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Social relationships of adolescent male Japanese macaques (Macaca fuscata)

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Abstract

Social relationships can be observed in primates not only between related but also between unrelated individuals. In macaque species, social relationships are influenced by various factors, such as sex-specific dispersal behaviour and kinship. Japanese macaques *(Macaca fuscata)* form despotic and matrilinear organized societies, in which females remain in their natal groups throughout their lifes. Males, in contrast, leave their natal groups upon reaching sexual maturation and live in bachelor groups or solitarily before joining new groups. These circumstances make it difficult to study the social relationships of adolescent males in the wild. The aim of this study was to contribute to a better understanding of the dispersal behaviour of male Japanese macaques in semi-free conditions, to investigate the social relationships between adolescent males, and to examine whether age influences their spatial positioning within the group and their age-dependent proximity to one another.

Data collection took place at Affenberg Landskron, which offers the opportunity to observe Japanese macaques in semi-free conditions. The main analyses focused on adolescent males under 8.5 years of age (N=23); socio-sexually mature males (N=4) were included for additional analyses. The study investigated age-related dispersal from the group in adolescent males by analysing their use of peripheral and central areas inside the enclosure (spatial positioning) and whether there is a correlation between age and co-presence. It also examined whether the males prefer to form relationships with related or unrelated adolescent males. Social relationships were determined for each possible dyad using the Composite Sociality Index (CSI) based on affiliative behaviours.

The results show that adolescent males were observed across all areas of the enclosure and that there was no significant correlation between age and co-presence. This indicates that age alone does not explain the distribution and proximity between young males. Analysis of the CSI values revealed that affiliative relationships increased with genetic relatedness, indicating that related adolescent males formed stronger social bonds. However, social relationships were also observed between unrelated adolescent males. Overall, these results suggest that although age did not influence spatial behavior, genetic relatedness played a significant role in shaping affiliation relationships among adolescent male Japanese macaques.

Zusammenfassung

Soziale Beziehungen können bei Primaten sowohl zwischen Verwandten, aber auch zwischen Nicht-verwandten Individuen beobachtet werden. Bei Makakenarten werden sozialen Beziehungen von verschiedenen Faktoren, wie den sex-spezifischen Ausbreitungsverhalten, sowie der Verwandtschaft beeinflusst. Japanmakaken haben einen stark despotischen Lebensstil, wobei die Weibchen lebenslang in ihren Geburtsgruppen verbleiben. Die Männchen verlassen hingegen ihre Geburtsgruppen mit Erreichen der Spermatogenese und leben vorerst in Bachelorgruppen oder solitär, bevor sie sich neuen sozialen Gruppen anschließen. Diese Umstände erschweren es, die sozialen Beziehungen der adoleszenten Männchen in freier Wildbahn zu erforschen.

Ziel dieser Studie war es, zu einem besseren Verständnis des Ausbreitungsverhaltens männlicher Japanmakaken unter semi-freien Bedingungen beizutragen und die sozialen Beziehungen zwischen adoleszenten Männchen zu untersuchen sowie zu prüfen, ob das Alter ihre räumliche Positionierung innerhalb der Gruppe und ihre altersabhängige Nähe zueinander beeinflusst. Die Datenaufnahme erfolgte am Affenberg Landskorn, der die Möglichkeit bietet, die Japanmaken in semi-freier Haltung zu beobachten. Die Hauptanalysen fokussierten sich dabei auf die adoleszenten Männchen unter 8.5 Jahren (N=23); für zusätzliche Analysen wurden bereits sozial-sexuell reife Männchen (N=4) inkludiert.

Die Studie untersuchte die altersbedingte Ausbreitung der Männchen innerhalb der Gruppe, indem sie deren Nutzung der peripheren und zentralen Bereiche innerhalb des Geheges analysierte und untersuchte, ob ein Zusammenhang zwischen Alter und Koexistenz besteht. Außerdem wurde untersucht, ob die Männchen bevorzugt Beziehungen zu Verwandten oder Nicht-verwandten adoleszenten Männchen aufbauen. Dabei wurden soziale Beziehung durch affiliative Verhaltensweisen für jede mögliche Dyade mittels des Composite Sociality Index (CSI) bestimmt.

