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The influence of closest female relatives on the centrality of adolescent males in a semi free-living group of Japanese macaques (Macaca fuscata)

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Abstract

This study investigated the social centrality of adolescent male Japanese macaques (*Macaca fuscata*) in relation to their closest female relative. Additionally, patterns of male dispersal and area use were observed. The study was conducted on 22 adolescent males at Affenberg Landskorn, Austria. Centrality was assessed by the proportion of time a male spent in central areas of the enclosure - the main gathering spot of the core group. Using a linear model, the centrality of the adolescent males in relation to both the dominance rank of their closest female relative and the strength of their social relationship (CSI) with these females was evaluated. The results suggest no significant relationship between male centrality and either the rank or the strength of the social relationship with their closest female relative. Furthermore, there was no clear evidence of dispersal behavior among the adolescent males. The only significant finding was a decrease in time adolescent males spent with their closest female relative as they aged. These results demonstrate that further research is necessary to identify the specific factors influencing male centrality and dispersal patterns under semi-free conditions, with particular attention to the role of the closest female relatives.

Table of contents

Acknowledgements 0

Abstract 0

1.Introduction 1

1.1 Japanese macaques as research animals 1

1.1.1 Taxonomy 1

1.1.2 Habitat 1

1.1.3 Morphology 2

1.1.4 Social Structure 3

1.1.5 Maternal influence and male dispersal 3

1.2 Research Questions 5

1.2.1 Aims 5

1.2.2 Hypotheses 5

2 Methods 6

2.1 Ethical Information 6

2.2 Study animals 6

2.2.1 Study site 8

2.3 Provisioning 9

2.4 Data collection 10

2.4.1 Focal sampling 10

2.4.2 Scan sampling 10

2.5 Variables of interest 11

2.5.1 Area Use 11

2.5.2 CSI 11

2.6 Statistics 12

2.6.1 Influence on centrality 12

2.6.2 Connection between CSI and age 12

3 Results 13

3.1 Centrality 13

3.2 Connection between CSI and age 16

4 Discussion 16

5 References 20

5.1 List of figures 23

5.2 List of tables 23

5.3 List of formulas 23

6 Appendix 24
6.1 Zusammenfassung 24
6.2 Ethogram 25
6.3 Enclosure map 32

1.Introduction

1.1 Japanese macaques as research animals

1.1.1 Taxonomy

Human behavior is a frequent subject in psychological as well as biological research. Over the last years, evolutionary perspectives increased in importance when addressing questions related to human behavior, cognition and social structure (Sandel et al., 2024). Since humans are a part of the order Primates (Suddendorf, 2004), primatology provides important insights when it comes to comparisons between human and non-human primates (Sandel et al., 2024). The aim of the comparison between humans and other primates is to gain a deeper understanding of the evolutionary traits we share but also the differences between the species. Over recent years, primatologists have demonstrated that gaining insights into human behaviors and social structure is not limited to studying great apes but also includes other non-human primate species (Kappeler and Silk, 2009; van Schaik, 2016).

The taxonomy of primates is diverse and consists of several major lineages and multiple subgroups (Fischer, 2012). Presently, there are over 500 living primate species (deutsches Primatenzentrum, 2017). The research animal of this study belongs to the genus *Macaca*, which belongs to the lineage of *Cercopithecoidea* or more commonly known as Old-World monkeys (Fischer, 2012). Macaques consist of about 20 to 30 species, making them one of the most widespread primate genus, with species well adapted to a broad range of different climatic conditions (Fleagle, 2013; Thierry, 2007; Thierry et al., 2004). Examples of the genus *Macaca* would be the rhesus macaque (*Macaca mulatta*) and the Japanese macaque (*Macaca fuscata*) – the latter being the focal animals analyzed in this work.

1.1.2 Habitat

Japanese macaques (*Macaca fuscata*), as the name suggests, are native to Japan and distributed throughout the country including the main islands Honshu, Shikoku, and Kyushu, as well as numerous smaller surrounding islands (Hanya, 2010) but excluding the most northern island Hokkaido. Japan covers a wide range of climatic zones resulting in different types of habitats.

In the northeastern regions of Japan where some of the Japanese macaques live, one can find a cold temperate or boreal climate, which includes one of the coldest climates within this

geographical zone. This region is characterized by deciduous forests, where the trees shed their leaves in winter (Hanya, 2010).

Contrary, in the southwest region of Japan one can find evergreen mixed forests, that mainly consists of broadleaf and coniferous tree species. The temperatures range from temperate to subtropical (Hanya, 2010).

One of the most ecologically extreme habitats found in Japan, that is still inhabited by Japanese macaques, is the mountain region. Here, the temperature can drop below -20°C during the winter months, which drastically reduces food availability and consequently presents a challenge for survival (Hanya, 2010).

Among all non-human primates Japanese macaques occupy the highest latitudes globally (Fooden and Aimi, 2005). The most significant difference between warmer and colder habitats is food availability. This leads to adaptations in physiology to cope with seasonal food scarcity and thermoregulation demands (Hanya, 2010; Inagaki, 1985).

1.1.3 Morphology

Japanese macaques are commonly referred to as “snow monkeys” or “red-faced macaques”. The name “snow monkey” comes from populations that reside in the mountain area of Japan, where they are nearly constantly surrounded by snow. The term “red-faced macaque” refers to the red coloration of their face and hairless body parts during the winter mating season (e.g., Wallner et al., 2011). Japanese macaques make use of both, the trees and the ground in their daily activities, moving between arboreal and terrestrial habitat (Hamada and Yamamoto, 2010).

As in many primate species, males are in general lager than females. Body size among individuals tends to increase with altitude and decreasing temperatures, which agrees with Bergmann’s rule (Hamada, 2002). In colder, mountainous regions, where food availability is narrow and often reduced to low-quality resources such as tree bark, a greater body mass plays a crucial role in thermoregulation and survival (Hamada and Yamamoto, 2010).

Japanese macaques possess relatively short tails, and the length correlates with climatic conditions: longer tails are typically found in individuals from warmer areas, while shorter tails are more common in colder regions (Fooden, 1976). Their fur changes seasonally from a lighter summer coat to a denser winter coat (Inagaki and Hamada, 1985). Groups living in high-altitude areas get extremely dense fur, which provides essential insulation against the intense winter temperatures (Fooden and Aimi, 2005). The coloration of their pelage varies geographically and agrees with Gloger’s rule (Hamada et al., 1992), thus individuals in warmer climates display

darker fur compared to individuals in colder regions who have lighter fur coloration (Hamada et al., 1992).

1.1.4 Social Structure

Japanese macaques live in multi-male multi-female groups (Fujita, 2010). Within these groups, females typically outnumber males (Beisner et al., 2012). This species has a highly despotic and nepotistic social organization (Thierry, 2000), which is displayed through a strict dominance hierarchy in which the social rank of females significantly influences the social rank of their daughters. There are three different dominance hierarchies coexisting within the group – one between only females, one between only males and one between females and males.

Japanese macaques display a matrilinear social system, meaning that daughters inherit the social dominance rank from their mothers (Fooden and Aimi, 2005). This results in stable hierarchies, because mother and daughter ranks are closely aligned (Chapais, 1988; Wolfe, 1984). Among female siblings, the youngest daughter often earns the highest rank (Gartland et al., 2021; Koyama, 1967), which is an occurrence also known as “youngest ascendancy rule” (Kutsukake, 2000).

