include

- suckling the infant
- holding the infant
- resting together
- cuddling
- playing
- assisting the infant while climbing etc.
- following the infant
- carrying the infant
- leading the infant through the enclosure while holding its hand
- supervising the infant's own activities, such as climbing, and social interactions, such as playing with other individuals.

It has to be noted that these interactions were not only observed between Struppi and Surya, but also between Noah and Rezeki, although to a lesser extent. Even though Rezeki is an adolescent animal by age and not an infant anymore, her bond to her mother is still very strong and she sometimes still tries to get breast-fed, which Noah allows most of the time.

Fig. 17 Struppi suckling Surya, Neunkirchen Zoo.

Interactions with infants

This category includes all interactions of infants with adolescent or adult animals other than their own mother, including their father. Surya in the Neunkirchen group was the only infant observed during the observation period as there was no infant in the Heidelberg group. This is why the behavioural patterns directed towards her are treated in this separate category, even though they could be included into several of the already existing categories. The biggest part of these interactions is sociopositive, with the exception of occasions when the infant's approach was ignored. No socionegative behaviours towards Surya were observed during the observation period from any individual in the group.

Behavioural patterns include

- making and keeping eye contact
- cuddling
- playing
- assisting the infant while climbing etc.
- observing the infant while it is involved in other activities such as climbing.

5.1.5 Sexual behaviour

Autosexual behaviour

Behavioural patterns that are classified as autosexual behaviour are masturbation and touching the own genitals or other sensitive body parts, sometimes followed by sniffing at the hand.

Fig. 18 Struppi inspecting her teat, observed by Masala (possible sexual interest, see below), Neunkirchen Zoo.

Impressing

This behavioural pattern is only performed by male individuals. Impressing may be carried out by emitting long calls, even though these were not recorded during the observation period, but also by movements, mostly swinging briskly at ropes or other enrichment elements in the enclosure.

Possible sexual interest

Some of the interactions between male and female individuals observed in both focus groups cannot definitely be classified as sexual interest in the partner, but seem to go beyond a simple sociopositive interaction taking place irrespective of the partner's sex. These include

- observing the other half of the dyad, usually the male, who is obviously not interested in obtaining or keeping contact, for longer than ten seconds
- following the other half of the dyad, usually the male, who is obviously not interested in obtaining or keeping contact, nevertheless for longer than ten seconds
- eye contact from close proximity so that physical contact could be possible at any given moment without greater locomotion activity necessary
- allogrooming involving an intensive use of lips, "kissing"/ touching the partner with the lips
- a female swinging along the same rope as a male during the male's impression behaviour
- a female searching contact to a male during or after the male's performance of impression behaviour
- a male performing impression behaviour after interacting with a female
- observing any of the interactions described above between a male and a female for at least ten seconds, and possibly trying to join them
- observing other behavioural patterns categorized as sexual behaviour.

The receiver of such behavioural patterns may move away from the individual performing them, allow, but otherwise ignore them, or respond, either in a similar way or with other sociopositive or sexual behaviours. A socionegative reaction was never observed in the context of any of the behavioural patterns described above.

Fig. 19 Masala and Struppi holding close eye contact through the bars, Neunkirchen Zoo.

Sexual interest

Sexual interest in a member of the opposite sex (and sometimes the own sex) is indicated through

- sniffing at the partner's genitals
- touching the partner's genitals, possibly with sniffing at the hand afterwards
- taking the partner's hand and directing it towards the own genitals
- a female offering herself to a male by lying down on front of him with legs open, possibly occurring after having performed a behaviour classified as possible sexual interest.

Forced mating/rape

In the wild, this behaviour is an essential part of the mating strategies of subadult males since they would otherwise not be selected as partners by females. But it has also been observed with non-dominant adult males (Mitani, 1985; MacKinnon, 1988; Delgado and van Schaik, 2000) and can also be observed in groups such as the focus groups with only one adult male present. The copulation is forced by the male, possibly after having performed an impressing behavioural pattern and sometimes after having dragged the female in position, with the female resisting copulation, trying to flee or showing other signs of fear such as uncontrolled urination.

Consensual mating

Consensual mating usually takes place as a result of female choice and thus is much more likely to involve an adult male rather than a subadult (Rijksen, 1978). The copulation is carried out without the female showing signs of fear or resistance and might be preceded by the female offering copulation to the male (see sexual interest). The female thrusting during copulation which has been observed in other zoos (Nadler, 1977; Maple et al., 1979) was not observed during the observation period.

5.2 Quantitative analysis – focal animal sampling

5.2.1 Comparison Heidelberg Zoo vs. Neunkirchen Zoo

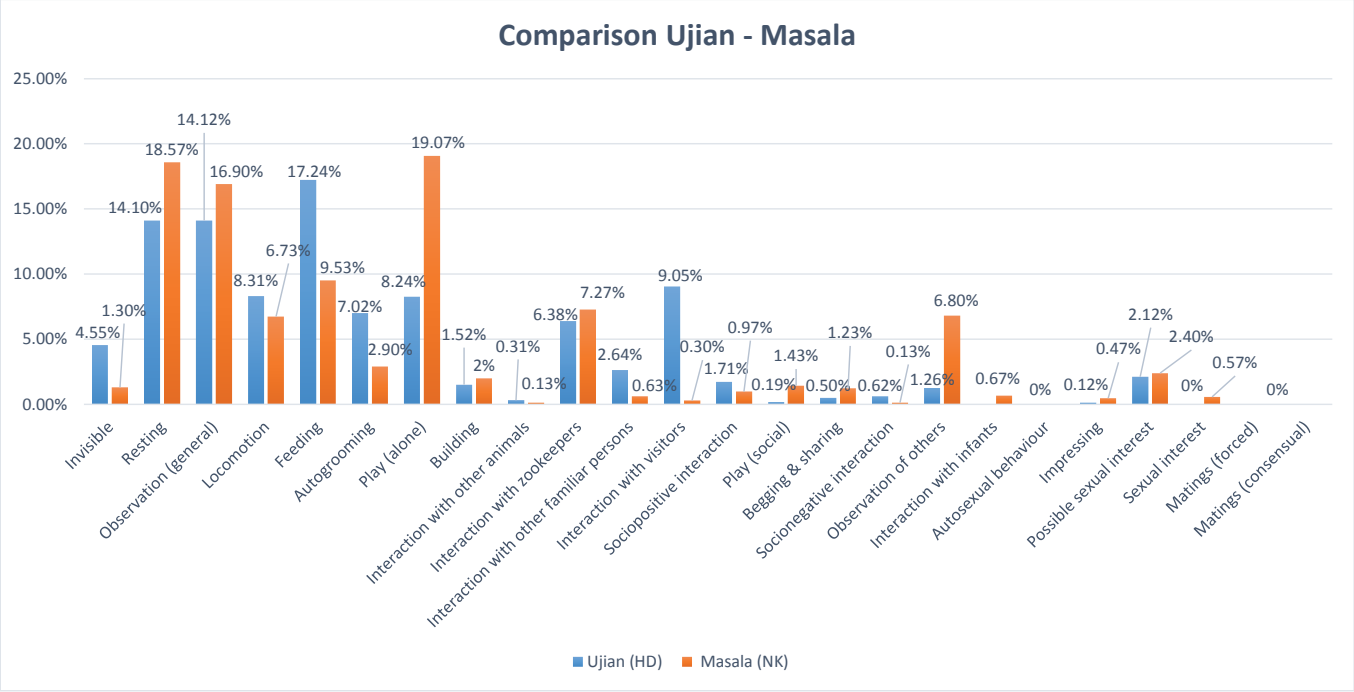


Fig. 20 Comparison of the proportion of behavioural patterns of male individuals in the Heidelberg and Neunkirchen group.

When contrasting the males of the two focus groups, many behavioural patterns are comparable. An exception is autogrooming, which generally is more important in the Heidelberg group than in the Neunkirchen group. The proportion of time spent on feeding and play are reverse between the two individuals, with Ujian spending twice as much time on feeding as on play and vice versa for Masala. While the amount of interaction with the respective zookeepers is comparable, the overall time Ujian spends on interacting with humans is more than twice as much as with Masala. In return, Masala interacts more than twice as much with the members of his group, even though a great amount of his interest is expressed through observation. Masala also engages in sexual interactions 1.5 times more often than Ujian.