Die Ergebnisse zeigen, dass die adoleszenten Männchen in allen Bereichen des Geländes gleichermaßen beobachtet wurden und kein signifikanter Zusammenhang zwischen Alter und Co-präsenz bestand. Das deutet darauf hin, dass das Alter allein nicht die Verteilung und die Nähe zwischen den Männchen erklärt. Die Analysen der CSI-Werte zeigte zudem, dass Männchen häufiger soziale Beziehungen zu verwandten adoleszenten Männchen aufbauen, aber auch, dass soziale Beziehung zu nicht-verwandten Männchen bestehen. Insgesamt deuten diese Ergebnisse darauf hin, dass das Alter zwar keinen Einfluss auf das räumliche Verhalten hatte, die genetische Verwandtschaft jedoch eine wichtige Rolle bei der Bildung der affiliativen sozialen Beziehungen zwischen adoleszenten männlichen Japanmakaken spielte.

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1. Introduction

1.1 Systematics and distribution area

Japanese macaque, *Macaca fuscata* (Gray, 1870), commonly referred to as the snow monkey, is a non-human primate species of the family *Cercopithecidae*. They are part of the subfamily *Cercopithecinae* and are classified in the tribe *Papionini*. They belong to the genus *Macaca*, which includes other species such as the rhesus monkey (*Macaca mulatta*) and the Barbary macaque (*Macaca sylvanus*) (Geissmann, 2003). Japanese macaques are the only non-human primates found exclusively on the Japanese archipelago. Their natural distribution covers three of the four main Japanese islands, primarily the highland regions of Honshu, Shikoku and Kyushu, as well as on other small Japanese islands (Aimi and Fooden, 2005). Overall, Japanese macaques are the the northernmost distributed non-human primate species, with a range extending from approximately 30°15'N to 41°30'N (Aimi and Fooden, 2005; Enari et al., 2022). Due to the wide variation in its range, the climate and vegetation can vary greatly (Hamada and Yamamoto, 2010). Japanese macaques live in the cool temperate broadleaf forests of northern Japan, as well as in the warm temperate evergreen broadleaf forests of the south (Aimi and Fooden, 2005). Lowland areas of Japan are rarely populated by macaques today (Amagasa and Ito, 1978). The population size of Japanese macaques has changed significantly over the years. In the mid-20th century, declining population numbers in rural regions of Japan led to a change in the use of forest resources (Enari 2021, cited in Enari et al., 2022). This resulted in an increase in macaque populations in these areas. The increasing macaque population led to increased crop damage (Suzuki and Muroyama, 2010) as well as property damage and physical injury (Tsunoda and Enari, 2020). This led to changes in governmental regulations permitting macaque hunting, which resulted in a decline in population numbers (Enari et al., 2022), as several thousand macaques were killed each year (Aimi and Fooden, 2005). In addition to restrictive measures, there are also management strategies to enable the protection of existing populations and ensure the coexistence of humans and Japanese macaques (Enari et al., 2022), and a geographical spread of macaques can be observed (Aimi and Fooden, 2005; Hashiba, 1989).

The current distribution range of *Macaca fuscata* (2025) can be seen in Figure 1. According to the Red List of the International Union for Conservation of Nature (IUCN), Japanese macaques are currently classified as a species of least concern (as of November 2015) (Watanabe and Tokida, 2020).

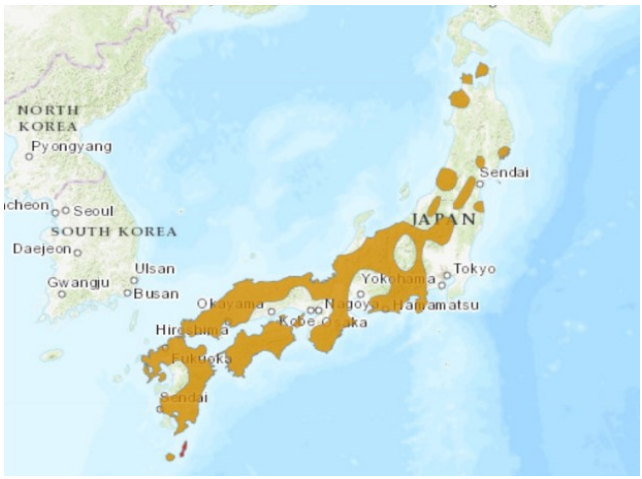

Figure 1: Geographic distribution of Japanese macaques. Orange: current distribution area; red: extinct (Source: Watanabe and Tokita (2020), IUCN Red List:https://www.iucnredlist.org/species/12552/195347803 Accessed: 01.08.2025)