In contrast, the male social dominance hierarchy is not based on kinship but rather shows a clearly defined alpha male at the top of the hierarchy, whose status is mostly earned by death of the predecessor (Sprague et al., 1998). Good social skills of males in both male-male and male-female relationship play more important role in determining the male rank than the display of aggression (Eaton, 1976). Still other factors like the age, physical attributes like body size and a males’ competitive ability are important (Beisner et al., 2011). In addition, a strong affiliative relationship between the alpha male and high-ranking females is essential to maintain a stable male dominance hierarchy (Gartland et al., 2021; Kutsukake and Hasegawa, 2005; Nakamichi et al., 1995).

1.1.5 Maternal influence and male dispersal

Like in humans, Japanese macaques go through different life stages: infant, juvenile, adolescent, subadult, adult, and elderly (Hamada and Yamamoto, 2010). As a female-philopatric and matrilinear species (Soltis et al., 1999), females typically remain in close proximity to their maternal kin throughout their lives (Fooden and Aimi, 2005). During the juvenile and adolescent life stage, female offspring tend to stay close to their mothers and other related females and hence strengthen both maternal bonds and social ties with unrelated female groups members (Nakamichi and Yamada, 2007).

In contrast, proximity between male offspring and their mothers declines during the juvenile phase (Nakamichi, 1989). Upon reaching sexual maturity, typically between 4 and 5 years of age (Wolfe, 1978), males emigrate from their natal group which is called male dispersal (Soltis et al., 1999). The emigration of the males serves important evolutionary functions, including the regulation of inbreeding and group size (Soltis et al., 1999). After leaving their natal group, adolescent males may either join new social groups, live solitarily (Chepko-Sade and Stone Sade, 1979), or form temporary all-male units known as bachelor groups (Kawazoe, 2016).

In many social mammals, maternal influence plays a crucial role when it comes to the development of social skills in the offspring (Maestripieri, 2018). Mother and son relationships vary across species and depend on which sex is philopatric. In male-philopatric species such as chimpanzees (*Pan troglodytes*), maternal bonds are essential for the development of social skills in the male offspring (Murray et al., 2014). Nevertheless, in female-philopatric species, such as rhesus macaques (*Macaca mulatta*) and Japanese macaques (*Macaca fuscata*), the maternal behavior towards their male offspring often differs (Amici et al., 2019). It can often be seen in rhesus macaques that mothers frequently display less affiliative and more aggressive behavior towards their sons. Therefore, a higher frequency of maternal aggression is associated with earlier male dispersal (Kulik et al., 2016). In Japanese macaques, male offspring who experience maternal rejection or aggression during their infantile phase tend to become independent earlier than those who receive more maternal care and protection (Amici et al., 2019). Additionally, in free living rhesus macaques maternal dominance rank appears to influence the timing of male dispersal. Males born to low-ranking females are more likely to disperse earlier that those born to high-ranking females (Weiß et al., 2016). Another study on rhesus macaques demonstrated that if males descend from a high-ranking matriline, they sometimes decide to stay in the natal group and try to form alliances with their maternal kin to gain better access to a high dominance rank or to resources (Beisner et al., 2011). Similarly, research in Tibetan macaques indicated that a female dominance rank had an influence on the social relationship of their offspring, i.e., the higher the social rank of the female the stronger the social relationships of their offspring with other group members (Liu et al., 2022).

Although several studies have addressed the relationship between adolescent males and their mothers, as well as how these relationships may affect male dispersal, there are still many gaps regarding this topic. Little is known about the extent to which the dominance rank of female relatives influences the dispersal behavior or the centrality of adolescent Japanese macaques. Even though there a few studies about how the availability of grandmothers effects the mother and the grandoffspring (Fairbanks, 1988) there is even less research about the role of other

female relatives, such as the aunt or sister. Furthermore, there is a big gap on the topic on the role of other female relatives on male behavior in absence of the mother. Lastly, there is also a lack of research in semi-free settings, which limits our understanding of partial or delayed dispersal patterns in adolescent males under these conditions.

1.2 Research Questions

1.2.1 Aims

To gain a deeper insight into the dispersal behavior of semi-free-living adolescent Japanese macaques, it is necessary to study their spatial distribution in relation to the presence of their closest female relative. The main goal of this study was to determine whether the centrality of adolescent males is influenced by their social connectivity to their mothers or to their next closest female relative in semi-free ranging Japanese macaques. Additionally, the dominance rank of these females was considered as a potential factor affecting the male spatial distribution. The reason we chose the closest female relative and not only the mother was that in some cases the mother was already deceased and there are studies that showed altruistic behavior coming from the grandmother (Chapais et al., 2001). In this study, centrality was assessed by the proportion of time a male spent in central areas of the enclosure.

In general, it was hypothesized that adolescent males would spend less time in central areas than in peripheral areas of the enclosure. Furthermore, age-related behavioral differences were expected: while younger adolescent males were expected to frequently stay near and interact with their closest female relative, we expected that the strength of these relationships decline as they grow older. It was also hypothesized that a high dominance rank of the female would have a positive influence on the males' spatial centrality as well as on their dispersal age. Specifically, it was assumed that adolescent males with high-ranking female relatives would spend more time in the central areas and with their closest female relative compared to males of lower-ranking matrilines.

1.2.2 Hypotheses

Hypothesis 1: After the dispersal age of 4.5 years, the adolescent males spend more time in peripheral areas than in central areas of the enclosure.

Hypothesis 2: Younger adolescent males have closer contact to their closest female relative than older ones (Amici et al., 2019), measured via Composite Sociality Index (CSI).

Hypothesis 3: Adolescent males of higher ranked female relatives show a higher centrality in regards of their area use compared to adolescent males whose closest female relative is lower ranked.

Hypothesis 4: The higher the rank of the closest female relative, the later in age the adolescent males tend to disperse into peripheral areas (Weiß et al., 2016).

2 Methods

2.1 Ethical Information

The study, which was carried out at Affenberg Landskron, was based on non-invasive behavioral observation (European Directive 2010/63). This method complies with the legally established requirements of Austria, the Affenberg Zoo (Affenberg Zoobetriebsgesellschaft mbH) and the ethical principles and guidelines of the American Society of Primatologists for the treatment of non-human primates in science (https://asp.org). No animals were isolated from their social group during the study.

2.2 Study animals

The animals observed for this study were Japanese macaques (*Macaca fuscata*) housed at the Affenberg Landskron in Carinthia, Austria. The macaques were brought from Osaka to Austria in 1996 and have lived in a semi-free living, constantly growing group ever since. The original animals from Japan were identified when they first arrived, and every birth and death was recorded since their arrival to keep track on changing demographics. At the beginning of data collection (February 5, 2024), the group consisted of 181 individuals, of which 66 were sexually matured males (≥ 4.5 years), 75 sexually matured females (≥ 3.5 years) and 40 juveniles. To prevent the group from becoming too large, birth control has been implemented since 2000 through ovarian tube ligation (sterilization) of selected females (Pflüger et al., 2021).

Focal animals of the present study were 22 adolescent males, aged between 4.5 and 7.5 years (mean $\pm$ SD = 5.7 $\pm$ 1.07 years). Adolescent males are sexually mature but not yet socially mature (Fooden and Aimi, 2005). Additionally, the identity of the closet living female relative of these males was assessed (Table 1) and their interactions with the focal animals was recorded. After two weeks of training, the focal males and their closest female relatives could be identified based on their different facial and body characteristics. The data concerning the female rank was taken from the study from Pia Giraudet (Giraudet, 2024), who did a female rank assessment

at the same time this study was collecting data (ranging from 1= highest social rank to 66= lowest social rank position).

Table 1: Overview of the focal animals (n = 22) including their age, closest living female relative and their closest living female relative's rank (1= highest rank position; 66= lowest rank position).