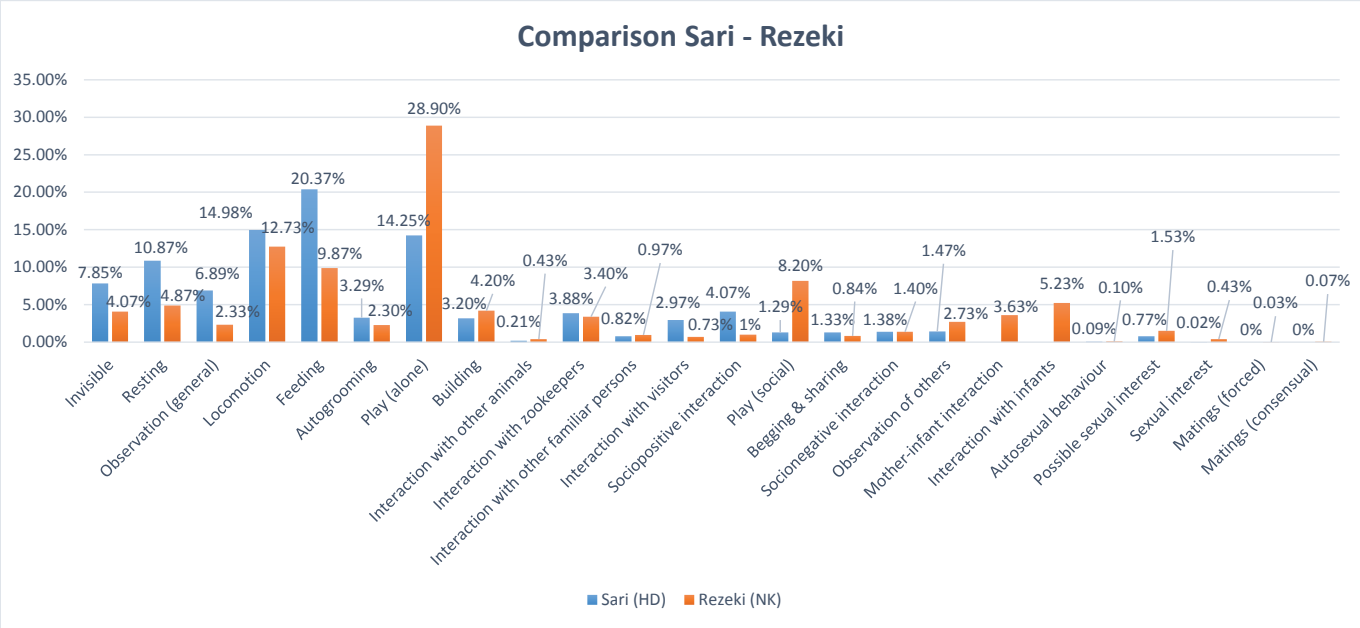


Fig. 21 Comparison of the proportion of behavioural patterns of the younger females in the Heidelberg and Neunkirchen group.

Comparing the behavioural patterns performed alone by the younger females of the two focus groups, four year older Sari plays only half as much, but rests and observes around 2.5 times more than Rezeki. While the time spent on interacting with humans is comparable, Rezeki interacts about 2.5 times more with members of her group than Sari. Comparing the proportion of time spent on sexual behaviour, Rezeki was also seen about 2.5 times more often than Sari performing behaviours from this category.

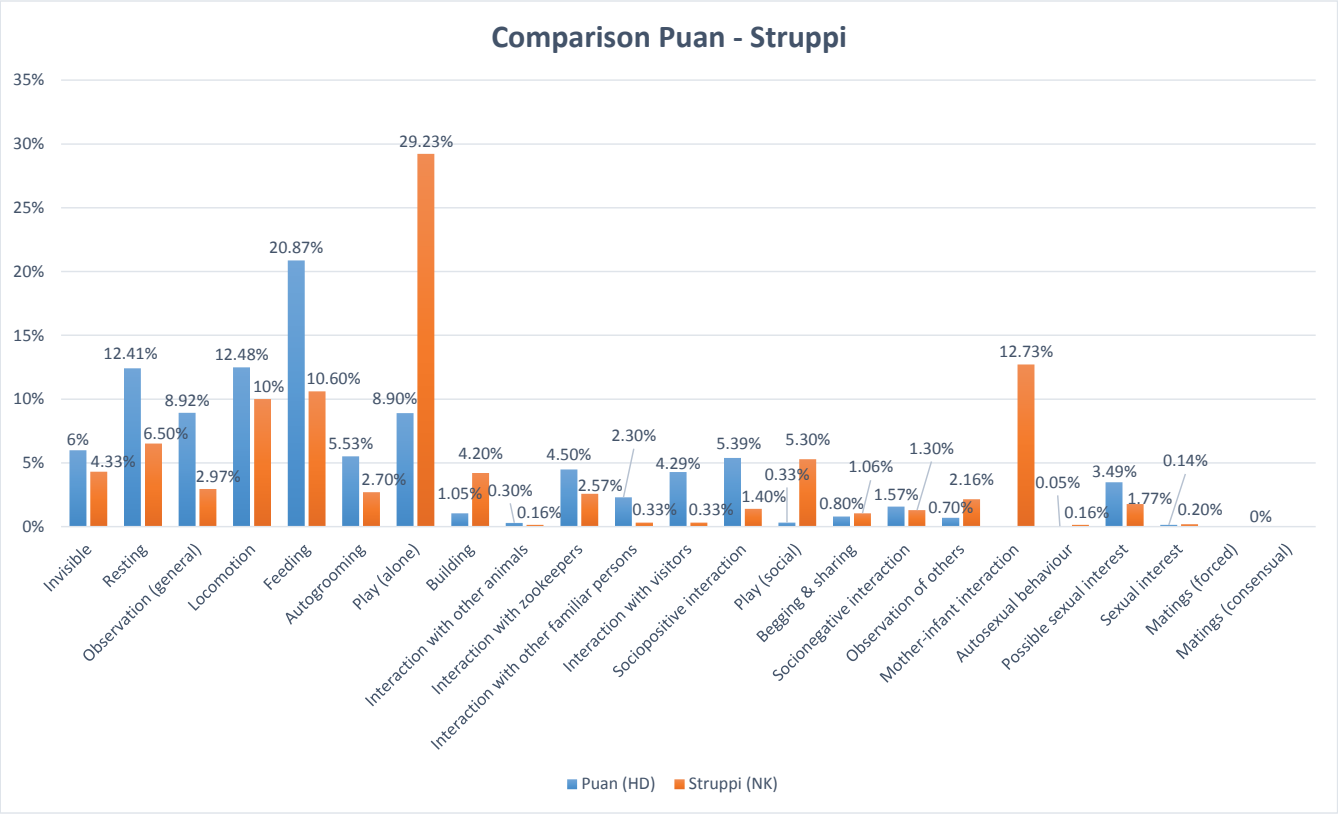


Fig. 22 Comparison of the proportion of behavioural patterns of the older females in the Heidelberg and Neunkirchen group.

Almost 16 year older Puan spends more than twice as much time on resting, observation and feeding than Struppi while Struppi, even though she is currently nursing an infant, plays around 3.3 times more often than Puan. Puan, on the other hand, interacts around 3.4 times more often with humans than does Struppi. Another difference which is consistent throughout the two focus groups is the much higher portion of autogrooming in Heidelberg which is performed around 3.3 times more often by Puan than by Struppi.

It has to be noted that Struppi devotes almost half of all her social interactions to her infant Surya. Without considering Surya, the time spent on social interactions would be comparable among the two. Yet, it has to be pointed out that this time is spent more with sociopositive interactions such as allogooming for Puan while for Struppi, social play, mostly engaged in with Rezeki, occupies the greatest percentage besides Surya. As for sexual interactions, Puan spends around 1.7 more time on these behavioural patterns than Struppi.