1.2 Morphology and lifestyle

The morphology of Japanese macaques varies depending on their habitat. While macaques in colder regions are larger on average and have thicker fur, animals in warmer areas are usually smaller and have thinner fur (Hamada et al., 1996). The coat colour of Japanese macaques can vary between different shades of brown. In addition to grey-brown macaques, there are also yellow-brown and dark golden-brown macaques (Aimi and Fooden, 2005). The coat colour of females is slightly lighter than that of adult males (Hamada et al., 1992). Their faces are pink and they have a short tail stump (Aimi and Fooden, 2005; Rowe, 1996). Sexual dimorphism can be observed between males and females, with female macaques being smaller and weighing less on average (8.4 kg) than males (11.3 kg). In accordance with Bergmann's rule, body size and weight tend to increase with latitude (Aimi and Fooden, 2005; Hamada and Yamamoto, 2010). While the life expectancy for males living in the wild is up to 28 years, females can reach an age above 30 years (Nakamichi et al., 1995). Animals living in captivity reach a significantly higher age, partly due to medical care (Gutleb et al., 2014). Japanese macaques are omnivorous and feed mainly on various plants, fruits, seeds and insects (Koganezawa, 1975; Tsuji et al., 2015), although their diet may vary depending on their distribution area (Tsuji et al., 2015). They not only move around by climbing and running, but can also swim up to several hundred metres (Aimi and Fooden, 2005). A wild population in Japan's Nagano Prefecture is well known for bathing in natural hot springs. This serves a thermoregulatory purpose and can be observed particularly in females and young animals (Zhang et al., 2007).

1.3 Life stages

The life stages of Japanese macaques can be divided into different phases. The infantile phase begins at birth and at around three months of age, the colour of their fur begins to change and their motor skills develop to the point where they can forage for food independently (Hamada and Yamamoto, 2010), while still being nursed by their mother. From the age of one year, the infantile phase changes to the juvenile phase (Aimi and Fooden, 2005).

For males, this juvenile phase ends at around 4.5 years of age, when they become sexually mature. Spermatogenesis begins during this adolescent phase (Hamada and Yamamoto, 2010). Females, on the other hand, reach sexual maturity at 3.5 years of age when they start menstruating for the first time. In females, sexual maturity is related to physical development. On average, females give birth to their first offspring between the ages of 5 and 6 years (Takahata et al., 1998). Japanese macaques show intensified red coloration of the hairless skin (face, hindquarter, nipples) during the reproductive phase (Aimi and Fooden, 2005; Wallner et al., 2011).

While female macaques remain in their natal groups and form bonds with their relatives, males disperse from the group upon reaching sexual maturity and thereby losing contact with their relatives (Drickamer and Vessey, 1973). Most male Japanese macaques leave their natal group by the age of 5 years (Sprague et al., 1998), and by emigrating they avoid inbreeding within the group. The adolescent phase in male Japanese macaques lasts several years, until they reach socio-sexual maturity. There are different ways in the literature to define the start of the socio-sexual lifestage. According to Aimi and Fooden (2005), males reach socio-sexual maturity at around 8.5 years of age. Hamada and Yamamoto (2010), however, place the onset of adulthood at approximately 10 years, when physical development is largely completed. Mori and Watanabe (2003) further demonstrated that males continue to gain body weight until they reach the age of 15 years.

The post-reproductive phase of life is determined by the onset of ageing or the end of the reproductive cycle. While no decline in reproductive function can be observed in males with increasing age, a reduction occurs in females at around 25 years of age (Hamada and Yamamoto, 2010).

1.4 Reproduction

The reproductive cycle of Japanese macaques is seasonal, with the animals' sexually active phase extending from autumn into the winter months (Aimi and Fooden, 2005). Female macaques have a promiscuous mating system, meaning that they mate with different males during the reproductive phase. This leads to a high degree of uncertainty regarding the paternity of the young (Manson, 1992).