Name	Closest living female relative	Female social rank score	Age adolescent male in years
James Bond	Marianne (grandmother)	6	7.5
Bud Spencer	Suzana (mother)	66	7.5
Hulk	Alice (mother)	5	7.5
Wolverine	Jessy (mother)	1	7.5
Albert Einstein	Augustine (grandmother)	8	6.5
Charles Darwin	Sandra (mother)	28	6.5
Nikola Tesla	Krato (mother)	20	6.5
Mark Twain	Marianne (grandmother)	6	5.5
Terry Prachett	Pippi (sister)	12	5.5
Leo Tolstoi	Suzana (mother)	66	5.5
Umberto Eco	Sakura (mother)	32	5.5
Ernest Hemingway	Magdalena (mother)	48	5.5
Edgar Allan Poe	Amy (mother)	42	5.5
Erich Kästner	Jessy (mother)	1	5.5
Johann Nestroy	Uschi (mother)	17	5.5
Tokio	Lucy (mother)	63	4.5
Edo	Sandra (mother)	28	4.5
Kyoto	Marylin (mother)	19	4.5
Fujimino	Augustine (grandmother)	8	4.5
Hokkaido	Bettina (mother)	46	4.5
Nagano	Pippi (sister)	12	4.5
Mito	Jessy (mother)	1	4.5

2.2.1 Study site

The study took place at Affenberg Landskron in Carinthia, Austria (46°37'60" N - 13°52'60" E). The area extends over four hectares and consists of a mixture of typical Austrian mixed forest and swamp. From 29th of March to 2nd of November the Affenberg Zoo opens for visitors who can view a selected area of the enclosure during a guided tour. During the winter months the park is only open to animal care staff and researchers who can access the whole enclosure while following the park rules. Due to a long touristic history of the Affenberg Zoo, the animals are well habituated to the presence of humans and are therefore not expected to change their behavior when observers are present.

For descriptive purposes, the enclosure was divided into different areas based on vegetation and natural borders inside the enclosure. To highlight area borders inside the enclosure, markings were made around trees and along the fence. The enclosure was divided into center (C) and periphery (P) areas. These areas are furthermore divided into smaller sections. Main entrance belonged to the periphery as well (Figure 1). Each section of the area had different vegetation and feeding or hiding places. The enclosure also entailed a pool, a field office for researchers and a monkey hospital that was only used in case of medical treatment and emergencies. In addition, a small area was separated in October 2020 during a fission event. The internal fence that separated the two areas comprised three fission-fusion gates that enable individual access to both areas (Figure 1 the blue marks in 3P, 6C, 6P). While the gates could be closed completely, they were left open ever since they were built (Hammer et al., 2023). A few months after the fission, the two groups fused back together and remained as one single group.

Figure 1: Map of the Affenberg enclosure with all the different areas (center area (C), Periphery area (main entrance and (P)). © Gernot Paulus & Ulf Scherling, SIENA, Carinthia University of Applied Science – Geoinformation and Environment.

2.3 Provisioning

The feeding stations were scattered throughout different areas of the enclosure, including center and peripheral areas. However, to preserve peripheral areas as resting and withdraw areas for low-ranking individuals, feeding spots mainly concentrated in central areas with only a few located in peripheral areas flanking the center areas. On a daily basis, 220 kg of food was provided. The food consisted of wheat grains, vegetables and fruits. The macaques also had unlimited access to forage on the vegetation within the enclosure and to a natural water source (a spring) located in the forest. In winter there was one feeding in the morning at 10:00 a.m. and in summer there were two feedings, at 8:30 a.m. before the first tour and at 06:15 p.m. after the last tour. Furthermore, the animals were provided with small pieces of fruit and vegetables during guided tours.

2.4 Data collection

Data collection started on the 19th of February 2024 and ended on the 15th of May 2024. A literature search was carried out in advance. Before the start of the data collection there was a two-week training session on individual ID, observation techniques and ethogram. After two weeks there was a reliability check (ICC (2,k); ICC = 1; 95% conf. int.: 1 < ICC < 1; p-value = 9.35e-216) together with established researchers at the Affenberg, and the official data recording started. Data collection consisted of two different techniques, focal sampling and scan sampling.

2.4.1 Focal sampling

For data collection the focal animal sampling method after Martin and Bateson (2007) was used. The behavior of the 22 focal males was recorded continuously for a period of 20 minutes per day. The observations were randomized so that every focal animal was observed approximately equally often at different times of the day (Range and mean of observation effort in minutes: min = 276.9, max. = 320, mean ± SD = 305.427 ± 10.145; total observation time 6719.4 minutes). In the beginning of each session the time and date, the weather conditions and the name of the animal was stated. During the observation all frequencies and durations of all the behaviors listed in the general ethogram of the Affenberg Research Station (see appendix) was noted continuously. In addition to the behavior variables, the position of the focal within the enclosure (area section names) was continuously recorded. Furthermore, the passive behavior of the interaction partners was recorded as well as if their ID was known. If the interaction partner was not identified, the sex (male/female) and age group (adult, juvenile, infant) of this individual was noted.

2.4.2 Scan sampling

The 20 min continuous focal sampling sessions were separated into 5 minute-instantaneous-scan-intervals (Martin and Bateson, 2007) at minute 0, 5, 10, 15 and 20. In these scan intervals the proximities of other group members in a 0 meter/1 meter/3 meter and 5 meter radius to the focal animal were recorded. The ID of the partner was recorded if it was known. If the identity of the partner was unknown, the sex (male/female) and age group (adult, juvenile, infant) of this individual was noted.

2.5 Variables of interest

2.5.1 Area Use

To determine the centrality of the adolescent males, the general area use had to be calculated first. In order to do this, the whereabouts of the animals were recorded continuously during the focal animal observation and every area change was documented. The proportion of time spent in the center was calculated by dividing the sum of time spent in all center areas by an individual's total observation time. In addition, the proportion of time spent in each enclosure area by the adolescent males was calculated to provide an overall impression. For the calculation of the centrality the proportion of time spent in the center was used.

2.5.2 CSI

The CSI value (= Composite Sociality Index) was calculated to assess the strength of the relationship between the adolescent males and their closest female relative (Silk et al., 2013).

Table 2: Variables of interest for the CSI calculation. Excerpt from the general ethogram from the Affenberg Research Station (University of Vienna).

Behavior	**Definition**
Body contact	Focal maintains contact with the body of another individual. Does include short touches.
Proximity	Focal is within 1 meter of another individual and is not passing by.
Cofeeding	Focal is feeding/foraging with another feeding/foraging individual while being within 1 meter from each other.
Grooming	Focal touches and strokes another individual's fur with one or both hands, accompanied by periodic hand contact with its own mouth. Focal pays close attention to the recipient's fur.

The calculation of the CSI (Formula 1) was performed using affiliative behaviors namely body contact, proximity, grooming and cofeeding (Table 2 for definitions).

$$CSI: \frac{\left(\frac{BCab}{\frac{OTa + OTb}{Bx}}\right) + \left(\frac{Pab}{\frac{OTa + OTb}{Px}}\right) + \left(\frac{Gab}{\frac{OTa + OTb}{Gx}}\right) + \left(\frac{Cab}{\frac{OTa + OTb}{Cx}}\right)}{4}$$

Formula 1: CSI calculation. Variables: BCab is the duration of the body contact for individuals a and b. Pab is the duration of the proximity for individuals a and b. Gab is the duration of the grooming for individuals a and b. Cab is the duration of the cofeeding for individuals a and b. OTa is the observation time for a. OTb is the observations time for b. Bx is the mean body contact rate across all dyads (n = 22). Px is the mean proximity rate across all dyads. Gx is the mean grooming rate across all dyads. Cx is the mean cofeeding rate across all dyads.