5.2.2 Comparison of sociopositive and socionegative interactions

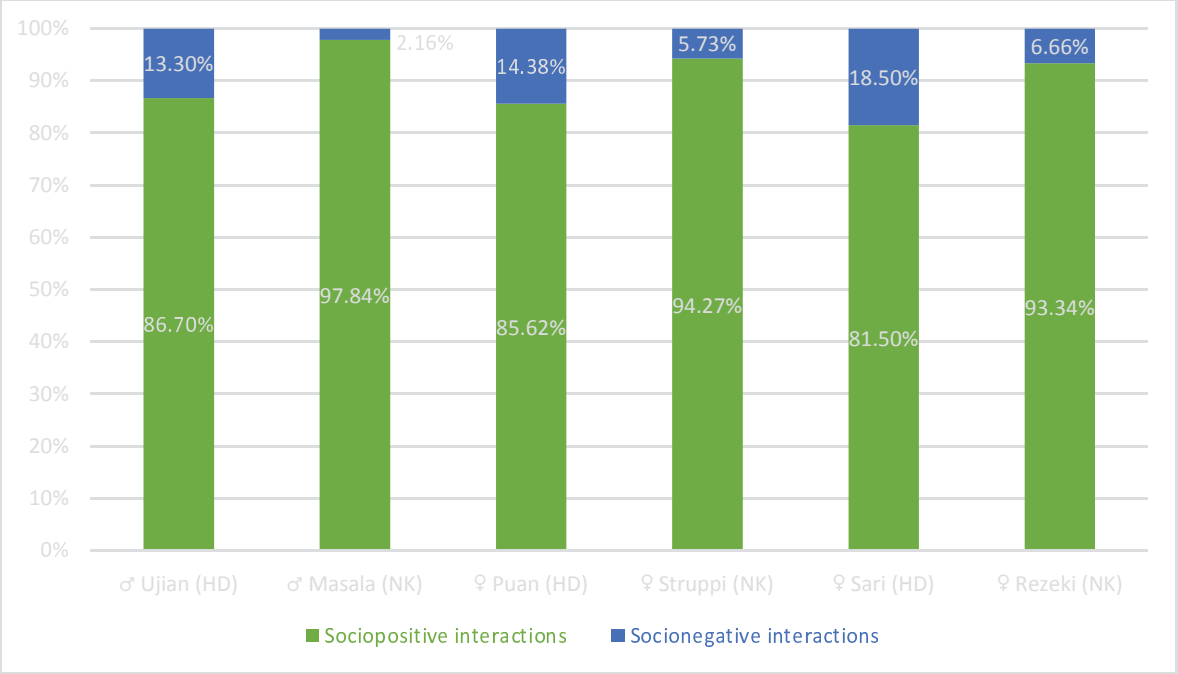


Fig. 23 Ratio of sociopositive to socionegative behaviour for all focus animals.

Overall, the proportion of socionegative interactions within the Heidelberg group is around 2.5 times higher than in Neunkirchen. For the males, the difference is even bigger, with Ujian engaging over 6 times more often in socionegative behaviour than Masala.

Within both groups, it is discernible that the proportion of socionegative interactions as compared to sociopositive interactions increases with lower social rank within the group (see 5.3.1), mostly due to conflicts about food or other items or, for the individual lowest in rank, due to getting supplanted by the others more frequently. Furthermore, Sari appeared to be more willing than usual to start a fight with Puan on a few of the observation days recorded which may also contribute to her higher percentage of socionegative behaviour.

5.2.3 Comparison of indices of association with members of the group and members of other species

Heidelberg

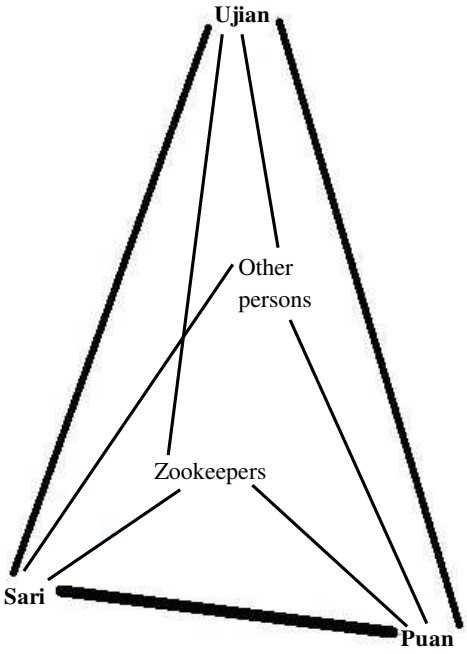


Fig. 24 Sociogram Heidelberg group.

Neunkirchen

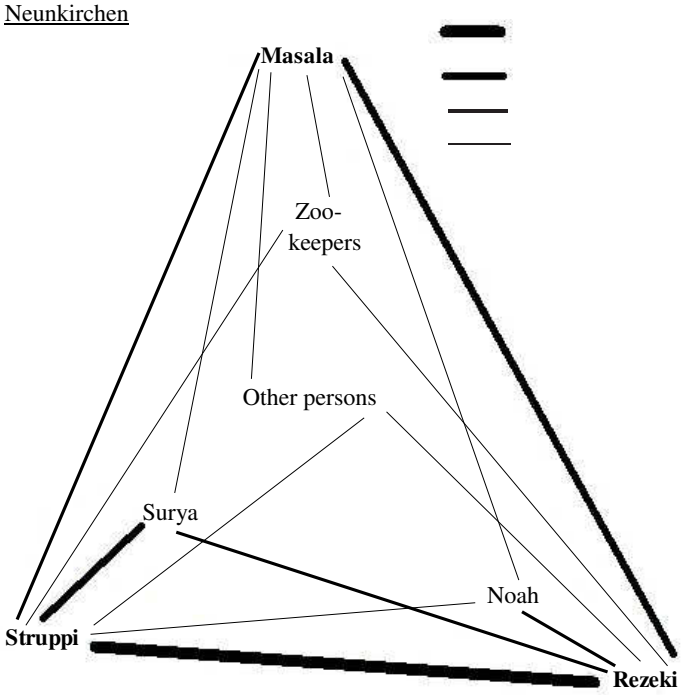


Fig. 25 Sociogram Neunkirchen group.

In both groups observed, the association among the two female focus animals is the strongest within the group. Also, the younger female associates stronger with the male than the older one both in Heidelberg and Neunkirchen.

When comparing the sociograms of the two groups, it is noticeable that the Heidelberg group overall associates much stronger with the persons around them, both zookeepers and visitors. In the Neunkirchen group, almost all associations with humans are considerably weaker than the ones within the Heidelberg group. Persons who are not zookeepers or do not belong to the zoo staff, that gets into contact with the animals on a more or less regular basis, hold virtually no importance at all for the Neunkirchen group, whereas in Heidelberg, visitors are generally associated with even to an even stronger degree than zookeepers, especially in regard to Ujian. (For detailed overview of values see app. 7.3, tab. 3-4)