During the reproductive period, they may engage in short-term sexual relationships known as consortships (Manson, 1997). In addition to copulating several times a day, the two animals also move and eat together. Consortships can last between 1 and 7 days, but can be interrupted at any time and then resume (Huffman, 1992). During the sexually active period, sexually mature females signal their attractiveness to potential partners through visual signals, with the skin on their face, hindquarter and nipples taking on a more intense red colour during the mating phase. Within the social groups in which they live together, males and females form a strict dominance hierarchy (see section 1.5 for further details). It is assumed that there is a positive correlation between rank and reproductive success (Cowlishaw and Dunbar, 1991). However, observations have shown that a higher rank is not automatically associated with greater reproductive success in males (Takahata, 1982). This could be due to the fact that females ultimately decide whether mating takes place, which is referred to as female mate choice (Gartland et al., 2021). Alternative mating strategies employed by low-ranking males can also lead to an increase in their reproductive success (Huffman, 1991). Nevertheless, it has been shown that higher-ranking males tend to be in longer-lasting consortships than lower-ranking animals (Aimi and Fooden, 2005; Huffman, 1992) and the reproductive success declines in high-ranking males with a long tenure in the group (Inoue and Takenaka, 2008). In addition to heterosexual consortships, homosexual consortships can also be observed in Japanese macaques (Vasey, 1995). The main birthing season begins in the spring and extends into summer, with some births also occurring in late summer (Aimi and Fooden, 2005).

1.5 Social system

Japanese macaques live in groups consisting of up to 40.8 ± 28.95 individuals on average (Aimi and Fooden, 2005). However, group sizes can vary, as they depend on the habitat and local resources, and groups that are fed can become significantly larger (Izumiyama et al., 2003). For example, one group in Japan reached a size of more than 1100 animals (Sugiyama and Ohsawa, 1988). According to Thierry et al., 2000, the social style of the genus *Macaca* can be divided into four grades. There are macaque species with an egalitarian dominance style, such as Tonkinese macaques (*Macaca tonkeana*) and Black crested macaques (*Macaca nigra*), in which the steepness of hierarchies is comparatively low. Aggression between group

members is rare and tolerance levels are significantly higher. Japanese macaques, rhesus macaques and long-tailed macaques, on the other hand, have a despotic social style. This is characterised by a high kin bias, with the animals establishing more social relationships with relatives than with unrelated members of the group. This social style is also characterised by very strong dominance hierarchies and a low tolerance threshold. Aggression occurs more frequently and is typically initiated by higher-ranking individuals and directed towards lower-ranking group members (Flack and Waal, 2004; Thierry, 2007; Thierry et al., 2004)

Along the macaque social style gradient, Japanese macaques together with rhesus macaques, are characterised as the most despotic and intolerant species (grade 1; Thierry et al., 2000). They live in multi-male and multi-female groups and the females form matrilines, consisting of related females. Females are the philopatric sex, meaning that they remain in their natal group for life (Gouzoules and Gouzoules, 1987). Within the matrilines, female kin remain in close proximity, support one another and social status is typically maternally inherited under strict rules of hierarchy (Thierry et al., 2004). Females born into one of the higher-ranking families gain a higher rank than females belonging to a lower-ranking family. Within these matrilineages daughters occupy the ranks directly below their mother, with the youngest daughter occupying the next place below the mother (Koyama, 2003). Males are the dispersing sex in Japanese macaques and usually do not remain in their natal groups for life. When spermatogenesis begins at the age of 4-6 years, males start leaving their natal group (Nigi et al., 1980) and from this point on, adolescent males live in solitarily for a certain period of time or join groups consisting of several males, known as bachelor groups (Aimi and Fooden, 2005; Sprague et al., 1998). Factors such as predation or potential aggression from other males determine whether males join bachelor groups or remain solitary (Pusey and Packer, 1987). Males usually join the dominance hierarchy at the bottom when they immigrate into a new group and can attain a higher rank within the group through tenure-length (Cooper et al., 2022). In addition to the integration of a new male into the group, the hierarchy can also change when a higher-ranking male leaves or dies. Group splits can also lead to changes in the hierarchy (Sprague et al., 1998, 2005). Social relationships within the group are another important factor that may influence social status in males. Males can influence their rank by engaging in affiliative behaviour with other members of the group. These connections can have a positive or negative effect on rank positions (Sprague et al., 2005). The relationship between the alpha male and high-ranking females plays a decisive role in maintaining the dominance hierarchy (Gartland et al., 2021; Nakamichi et al., 1995).

1.6 Social relationships

Animals that live together in groups usually have only a few close social relationships with other members of their group (De Moor et al., 2020). According to Hinde (1976) social and affiliative relationships are characterised by the fact that they are structured in terms of time. Social relationships have been documented in many primate species and have been studied particularly well in the genus *Macaca* (Kawazoe, 2021). These interactions can be divided into short-term and long-term relationships. Long-term affiliative relationships between two individuals can be referred to as social bonds. The strongest social bond can be found between a mother and her children (Curley and Keverne, 2005). In general, social relationships with group members can play a key role in the further course of an individual's life and may increase fitness (Amici et al., 2019). For example, strong social relationships can enhance an individuals ability to cope with stressful situations (Young et al., 2014), improve their reproductive success (Schülke et al., 2010) or gain tolerance to food (Tiddi et al., 2011). Overall, this can enhance the longevity of macaques (Silk et al., 2010) or improve the survival chances of their offspring (Silk et al., 2009).