A high CSI value indicates many and/or long affiliative interactions between the males and their respective female relative, and a low value indicates very little interaction based on the four pre-determined variables. Consequently, the higher the final CSI value, the stronger the relationship between adolescent males and their closest female relative. Conversely, the lower the value, the weaker the relationship between relatives (Silk et al., 2013).

2.6 Statistics

All data were recorded via pen and paper and digitized at regular intervals using Microsoft Excel from the Microsoft Office 356 suite. For subsequent statistical evaluation the statistics program R Studio (version R 4.4.0, R Core Team, 2024) was used.

2.6.1 Influence on centrality

A linear model was run to investigate factors that might the influence the centrality of adolescent males. The centrality was measured through the proportion of time spent by the adolescent males in the central areas of the enclosure. The CSI between the adolescent males and their closest female relative, the female rank and the age of the adolescent males entered the model as predictor variables.

2.6.2 Connection between CSI and age

To determine if the relationship (CSI value) between younger adolescent males and their respective female relative is stronger than the relationship between the older adolescent males and their closest relative, a spearman correlation was used. The correlation was done to investigate whether the relationship between adolescent males and their closest female relative declines with male age.

3 Results

3.1 Centrality

Neither the rank of their closest female relative (Estimate = -0.002, SE = 0.009, t = -0.3, p = 0.8, n = 22), the age of the adolescent males (Estimate = -0.007, SE = 0.05, t = -0.2 p = 0.9, n = 22) nor the relationship (CSI value) between the adolescent males and their closest female relative (Estimate = 0.01, SE = 0.04, t = 0.3 p = 0.8, n = 22) had a significant influence on the centrality of adolescent males. The centrality was measured by the proportion of time spent in the center. The correlation between male centrality and social rank of the related female is shown in Figure 2, separated for each male age group.

The correlation between male centrality and strength of relationship with closest related female (CSI) is shown in Figure 3, separated for each male age group (Range of the CSI values: min. = 0, max. = 3.6943, mean ± SD = 1 ± 1.1903, n = 22).

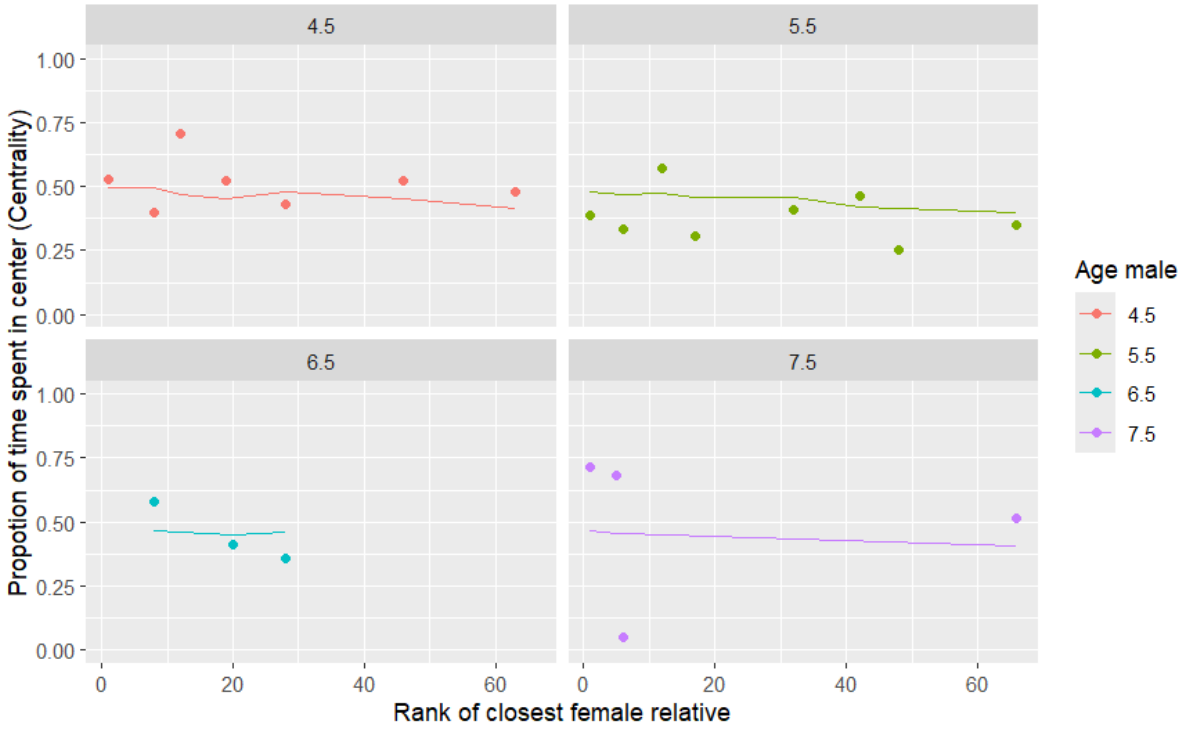

Figure 2: Relation between the centrality of adolescent males measured by the proportion of time spent in the center and the rank of their closest female relative (1-66). The lower the value the higher is a female's rank. The graph is divided into the four age groups of the males (4.5, 5.5, 6.5, 7.5 years). Each male is represented by a dot (n = 22).

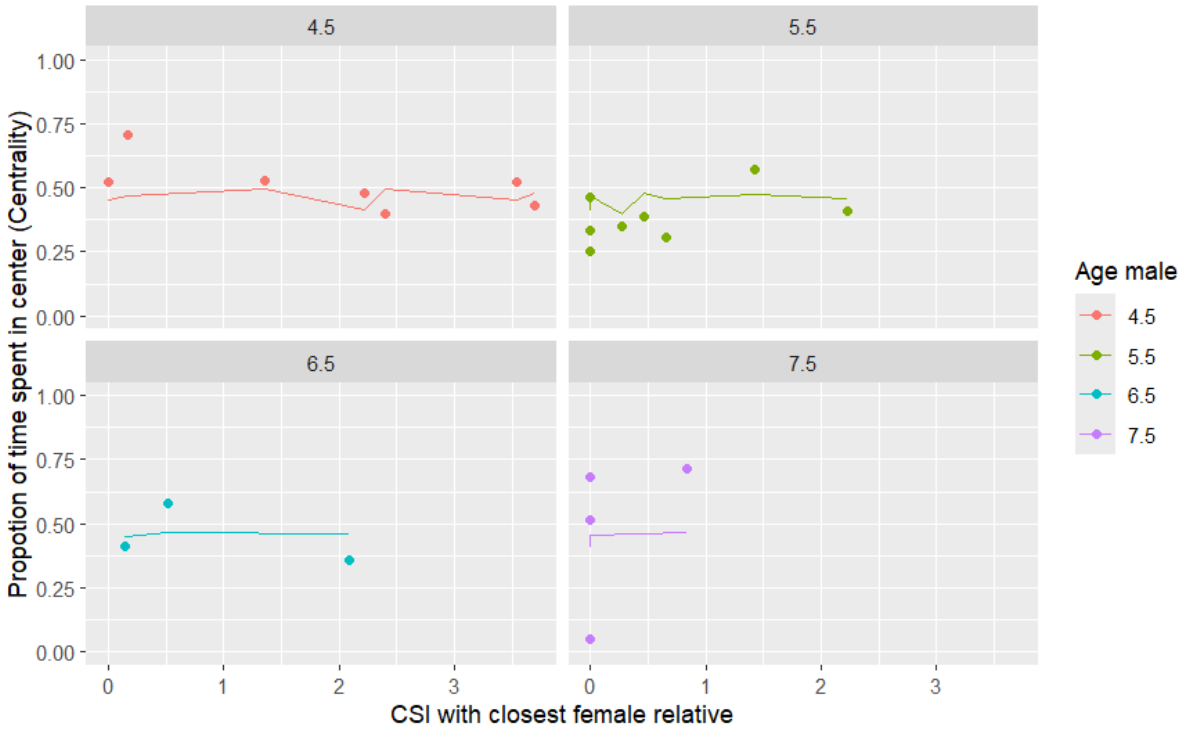

Figure 3: Relation between the centrality of adolescent males and the CSI with their closest female relative. The x-axis represents the CSI with the closest female relatives, and the y-axis represents the centrality of adolescent males measured by the proportion of time spent in the center. The graph is divided into the four age groups of the males (4.5, 5.5, 6.5, 7.5 years). Each male is represented by a dot (n = 22).