5.3 Quantitative analysis – ad libitum sampling

5.3.1 Dominance indices

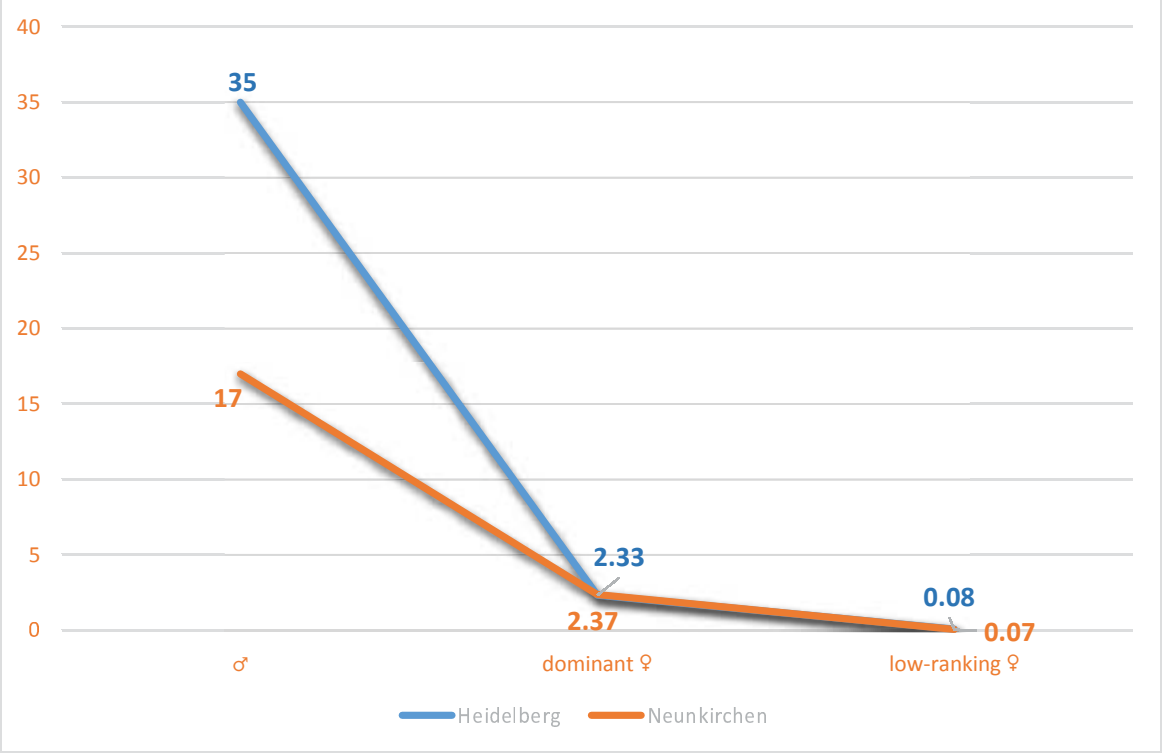


Fig. 26 Dominance indices for both focus groups.

The dominance indices for the two groups portray a similar picture for Heidelberg and Neunkirchen, with the sole adult male of the group clearly being the dominant individual and the youngest female lowest in rank.

Both in Heidelberg and in Neunkirchen, the younger females occasionally had to apply rather elaborate methods in order to be sure to get their desired share of food. While Rezeki was most successful with begging, mostly from Masala, Sari rather relied on collecting food faster and at other places than the others or leaving a small piece of food behind when fleeing from a potential stealer.

Noah in Neunkirchen was not observed as focus animal and therefore cannot be considered in this ranking. However, ad libitum observation show that she takes food and objects she wants from the other females without meeting resistance on several occasions while the other females, Struppi in particular, avoid her at times of an increased number of conflict situations. Although the relationship between Noah and Masala is very different from the other relationships in the Neunkirchen group due to the special situation of partial separation, a certain level of interaction can still be observed, e.g. mutual observation or Masala approaching the bars when Noah walks along on the other side. On some of these occasions, Noah was observed backing off the bars when Masala approached, while Masala was never seen moving away from her.

5.3.2 Frequency of sexual interactions

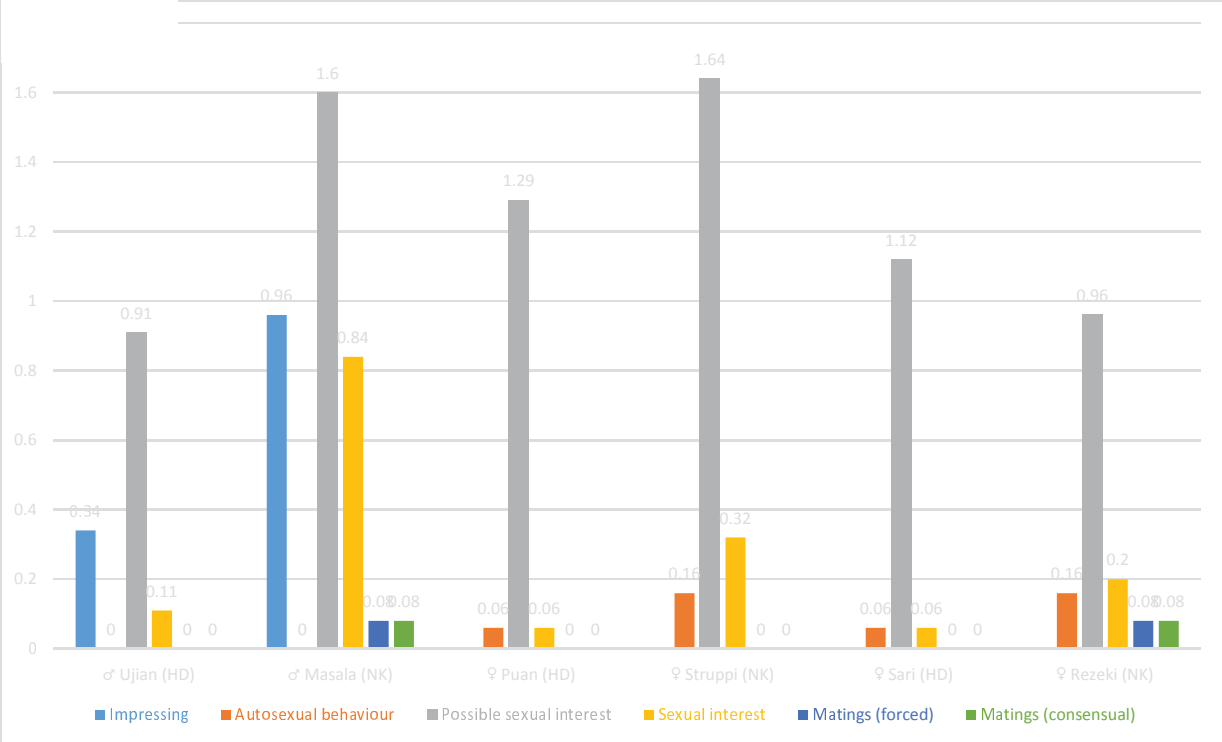


Fig. 27 Comparison of average numbers of occasions sexual behaviours were performed by focus animals per hour.

Both in the Heidelberg and the Neunkirchen group, behavioural patterns within the category of possible sexual interest were observed the most frequently.

The two males as well as the females from the different age classes are all roughly comparable in qualitative terms of behavioural patterns. However, the animals in the Neunkirchen group overall engage more frequently in sexual interactions than the ones at Heidelberg Zoo. Masala performs sexual behaviour about 2.6 times more often than Ujian and Struppi around 1.5 times more often than Puan while Sari and Rezeki are approximately comparable. While no autosexual behaviour was observed for the males in both groups, the females at Neunkirchen Zoo perform it around 2.6 times more frequently than the females in Heidelberg.

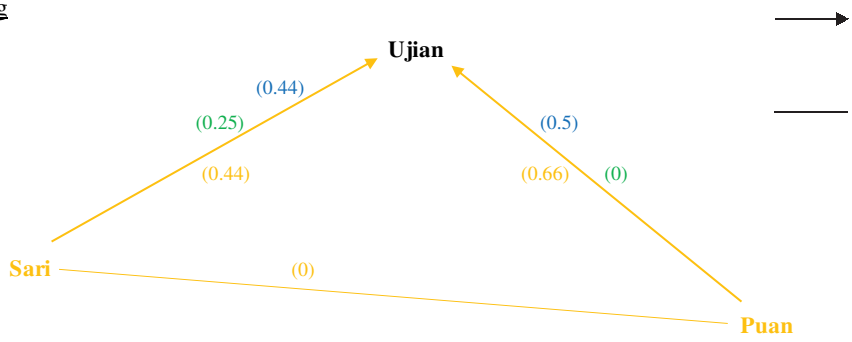
One incidence of Ujian showing sexual interest in Sari outside of observation time was reported to the observer by a regular visitor. The occasions of sexual interest observed for Ujian all took place during the last observation week and were directed towards Puan.

Even though Struppi shows more interest in sexual interactions than Rezeki, the three matings that were observed in Neunkirchen during the observation period took place between Rezeki and Masala. The first mating observed was forced by Masala. For the second one, it could not be observed whether copulation took place without a doubt. In any case, the interaction was initiated by Rezeki who showed no sign of fear at any stage. The third mating was initiated by Rezeki who, however, during copulation began to struggle and finally escaped Masala. Therefore, this mating cannot clearly be classified as forced or consensual.