1.6.1 Rearing phase before entering sexual maturation

During the early stages of development, offspring are highly dependent on maternal care and the mother represents their primary social environment. Offspring form their first and closest social relationships within the maternal matriline, where they gain access to social partners through their mother (Hamada & Yamamoto 2010).

However, studies show that mothers care for their offspring differently depending on their sex and terminate the close relationship with their sons more often than with their daughters (Eaton et al., 1986; Nakamichi, 1989).

Grooming by the mother towards her sons also decreases more sharply over the first few months than grooming of her daughters. In contrast, sons are more likely to experience aggressive behavior from their mothers in their first months of life than female offspring. This maternal aggression can lead males to reduce social interactions with maternal family members and initiate the search for other social partners outside the family (Kulik et al., 2016). Another reason for maternal aggression towards male offspring could be that it promotes the independence of males (Bardi and Huffman, 2002) and causes them to separate from their natal group at an early age (Kulik et al., 2016).

While females are the philopatric sex and remain in their natal groups for life (Gouzoules and Gouzoules, 1987), males are the dispersing sex. Upon reaching sexual maturity, they leave their natal groups (Nigi et al., 1980) and lose their social relationships with group members as a result of migration. The males must then establish their social relationships independently

outside the maternal matriline. During this period, adolescent males may form social relationships with both related and unrelated males (Aimi and Fooden, 2005; Sprague et al., 1998).

1.6.2 Social relationships with kin and non-kin

Social relationships in primates occur both among relatives (kin), but also between unrelated individuals (non-kin) and studies show that various macaque species form stronger and more social relationships with kin compared to non-kin (Silk et al., 2006).

This pattern can be explained by the theory of kin selection (Hamilton, 1964), which states that individuals can increase their own fitness not only through reproduction, but also by helping relatives to survive and reproduce. Behaviour that benefits relatives and thus increases the probability of their reproduction allows individuals to pass on their own genes indirectly.

The strength of social relationships is also influenced by sex-specific patterns of dispersal. Stronger social relationships can be observed more frequently among the philopatric sex than among the sex that separates from the natal group. Individuals who remain in their natal groups have more relatives available and therefore more opportunities to form stronger kin-based social relationships (Silk, 2002a). Social relationships can also be observed among males, who are the dispersed sex (Ostner and Schülke, 2014). In macaque species, males are typically the dispersing sex and usually separate from their natal group. As a result, the degree of kinship between males within groups is generally lower, compared to female macaques (Pusey and Packer, 1987). The likelihood of full siblings within the group is particularly rare among macaques because females often mate with multiple males across a reproductive season (Inoue et al., 1990). Despite the low levels of kinship among males, social relationships between unrelated males have been observed. For example, the study by De Moor et al., 2020 showed that Assamese macaques sometimes preferred non-kin males over kin males for coalitions, even though related males were available to form coalitions within the group. Additionally, young males can also be important social partners in the long term, as males usually emigrate together with peers of similar age classes (Widdig et al., 2002). Observations showed that males preferred contact with unrelated males of the same age compared to younger or older males (Nakamichi et al., 1995).

Male–male relationships in non-human primates remain comparatively understudied and existing literature presents mixed findings. Social relationships between males are less commonly observed, because they are usually in constant competition with each other for females that are ready to reproduce (Paul 2002). Therefore, male-male relationships are generally considered rare (Clutton-Brock, 2009), but recent research suggests that male social bonds do occur and can develop into long-term alliances that are important for within-group

competition and social stability (Ostner and Schülke, 2014).It is evident that more factors than kinship, such as dominance rank, play an important role in the formation of social relationships between individuals. High-ranked partners are often preferred and social relationships between males are associated with increased tolerance rather than cooperation (Kawazoe, 2021; Ostner and Schülke, 2014) and these mutual tolerance has also be observed in social relationships between male Japanese macaques (Kawazoe, 2021).