Figure 4 illustrates that the proportion of time spent in central areas was equally distributed across the different age groups. However, individual variability is evident within the age groups, particularly among adolescent males in the 7.5-year-old age group.

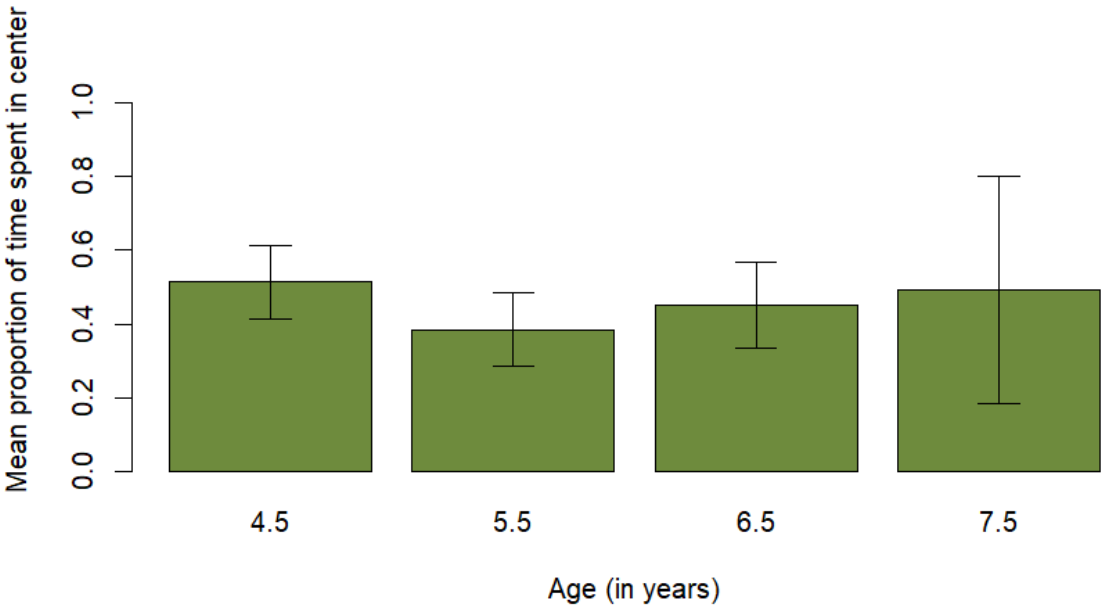

Figure 4: Proportion of time spent in the center across different age groups: Age 4.5 years: n = 7, age 5.5 years: n = 8, age 6.5 years: n = 3, age 7.5 years: n = 4. Given are mean ± standard deviation.

Figure 5 displays the proportion of time spent in the different areas by the adolescent males. Certain areas were preferred across the entire enclosure. Among adolescent males, area 4p showed the highest proportion of time spent, while area 5c showed the lowest. Notably, individual differences in spatial preferences are also evident in this context.

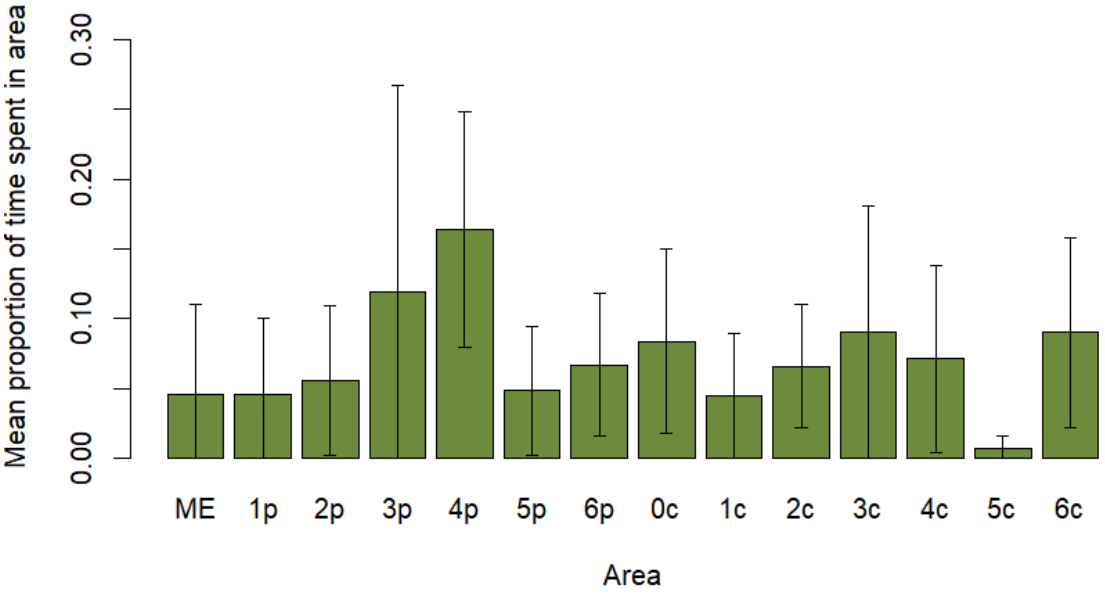

Figure 5: Proportions of time spent in different areas across all adolescent males (n = 22). ME-6p are the periphery areas, 0c-6c are the center areas. Given are mean ± standard deviation.

3.2 Connection between CSI and age

Younger adolescent males had higher CSI values and therefore stronger relationships with their closest female relatives than older individuals (r_s = -0.456, p = 0.03, n=22, Figure 6). The correlation shows a clear decrease in the CSI values as the age increases. Despite the clear result, you can see that there are individual differences within each age group regarding the CSI value between males and their female relatives.