No matings were observed in the Heidelberg group during the observation period.

5.3.3 Maintenance of sexual proximity

Heidelberg



(1) possible sexual interest

(1) sexual interaction

(1) both values combined

Fig. 28 Sociogram representing the maintenance of sexual proximity for the Heidelberg group.

Neunkirchen

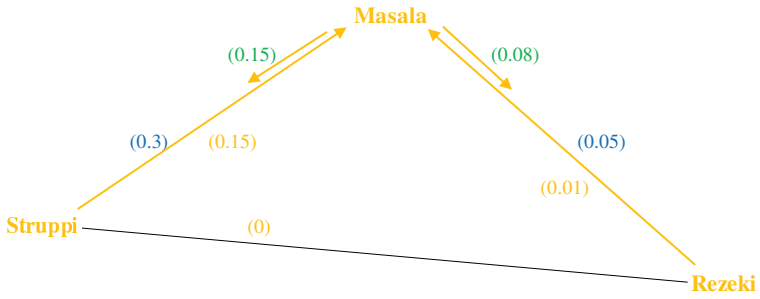


Fig. 29 Sociogram representing the maintenance of sexual proximity for the Neunkirchen group.

Overall, in both focus groups the females are responsible for the maintenance of interactions that are listed as sexual interest or interaction. While Ujian is still responsible for the maintenance of definite sexual interactions with Puan to the same extent as she is, he is neither responsible for any interaction of possible interest nor for any interaction with Sari that falls in the category of sexual interaction. Masala, on the other side, even though he is less responsible for the maintenance of interactions based on possible sexual interest than the females, is more responsible than the females for interactions based on definite sexual interest and for matings. Struppi is about 20 times more responsible for maintaining interactions of sexual interest with Masala than Rezeki.

Both in the Heidelberg and the Neunkirchen focus group, the two female focus animals were equally responsible for maintaining sexual interactions among themselves. However, it has to be pointed out that sexual interest among females was only observed once in Neunkirchen and twice in Heidelberg.

6. Discussion

6.1 Methodology

First and foremost, the greatest inconvenience with the data obtained in the course of this study is the length of the observation period which is too short to be statistically representative.
This can easily be distinguished by comparing the results obtained at the observation days the animals had access to the outside enclosure with the days they were restricted to the inside enclosure. Since the outside enclosures offer different elements of enrichment, more free moving space and more opportunities to interact with visitors than the inside enclosures, overall behavioural is different when animals have access to the outside enclosure. Due to the longer and more outspread observation period at Heidelberg Zoo which went on into spring, the Heidelberg group had access to the outside enclosure on about two fifth of the observation days. The Neunkirchen group, on the other hand, was allowed to access the comparatively much larger outside enclosure on only a few relatively calm and sunny days during the observation period which still took place during the winter season. However, owing to the overall shorter observation period in Neunkirchen, these few days still make up for a proportion

between 10% and 16% of overall observation time at Neunkirchen Zoo and thus are significant. Especially for a short observation period it would therefore be desirable to have similar observation periods for the occasions when the group can access the outside enclosure compared to when it does not. It is likely that only if this assumption is given, statistical approaches to verify whether enough data has been collected such as the split-half analysis (Martin and Bateson, 2007) will yield reliable results.

But already with the total observation time recorded here, the differences found when splitting the data obtained in half and comparing the results hint at an observation period that was not long enough (Martin and Bateson, 2007). In Heidelberg, with more occasions to observe the group in the outside enclosure, it seemed rather clear that the group was less stressed, the conflict potential lower and the practical possibility to interact more directly with visitors and zookeepers alike greater just from anecdotic record. However, for an observation period sufficiently long a more in-depth study than the Bachelor thesis presented here would be necessary.

Due to the practical constraints already mentioned (see 4.2.2) and the thus resulting differences in observation times on different observation days, the data obtained is less representative and comparable than it could have been if observation had been carried out at the same hours every observation day. Partly caused by the behaviour of the focus animals, observation hours differed slightly on each observation day and sometimes longer observation periods had to be discarded from the final data when the focus animals were out of sight for a longer period of time. Especially for Ujian it proved to be difficult to obtain an observation period that would be comparable to the females'. Furthermore, part of the differences among focus individuals, especially in the category of feeding and resting, might be explained through feeding times differing slightly every day in both of the zoos on one hand. On the other hand, phenomena like Ujian regularly retreating into the area of refuge soon after the afternoon feeding and usually staying there until the zoo's closing time, thereby becoming unobservable during late afternoon, entail bias in the data. The latter, in combination with Ujian's generally prolonged periods of absence, biases the data for two female individuals of the Heidelberg group slightly towards the late afternoon as it was always one of them who was observed as the last individual of the given observation day.

For the ethogram, some of the categories chosen to analyse the data further are disputable and the boundaries between them are often blurred. For example, resting while not sleeping often implies a certain observation of the surroundings or time-filling activities while searching the enclosure might, depending on the context, be evaluated as exploratory or food-collecting behaviour. Hence, not only may an activity not always fit into the given categories at all, but it may also fit into several categories at the same time. For the categories describing social interactions, this lack of clarity is especially important for the category describing possible sexual interest in another individual. These interactions cannot be included into the category of sexual interest as described in the literature (Maple et al., 1979) and may sometimes be nothing more than a regular sociopositive interaction between a male and a female. However, they were rarely or never observed between two females without involving the respective male. On the other hand, listing this category separately makes the definition of a regular sociopositive, non-sexually motivated interaction between a male and a female difficult. Hence, the line between the categories of sociopositive interactions, possible sexual interest and definite sexual interest is probably the most blurred among all categories used here.

All these uncertainties regarding categorization of behavioural patterns almost inevitably entail bias in the data obtained.

As for the index of association, it is important to also consider the members of the group which were not observed as focus animals as well as human interaction partners. However, the data about the number of occasions these individuals did not associate with the focus animal in question was not recorded and would also be very difficult to record precisely for members of other species. The approach of comparing the original number of occasions the respective individual interacted with the focus animals is the only possibility of still considering these relations. However, since this is a different methodical approach than calculating the index of association, the data is not comparable.

Also, when calculating the number of occasions when one individual was observed without the other, the number of occasions when it had been observed either alone or with another individual was added up. However, this approach does not take into account the times when two animals interacted with the focus animal in question. As the necessity of this information was not known at the time of recording, on many occasions the record for interactions with

multiple partners are not complete enough to be included into the calculation. Hence, the indices of association calculated here are probably slightly too low.

Both for dominance indices and the maintenance of proximity between two individuals, the difficulty of the exact calculation is that sometimes the categories required for the calculation do not apply to the behaviour observed. Conflict situations may end without an explicit winner and it is not always clear who started or ended an interaction. Sometimes, an interaction between two individuals may even be ended by a third individual which, for example, is often the case for interactions of possible sexual interest between Ujian and Sari. On numerous occasions over the whole observation period, Puan ended the interaction between them by making contact with Ujian herself while steadily pushing Sari away.

All these occasions had to be left unconsidered in the calculation of both dominance indices and maintenance of sexual proximity which will certainly have entailed bias in the data obtained.

All observational behavioural research entails similar difficulties due to the nature of the study subjects. The animals observed will still behave in ways that always remain unpredictable to a greater or lesser extent. Even in the comparatively favourable observation conditions of the zoo environment, there are situations in which the focus animal is hidden, performs a behaviour that cannot precisely be observed or categorised or simply remains out of sight. Hence, it is virtually impossible to deliver data that is as reproducible and comparable as data which is obtained under laboratory conditions.

Finally, the quality of the data recorded during the observation of animals' behaviour also depends on the length of the study as well as the experience of the observer (Martin and Bateson, 2007). The data recorded towards the end of the second observation period at Heidelberg Zoo is likely to be more reliable than the data recorded at the very beginning of the first observation period of the Heidelberg group. This is not only due to the gain of experience during the months in between, but also due to better knowledge of the focus groups and the overall behaviour of the different individuals.

6.2 Results

Comparing both the activity budgets and the sociograms, the age difference between the females at Heidelberg Zoo and Neunkirchen Zoo are instantly revealed. In the Heidelberg group, Sari, who may still be considered an adolescent (Noordwijk et al., 2009), engages in play behaviour, both alone and social play, about 1.6 times more often than Puan who is almost 15 years older than her. Nevertheless, both Heidelberg females fall completely short of the females at Neunkirchen Zoo in this category. Not only their actual age, but also the considerably greater proportion of time the Neunkirchen females spend on play behaviour of any kind clearly reveals them as adolescents. Strictly speaking, Rezeki even may still be considered an infant since she is not yet entirely weaned (Noordwijk et al., 2009).

Furthermore, when comparing the animals from the different zoos, the difference in who spends more time interacting with whom instantly catches the eye. The females in the Heidelberg group devote little more than a tenth of their time to interest in or interactions with other group members while a portion only little less than this is spent on interacting with humans as well. This does not only apply to zookeepers, but in Puan's case also almost equally much to interacting with visitors. At Neunkirchen Zoo, on the other hand, both females devote almost a fourth of their time to social interactions within the group while interactions with humans are almost exclusively restricted to the zookeepers and even these do not occupy an important part of their time.

However, it has to be underlined that in the Neunkirchen group an important part of the females' time spent on social interactions is devoted to interacting with Surya or, in Rezeki's case, with her mother Noah and that the already mentioned playfulness also plays a great role in the Neunkirchen females' social interactions. Hence, the difference between the two groups is in fact not that astonishing since the bond between mother and infant is and has always been considered the strongest bond in the social system of both Pongo species, even in the past when still little evidence had been found that orangutans do have a social structure despite spending much of their time solitary. Also, infants and as well as young adolescent orangutans of Rezeki's age are known to be partially socialized within the frame of temporary travel communities (van Schaik, 1999). Another piece of evidence that the comparatively stronger social interactions in the Neunkirchen group are owed to the focus females' younger age and the family relationship structure is the fact that Noah was observed in engaging in much less

social interactions than the two younger females and might yield data which could be roughly comparative to Puan's activity budget for social interactions.

Still, this cannot explain why the interest in humans is so much greater among the Heidelberg group. One possible explanation may be the imitation of each other. All animals in the group with the exception of Sari are hand-reared and at least one out of the two others may have maintained a close bond to humans beyond infancy and adolescence. It is improbable that different keeping methods play a primary role. Comparing the activity budgets of the Heidelberg group for the days spent entirely in the inside enclosure to those when the animals had access to the outside enclosure, there is evidence that the comparatively smaller and less enriched outside enclosure at Heidelberg Zoo might invite animals to interact with visitors more than the bigger and more outspread outside enclosure at Neunkirchen zoo. However, it is unlikely that this difference plays a major role since for the inside enclosures, opportunities to interact with visitors are approximately equal in both zoos. The inside enclosure at Heidelberg Zoo is even larger and offers somewhat more freedom to move than the one in Neunkirchen. Still, the overall interest in visitors of the Neunkirchen animals, which were almost solely observed in the inside enclosure, is much lower than with the Heidelberg group. It is more likely that the reason for the greater interest of the Heidelberg animals in humans in general can be found in the animals' life history or may simply expose a difference in personality.

The comparison of the activity budgets and sociograms of the two males from the two focus groups reveals both similarities and differences. They both devote almost half of their time to resting, feeding and observing their surroundings and thereby behave typically for an adult male Sumatran orangutan with high energetic needs and a "sit and wait" technique as overall mating strategy (Mitani, 1985; Atmoko et al., 2009). A possible reason for the differences in play and feeding behaviour between the two individuals might be that Ujian's food searching behaviour is more easily recognized as such, also due to a longer observation period in Heidelberg and therefore better knowledge of the group by the observer, whereas parts of Masala's food searching behaviour might have been interpreted as exploratory behaviour. Another aspect of Masala's bigger share of play behaviour might be the fact that he performs more time-filling activities since he is far less interested in interacting with visitors than Ujian.

This leads to the important differences between the two individuals concerning social behaviour. It is astounding that two animals with the similar background of being hand-reared have developed such a differing interest in humans and that both of them are the extreme end within their focus group concerning this category. While Ujian shows even more interest in visitors than in the zookeepers, Masala ignores virtually all humans which do not belong to his most direct contact persons. This difference very well reflects the overall differences between the two groups.

The different proportions of socionegative interactions in the two groups as well as the difference between the two males concerning dominance indices are also noteworthy. While the dominance indices calculated overall represent a social ranking that was expected for both groups with the adult male being the dominant individual and the youngest female ranking lowest, it is surprising that Ujian's index value is twice as high as Masala's. Perhaps this is due to Masala still being willing to positively respond more to Rezeki's invitations to play while Ujian is rather unwilling to engage into social play and avoids the individual inviting him or pushes it away. In general, it is possible that Ujian dominates the other group members a bit more than Masala by more often taking items such as food away from them. On the other hand, due to the separation of Masala and Noah, probably the greatest share of possible conflict situations in the Neunkirchen group is kept away from Masala. The ad libitum observations of Noah interacting with the focus animals clearly hint at her being the dominant female in the group, but submissive to Masala. Therefore, if they were not separated, Masala's dominance index could well be much higher than recorded and possibly even higher than Ujian's.

The same reasons might be a part of the explanation for the overall higher proportion of socionegative behaviour in the Heidelberg group. However, it is probable that the different relation between the females plays a more important role here. Even though the general relationship between Sari and Puan is good and they can be much more often observed engaging in sociopositive interactions such as allogrooming than in conflict situations, Sari may have reached an age at which Puan begins to consider her a risk for her own position within the group. This assumption is supported by Sari actively seeking to start a conflict with Puan on a few observation days which can be interpreted as testing her boundaries while on the other days, she rather avoided Puan at times of enhanced conflict potential, especially during feeding times and particularly during the second observation period. Puan, on the other

side, supplanted Sari from close contact with Ujian on numerous occasions and showed openly aggressive behaviour directed against Sari on a few rare occasions. Still, the few occasions Sari appeared stressed due to these conflict situations with Puan were negligible in terms of total observation time. It is improbable that enhanced stress levels are responsible for her lack of a menstrual cycle. However, in order to reliably verify or neglect this hypothesis, more elaborate hormone measurements including the evaluation of stress hormone levels would be necessary. In Neunkirchen, while Struppi and Rezeki engage in playful fights very frequently, no openly aggressive behaviour could be recorded during the observation period. Overall, the composition of younger animals and the resulting higher proportion of play behaviour in the Neunkirchen group as well as the more clearly set ranking of dominant and subordinate individuals seems to be mostly responsible for the lower share of socionegative interactions.

Comparing the frequency and maintenance of proximity for sexual behaviour among the two groups, the differences are quite obvious. The females are still roughly comparable in terms of possible and definite sexual interest as well as in being responsible for maintaining interactions of sexual nature with the respective male. As for both Sari and Rezeki, their comparatively young age, reproductive status and lack of experience as well as Rezeki's partial insecurity and struggle during matings and male impression behaviour hint at the exploratory nature when expressing behavioural patterns of this kind. On the other hand, the quantitative and qualitative difference between the two males' sexual behavioural patterns is striking. Masala is also always responsible for the maintenance of all sexual behaviours except possible sexual interest while in the Heidelberg group, the maintenance of sexual interactions is solely due to the females, particularly to Sari whose invitations to interactions are very frequently ignored by Ujian.

However, the combination of a highly enhanced interest in interacting with humans and a general lack of interest in sexual interaction does not necessarily imply that Ujian would not be able to reproduce from a behavioural point of view. The sexual interest displayed by both males might be considered quite normal when taking the current reproductive state of the females present into account: Masala shows less interest in Struppi than in Rezeki because Struppi is currently nursing an infant and therefore probably is not fertile while Rezeki might in theory already have undergone her first ovulatory cycle. Ujian's lack of interest, on the other side, may be explained as easily as by the current infertility of both females present. The few

occasions on which he did express sexual interest may be a hint that in case of fertility, he may well be engaging in increased sexual interactions including matings.