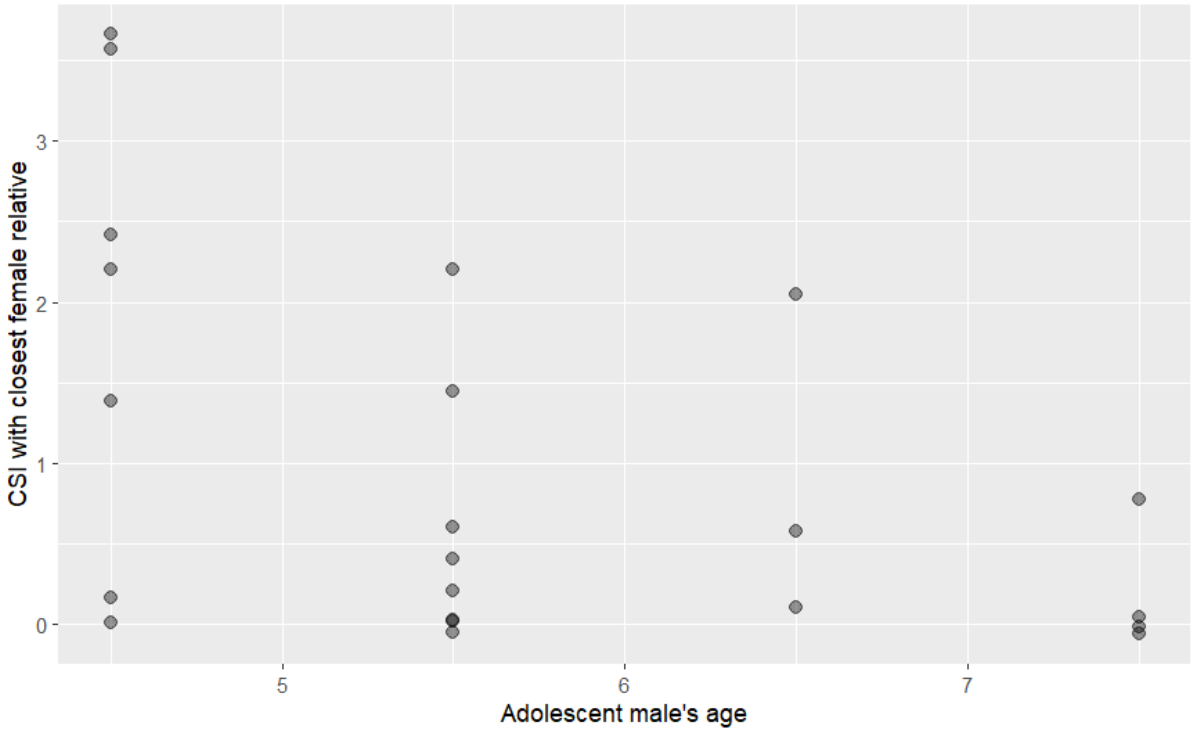

Figure 6: Correlation between the CSI values of adolescent males and their closest female relative and the male age (n = 22).

4 Discussion

The primary goal of this study was to determine whether the centrality of adolescent males is influenced by the presence of their closest female relative in a semi-free ranging group of Japanese macaques (*Macaca fuscata*). In addition, it was investigated if the rank of the closest female relative has an effect on the males' centrality and whether males lose their connection to their closest relative with increased age. Centrality was assessed by the proportion of time a male spent in central areas of the enclosure. Connectivity between males and their relatives was measured via the Composite Sociality Index (CSI).

The results indicate no significant association between the relationship (measured by the CSI value) between adolescent males and their closest female relative, nor between the rank of these females and the centrality of the males. Regarding area use, the data showed an approximately equal distribution, where the males spend nearly the same amount of time in the central and peripheral areas of the enclosure. One finding, however, clearly shows that the time adolescent males spend with their closest female relative decreases as males grow older.

The results were surprising given that, in the wild, adolescent males typically disperse from their natal group upon reaching sexual maturity around 4.5 years of age (Soltis et al., 1999). It was therefore hypothesized that the adolescent males would spend more time in peripheral areas to imitate dispersal-like behavior. However, contrary to expectations, their area use was nearly equally split between peripheral and central parts. Yet a slight increase in peripheral area use could be seen among the 5.5-year-old males. Although some outliners were present, especially among the 7.5-year-old males, no clear patterns appeared when looking at different age classes individually. A reason for the lack of preference regarding the peripheral areas could be that the group as a whole can move freely in the enclosure. Therefore, it could be possible that the adolescent males avoid the high-ranking monkeys who visit the peripheral areas by going in the center areas. Even though some preferences for specific enclosure areas could be identified, they were not surprising since these areas were largely located near or adjected to feeding sites. The low value recorded for area 5c is likely due to the limited size of this area. One surprising result was that the additional area 6p, which – with its partial separation and feeding sites – could serve as an ideal dispersal retreat, was not used more frequently than other areas.

Another initial assumption was that the rank of the closest female relative would influence the centrality of the males and consequently the timing of dispersal, as suggested by studies such as Weiß et al. (2016) and Beisner et al. (2011). Therefore, the absence of a significant correlation between female rank and the adolescent male dispersal behavior was unexpected. A possible explanation could be that the semi-free conditions of the enclosure do not create the same amount of pressure a natural habitat would thereby reducing the need to disperse from the group.

At last, the hypothesis that younger adolescent males spend more time in proximity to and interaction with their closest female relative (measured via CSI) than older adolescent males was supported. This suggests an age-dependent social distancing which is potentially linked to the gradual process of dispersal (Onyango et al., 2013). However, no connection was found between male's CSI with their relatives and female relative's social rank score. These findings suggest that adolescent males aim to receive benefits, such as support or social connections,

from their closest female relative for as long as possible, irrespective of the rank of their relatives, before eventually separating from the group.

In general, there are still several gaps in our understanding of this topic. For instance, in studies of matrilinear groups, the focus on kinship relationships is mainly centered in mother-daughter bonds, while much less attention has been given to the relationship between females and their male offspring. Even in studies where mother-son bonds (Amici et al., 2019; Kulik et al., 2016) or grandmother-grandoffspring bonds (Fairbanks, 1988) are investigated, the role of other female relatives, such as sisters or aunts is often overlooked despite the influence they might have on the adolescent male (Quiatt, 1979).

Another issue found in some studies is that male age classes are often grouped together (typically age 1-4), even though significant differences in social behavior and sexual development already emerge early in life of both, male and female (Kulik et al., 2015). As a result, little is known about the female role on the male dispersal process at the start of sexual maturity.

This issue is even less explored in semi-free conditions, where adolescent males are unable to fully disperse, may form all-male groups in the periphery and later re-integrate back into their natal group.

To address these gaps in knowledge, future research could include additional data collection methods alongside focal sampling approach. For example, a scan sampling twice a day in each enclosure area could provide a broader overview of spatial distribution, revealing whether adolescent males actively avoid their closest female relative or co-occupy the same area without proximity. Another method that should be included is network analysis. As mentioned above, the whole group moves freely in the enclosure and therefore it is important to have an overview of the whole group activity. Consequently, a network analysis should be used for the measurement of “Centrality” since it gives a broader understanding of the group dynamics and location preferences without having to stick to section markers (Farine et al., 2015; Croft et al., 2004).

Additionally, future studies could put a specific focus on bachelor groups. The formation of such groups could be expected since the males are on one hand in the right age to disperse from the group and on the other hand have the connection to other adolescent males (Kawazoe, 2016). This topic could not be addressed in the present study. However, future research could build upon the present findings and explore which demographic factors influence male co-dispersal and bachelor group formation, such as similar female relative ranks, same age class, kinship

(e.g., brothers) or whether groupings are more complex than expected (Cheney and Seyfarth, 1983).

Moreover, a longtime study beginning prior to the start of the dispersal and continuing through reintegration into the group could provide valuable insights into how affiliative relationships between adolescent males and their female relatives evolve over time.

At last, comparative studies involving other semi-free ranging matrilinear primate species would be beneficial to gain a broader understanding of social dynamics, particularly concerning male dispersal in semi-captive settings.

To conclude, the findings of the present study highlight the complexity of the social structure and dispersal dynamics under semi-free conditions, where environmental constraints differ from those in the wild. They also underscore the need for a clearer understanding of the extended maternal kin network, beyond the mother-son-dyad. Therefore, this study contributes to the growing body of research on primate social structures by addressing lesser studied aspects of male dispersal in matrilinear systems. However, it also reveals limitations, such as the need for an additional data collection method, and opens new ways for future studies especially in terms of a broader kinship analyses between males and females and long-term tracking of social bonds between adolescent males and their relatives.

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5.1 List of figures

Figure 1 Map of the Affenberg enclosure with the different areas marked.....9

Figure 2 Relation between the centrality of adolescent males and the rank of their closest female relative.....13

Figure 3 Relation between the centrality of the adolescent males and the CSI with their closest female relative.....14

Figure 4 Proportion of time spent in the center across different age groups.....15

Figure 5 Proportions of time spent in different areas across all adolescent males.....15

Figure 6 Correlation between the CSI values of adolescent males and their closest female relative and the age of the male.....16

5.2 List of tables

Table 1 Focal animals. 22 adolescent male Japanese macaques (*Macaca fuscata*) including age, closest female relative and rank of closest female relative.....7

Table 2 Variables of interest for the CSI calculation.....11

5.3 List of formulas

Formula 1 CSI calculation.....12

6 Appendix

6.1 Zusammenfassung

Diese Studie untersucht die soziale Zentralität von adoleszenten männlichen Japanmakaken (*Macaca fuscata*) in Bezug auf ihren nächsten weiblichen Verwandten. Weiters wurden Abwanderungsmuster und Arealnutzung untersucht. Diese Studie wurde an 22 adoleszenten Männchen am Affenberg Landskron in Österreich durchgeführt. Die Zentralität wurde anhand des Anteils der Zeit, die ein Männchen in den zentralen Bereichen des Geheges verbracht hat, ermittelt. Mit Hilfe eines linearen Modells wurde die Zentralität der adoleszenten Männchen in Beziehung zum Dominanzrang ihrer nächsten weiblichen Verwandten sowie zur Stärke ihrer sozialen Beziehung (CSI) zu diesen Weibchen analysiert.

Die Ergebnisse deuten darauf hin, dass kein signifikanter Zusammenhang zwischen der Zentralität der adoleszenten Männchen und weder dem Rang noch der Stärke der sozialen Beziehung zu den nächsten weiblichen Verwandten besteht. Außerdem konnten keine eindeutigen Hinweise auf Abwanderungsverhalten bei den adoleszenten Männchen festgestellt werden. Das einzige signifikante Ergebnis war der Rückgang der Zeit, die die adoleszenten Männchen mit ihren nächsten weiblichen Verwandten verbracht haben, je älter sie waren.

Diese Ergebnisse zeigen, dass weitere Forschung notwendig ist, damit man herausfinden kann welche Faktoren bei sowohl der Zentralität als auch der Abwanderung der adoleszenten Männchen eine Rolle spielen in Bezug auf ihre nächsten weiblichen Verwandten.

6.2 Ethogram

General Ethogram Affenberg Field Research Station - University of Vienna

General application

This is the general ethogram used at the Affenberg field research of the University of Vienna. This list of variables has been created to form a long-term database that contains general behavioural data that can be applied to several different research topics. This ethogram will form the basis for any research that occurs at the Affenberg and uses focal sampling as an observation method. This means that these variables have to be included in such studies. For specific research questions additional and more specific variables may be added to a project-specific ethogram but should not replace existing variables in the general ethogram.

Spatial information

Combination of:

Area: Area number + centre or periphery (e.g. 4c)

Environment events: Conflict, feeding, guided tour, veterinary, construction site, bird of prey, other events

Height: 0 m / 1-3m / 4-10 m / + 10 m

Weather: Sunny / Sun with clouds / Cloudy / Rain / Mist / Snowfall / Snow
(Snow indicates presence of snow on the ground. It can be combined with any other wheathertype.)

Durational labels:

These labels indicate the durational characteristics of a behaviour and in which column the behavioural variables should be digitalised in the focal templates:

Durational movement	=	DM
Durational behaviour	=	DB
Event behaviour	=	EB

Ten-second rule:

When a durational movement/behaviour (DM's & DB's) is interrupted for less then 10 seconds, it is still the same bout. Interruptions longer than 10 seconds mean a new bout has started (e.g.: a pause between grooming longer than 10 seconds, means two different bouts happened). If the observer feels confident enough to include shorter interruptions between bouts, the ten-second rule does not have to be applied.

Behavioural variables

Active encouragement (EB): Focal looks at the individual who mounts them and/or grabs behind (on hip, leg, genital region) or pulls the arm or other body part of another individual while being mounted.

Active solicitation (EB): Focal actively grabs or pulls the arm or other body parts of an individual to invite it for mounting or being mounted.

Approach (EB): This behavioural variable occurs in the following contexts:
1) Focal enters a 1-meter radius of another individual.
2) Focals moves towards another individual with a clear focus towards this individual.

Approach conflict (EB): Focal moves in the direction of a conflict. Focal might display vocalisations (e.g.: grunt, scream). When focal enters a conflict and displays (non-)aggressive variables, additionally write (non-)aggressive-intervention (see below). If a conflict dissolves before the focal reached the conflict, it is still seen as an approach conflict.

Attempted mount (EB): Focal tries to mount (see Mount (EB)).

Attention (EB): Focal looks towards a specific event (e.g. conflict, disturbance or vocalization) or towards an individual with a clear focus and with a frozen body posture.

Autogroom (DB): Focal grooms oneself.

Avoid (EB): Focal animal changes its path/sitting spot in order to avoid getting close to another individual with the focus on that other individual and was not in proximity (1-meter) with the other individual before.

Avoid conflict (EB): Focal focuses its attention on a conflict without approaching the conflict and moves away.

Avoid in proximity (EB): Focal animal avoids an individual within a one meter radius, while having focus on that individal, without leaving the proximity radius. (Do not write down change position.)

Bipedal walk (DM): Focal walks standing up on both hindlegs.

Bite (EB): Focal places its teeth on the body of another individual and closes its jaws.

Body contact (DB): Focal maintains contact with the body of another individual. Does include short touches (see below).

Body spasm (EB): Focal displays spastic movements, often combined with calls or slapping an object or the ground.

Body shake (EB): Focal rapidly turns the whole body along its spine in at least two different directions.

Carry (DB): Focal carries a juvenile on the back/belly.

Change position (EB): Focal adjusts position by moving less than 1 meter. Can be recorded passive as well if a partner stops being in body contact or in proximity through a change position.

Chase (EB): Focal runs after another individual for at least 3 meters.

Climb (DM): Focal moves in a non-horizontal direction on a tree, building or construction.

Consort sit:

Close consort sit (DB): Focal is sitting in body contact with a partner in a context where other sexual variables are displayed (e.g.: active solication, mount). Focal can sit directly in front of the partner (i.e.: back touches belly of the partner); or sit directly behind the partner (i.e.: belly touches back of the partner). If possible, indicate position in notes (F=front; B=behind). If the focal holds the buttocks or hips of another individiual from behind (either shortly or for longer duration), note down 'Hold Bottom' additionally. Mutually exclusive with body contact.

Loose consort sit (DB): Focal is sitting within an arm-length reach of a partner in a context where other sexual variables are displayed (e.g.: active solication, mount). Focal can sit directly in front of the partner (i.e.: back directed towards belly of the partner); or sit directly behind the partner (i.e.: belly directed towards back of the partner). If possible, indicate position in notes (F=front; B=behind). If the focal holds the buttocks or hips of another individiual from behind (either shortly or for longer duration), note down 'Hold Bottom' additionally. Loose consort sit is mutually exclusive with proximity.

Consort interruption:

Aggressive consort interruption (EB): Focal interrupts a consortship by aggressively trying to displace one or both consort partners or make them split their proximity. Possibly with body contact (hit/bite/grab) or without (chase/lunge/threat).