6.3 Recommendations

Despite the currently low interest Ujian shows in sexual behaviour, it is recommendable to re-evaluate the situation after one of the female group members, most probably Sari, has reached fertility. Therefore, an ongoing evaluation of her hormonal status as already performed during the second half of 2013 is advisable, as well as a close evaluation of the relationship between her and Puan. In case Puan becomes more hostile against Sari, inducing higher stress on her, a re-evaluation of the keeping conditions or group composition may be necessary. If this is not the case, but Sari will still not have undergone her first menstrual cycle in about one year, it may be advisable to take further medical steps to diagnose and possibly resolve her fertility problem, as it has already been tried for Puan.

In case Sari will remain infertile despite all efforts, exchanging one of the two females for a female that is known to be fertile and ideally has already raised offspring should be considered. Exchanging Ujian for a sexually more active male only needs to be an option if his interest in sexual activity remains as low as it currently is even in the presence of a fertile female.

7. Appendix

7.1 Enclosure at Heidelberg Zoo

Fig. 30 Inside enclosure at Heidelberg Zoo.

Fig. 31 Outside enclosure at Heidelberg Zoo.

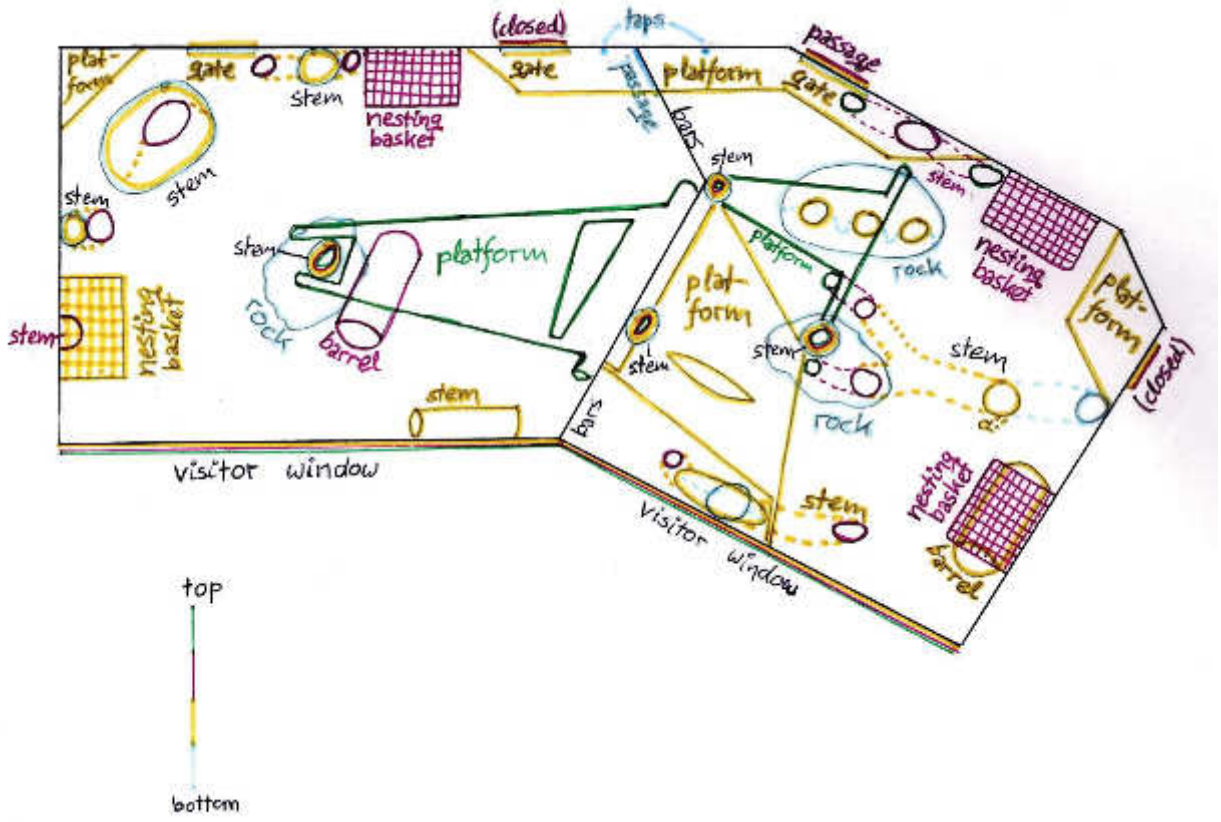


Fig. 32 Floor plan of the inside enclosure at Heidelberg Zoo.

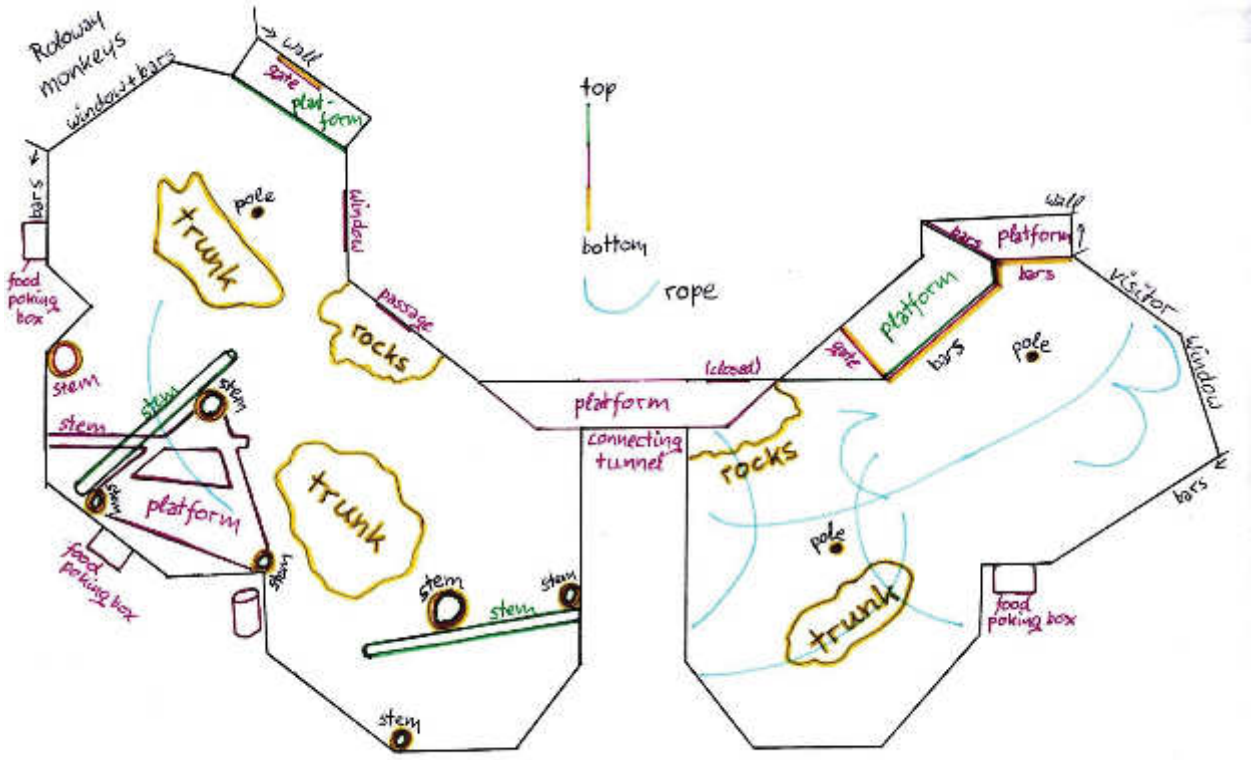


Fig. 33 Floor plan of the outside enclosure at Heidelberg Zoo.

7.2 Enclosure at Neunkirchen Zoo

Fig. 34 Inside enclosure at Neunkirchen Zoo.

Fig. 35 Outside enclosure at Neunkirchen Zoo.