Non-aggressive consort interruption (EB): Focal interrupts consort without showing aggressive behaviour but displacing one or both consorting partners or make them split their proximity.

Copulation call (EB/DB): Focal vocalizes towards a (potential) sexual partner. Can be continuous when pauses between copulation calls are shorter than 10 seconds (then digitalised in the DB-column).

Curl up (DM): Focal sits hunched forwards, head tilted towards chest, arms and legs tight at body core.

Cofeed (DB): Focal is feeding/foraging with another feeding/foraging individual while being within 1 meter from each other.

Cower (EB): Focal shows a lateral flexion of the spine, away from another individual, human or environmental event.

Cry for support (EB): Focal makes a high pitch vocalization accompanied by hectic looking and searching for another individual during or after an aggressive encounter.

Displace (EB): Focal approaches another individual who then leaves, after which the focal remains within 1m radius where the other animal used to stay. The approach is written separately, as well as any potential reaction towards the displace (e.g., leave or avoid).

Embrace (DB): Focal holds another individual in its arms (can be combined with huddle).

Face to face (EB): Focal pushes its own face close to the face of another individual. Usually involves grabbing the face of the other individual and pulling it towards its own.

Feed (DB): Focal takes repeated bites of the same food item (e.g.: potato; pine cone) without having to search for that item.

Forage (DB): Focal moves slowly while looking for food on the ground or focal is sitting while looking for food on the ground.

Follow (DB): Focal walks behind another individual in the same direction and stays within a radius of 5 meters.

Fear grin (EB): Focal retracts lips and the teeth become visible. May be accompanied with partly opened jaws.

Flee (EB): Focal runs away from another individual after being approached/chased/lunged by that individual.

Grab (EB): Focal holds body parts of another individual with one or two hands for a few seconds.

Groom (DB): Focal touches and strokes another individual's fur with one or both hands, accompanied by periodic hand contact with its own mouth. Focal pays close attention to the recipient's fur.

Ground hit (EB): Focal hits or wipes the floor with the hand.

Groom displace (EB): Focal displaces one monkey in a grooming dyad to form a new grooming dyad with the remaining monkey. Is alway accompanied with 'groom (passive)' of the remaining monkey.

Grunt (EB): Focal makes a low-pitched rumbling vocalization in an aggressive context or in direction of a conflict. Could be with clear focus towards another individual.

Hit (EB): Focal slaps another individual by hand.

Huddle (DB): Focal is in body contact to another individual and rests its head on this individual (mutually exclusive with body contact; can be combined with embrace).

Intervention:

Aggressive intervention (EB): Focal enters a conflict and displays aggressive behaviours (e.g. lung, threat, physical attacks, chase). Focal was not involved at the start of the conflict. If focal displays aggressive behaviours on the side of one specific individual, note support instead (see below).

Non-aggressive intervention (EB): Focal enters a conflict and displays non-aggressive behaviours. Focal was not involved at the start of the conflict.

Leave (EB): This behavioural variable occurs in the following contexts:
1) Focal stops being in proximity with another individual by moving away (if the 1-meter radius is left through a change position (passive), write change position instead);
2) Focal walks away after having displayed aggressive or dominance behaviours (e.g.: face to face; grab; threat) to another individual;
3) Focal walks away after having received aggressive or dominance behaviours (e.g.: face to face; grab; threat) from another individual. Might result in leaving proximity but is not required.

Lie down (DM): Focal is lying down, either on side, belly or back.

Lip smack (EB): Focal pouts and repeatedly opens and closes the lips.

Lunge (EB): Focal jumps a maximum of two body lengths forwards towards another Individual.

Mate (EB): Focal mounts and ejaculates, which is indicated by a pause before dismounting and/or the appearance of visible semen.

Masturbate (DB): Focal rubs own genitalia with fingers, on objects or on the ground.

Mock leave (EB): Focal walks away from another individual while turning around at least once to lunge/scream/threat the other individual.

Mock flee (EB): Focal runs away from another individual while turning around at least once to lunge/scream/threat the other individual. Mock flee is not the same as fleeing while crying for support.

Mount (EB): Focal climbs on another individual with its hands on the receivers back or rump. Note whether it involves thrusts.

Muzzle contact (EB): Focal brings its own mouth region close to another individual's mouth region.

Nurse (DB): Focal enables infant to breastfeed.

Object interaction (DB): Focal uses objects in movements that serve no obvious, immediate purpose.

Pass by (EB): Focal enters a radius of 1 meter around another individual and leaves this radius within the same movement without displaying any other social behaviours (to distinguish from approach definition #3 (see above)).

Physical attack (EB): Focal aggresses another individual with repeated and consecutive physical aggressive behaviours (e.g.: a succession of grab, hit and/or bite).

Present (EB): Focal displays its rump and/or anogenital region to another individual by bowing forward and/or raising hindquarter. Focal might also sit in front of a potential partner and displays the back towards another individual. Could involve hitting the ground.

Proximity (DB): Focal is within 1 meter of another individual and is not passing by.

Play face (EB):	Focal opens mouth with open jaws without retracting lips towards another individual. Focal makes no vocalisations.
Refusal (EB):	Focal leaves or changes position away from the partner without aggression while the partner shows interest in mounting (through presentation, holding bottom or active solicitation).
Rejection (EB):	Focal leaves or changes position away from the partner with aggression while another individual shows interest in mounting (through presentation, holding bottom or active solicitation).
Redirection (EB):	Focal that was involved in a conflict displays aggression to another, not previously involved individual within 10 seconds after the conflict (e.g. threats and/or physical aggression/chase/lunge).
Scratch (EB):	Focal uses finger(s) or foot to rake across own skin.
Scream (EB/DB):	Focal utters high pitched, intense vocalization. Can be continuous when focal screams every 10 seconds (then digitalised in the DB-column).
Sit (DM):	Focal rests in a posture supported by the buttocks or thighs.
Sunbathe (DB):	Focal sits upright with chest turned towards the sun.
Stand (DM):	Focal stands on four legs.
Social play (DB):	Focal displays behaviours of physical aggression (e.g. hit, grab or bite) with other individuals without vocalizations and with less intensity than regular physical aggression. Can be accompanied by playface.
Stare (EB):	Focal looks intensively at another individual with a straight back and raised eyebrows.
Startle (EB):	Focal jerks or twitches in response to an event or another individual that has approached while the focal individual was occupied with another activity.
Support (EB):	Focal actively approaches another individual who is in a conflict and together they display joined aggression towards one opponent. When a juvenile is supported, the juvenile might leave the conflict while the focal is chasing.
Threat (EB):	Focal moves its head with an O-shaped mouth and raised eyebrows towards another individual.
Travel (DM):	Focal walks or runs around.
Touch (EB):	Focal makes gentle and short body contact with another individual.
Travel together (DB):	Focal travels parallel to another individual. Distance between the individuals is less than 3 meters.
Tree shake (EB):	Focal holds a tree or object and shakes its body intensively.

Vigilance (EB/DB): Focal has a tense body posture and looks around with hasty movements of head and/or eyes without an imminent reason. Might be accompanied by standing on the hind legs. Can be continuous when focal is vigilant for more than 10 seconds (then digitalised in the DB-column).

Vocalization (EB/DB): Focal utters a vocalization that is not a copulation call, grunt or scream. Can be continuous when focal vocalizes every 10 seconds (then digitalised in the DB-column).

Yawn (EB): Focal opens mouth wide and inhales intensely, which can be seen by the expansion of the chest.

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6.3 Enclosure map

N
W E
S

0 12.5 25 50 75 100
Meters

Drohnenbefliegung Affenberg
Auflösung: 3cm/Pixel

23. März 2023