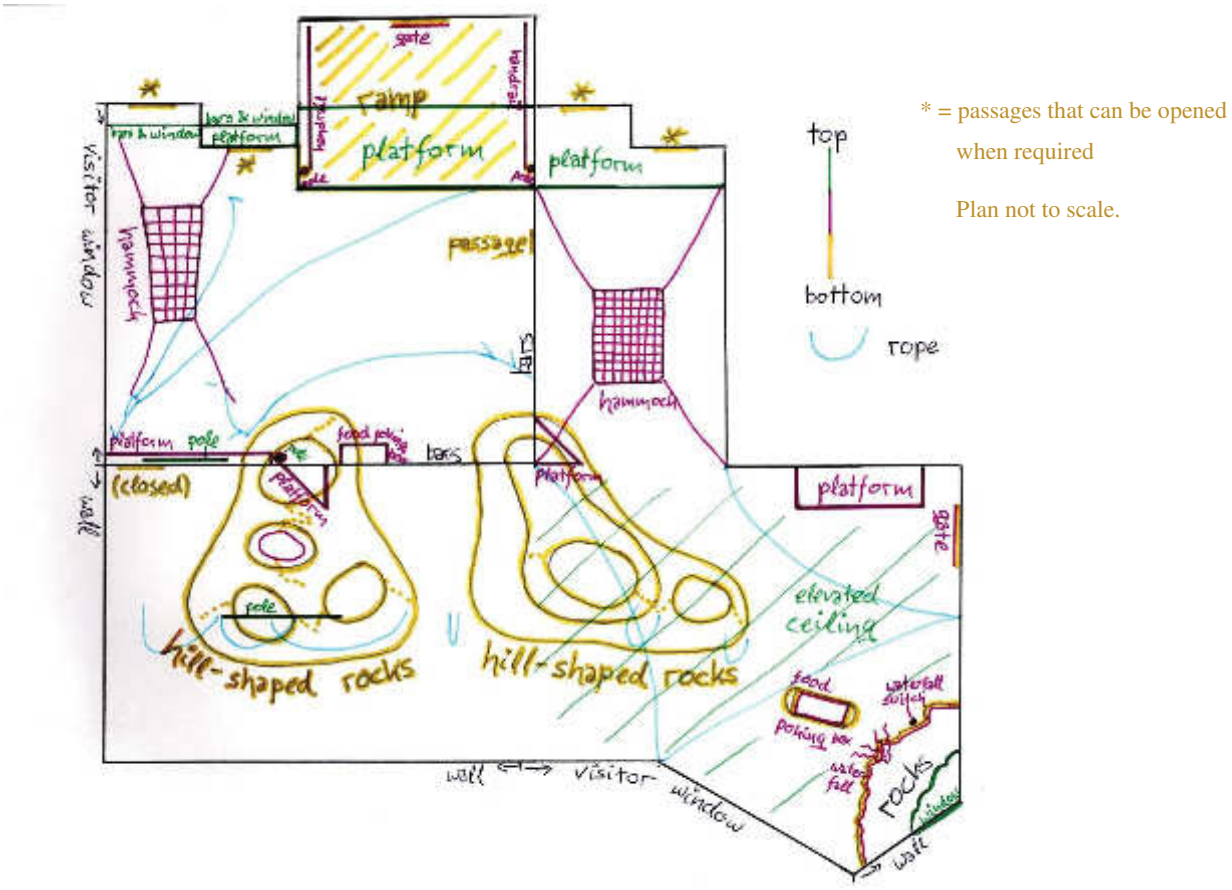


Fig. 36 Floor plan of the inside enclosure at Neunkirchen Zoo.

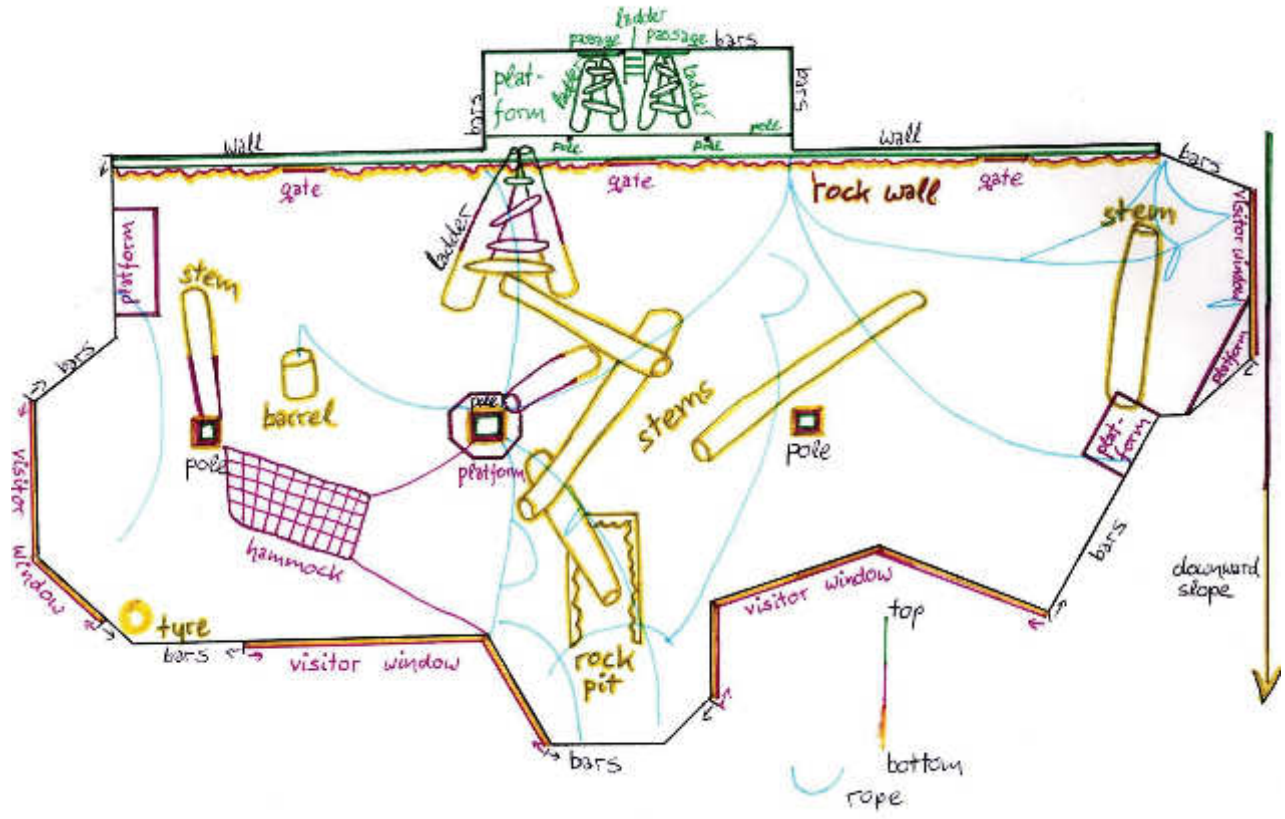


Fig. 37 Floor plan of the outside enclosure at Neunkirchen Zoo.

7.3 Values used for sociograms in 5.2.3 (fig. 24 – 25)

Dyad	Index of association	No. occasions together
Sari-Puan	0.189	251
Sari-Ujian	0.147	189
Ujian-Puan	0.111	136
Ujian-other persons		91
Puan-other persons		72
Ujian-zookeepers		62
Puan-zookeepers		56
Sari-humans		53

Tab. 3 Values used to create sociogram of the Heidelberg group (fig. 24).

Dyad	Index of association	No. occasions together
Struppi-Rezeki	0.158	194
Struppi-Surya		167
Masala-Rezeki	0.139	153
Masala-Struppi	0.094	94
Rezeki-Surya		76
Rezeki-Noah		68
Masala-zookeepers		48
Struppi-Noah		44
Rezeki-zookeepers		35
Masala-Noah		22
Masala-Surya		20
Struppi-zookeepers		17
Struppi-others		15
Rezeki-others		10
Masala-others		6

Tab. 4 Values used to create sociogram of the Neunkirchen group (fig. 25).

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