Most studies on social relationships among adolescent male primate species have been conducted on male-philopatric or both-sex philopatric species. There are significantly fewer study results on species in which males disperse and usually leave their natal groups, and thus have fewer relatives available (De Moor et al., 2020). Japanese macaques are a female-philopatric species, with females remaining in their natal group (Aimi and Fooden, 2005; Gouzoules and Gouzoules, 1987) while male Japanese macaques are the dispersing sex (Nigi et al., 1980) and form social relationships with both related and unrelated individuals (Silk et al., 2006). Overall, male-male relationships are considered rare (Paul 2002), but in observed cases, males seem to prefer relationships with related individuals (Silk et al., 2006). In general, the relationships of adolescent males have not been sufficiently researched (Ostner and Schülke, 2014; Paul, 2002) and the results of this work should shed more light on the social relationships of adolescent male Japanese macaques, who are the dispersal sex.

1.6.3 Measures of Social Relationships

In primatology, different affiliative behaviours, such as grooming, proximity and social play, are used to measure social relationships (Amici et al., 2019). Young males show social relationships with other males of the same age, increasingly through social play, which can initiate the first steps towards peripheralisation. During this phase, males separate from their group and increasingly move to the outer areas, accompanied by reduced affiliative interactions and increasing spatial distance from group members (Nakamichi, 1989). It is also assumed that social play can be seen as training for fights in adulthood (Groos, 1898). Social play is a decisive social behaviour, as it can be observed more frequently in male primates in all phases of life than in female primates (Eaton et al., 1986; Nakamichi, 1989). Observations show that social play decreases with age, while other affiliative behaviours, such as social grooming, increase (Shimada and Sueur, 2018). Overall, social grooming is the most frequently observed affiliative behaviour in non-human primates (Goosen, 1987). In addition to hygienic aspects, mutual grooming is also important for social cohesion and serves to strengthen social relationships (Majolo et al., 2005). It also serves to reduce tension (Terry, 1970) and to mediate social relationships after conflicts (Muroyama, 1991). Social grooming can be observed primarily among related individuals, but also occurs between unrelated

individuals (Nakamichi and Shizawa, 2003). More than half of all grooming interactions can be observed between relatives (Nakamichi, 2003). Grooming also plays an important role in the long term, as studies have shown, that individuals who groom each other more frequently also tolerate each other during feeding and accept each other's proximity (Kawazoe, 2021; Ventura et al., 2006). Studies also show that males tolerate the proximity of individuals of the same age, sex and similar dominance rank more than that of younger or older group members (Nakamichi, 1996). The affiliative behaviour of co-feeding also serves to determine social relationships between two individuals. Since food is usually limited, competition for food arises between members of the group. Co-feeding is a good indicator of the acceptance of a partner within a certain radius. Studies show that co-feeding decreases with decreasing kinship (Belisle and Chapais, 2001).

These affiliative behaviours such as grooming, social play, proximity including body contact and co-feeding can be observed and used to evaluate social relationships between individuals (Nakamichi, 1996). In primatology, a common measure to determine the strength of a social relationship between two individuals is the Composite Sociality Index (CSI). This index combines multiple affiliative behaviours (e.g., grooming, proximity, co-feeding, social play) by standardising each dyad's interaction rate relative to the group mean for that behaviour, then averaging across behaviour types. The higher the CSI value, the stronger the relationship of a dyad (Kawazoe, 2021; Silk et al., 2006).

1.7 Aims and questions of the study

The aim of this master's thesis was to improve our understanding of dispersal behavior and the social relationships of adolescent males in a semi-free ranging group of Japanese macaques (*Macaca fuscata*).

Research on this topic in free-ranging macaques is limited because adolescent males leave their natal group upon reaching sexual maturity and do not maintain contact with their family members after separation (Beisner et al., 2011). After leaving their natal group, adolescent males are difficult to track in the wild and behavioural observations are rarely possible due to these circumstances. This study was conducted on adolescent males (N=23, aged between 4.5 and 8 years) of a semi-free-ranging group of Japanese macaques, housed at Affenberg Landskron in Austria. Four males who already reached social maturation (8.5 years) entered the study for additional analyses on group reintegration. The enclosure is a fenced-in area covering several hectares of a natural forest. The enclosure allows the macaques to move freely, to socially interact with group members or retreat to peripheral areas. Under these semi-free conditions, adolescent males may leave the core of the group upon reaching sexual

maturity but are unable to fully disperse (Pflüger et al., 2021), offering an opportunity to study their behavior in semi-natural yet accessible settings.

The following hypotheses were formulated:

H1a) Male Japanese macaques leave their natal groups when they reach sexual maturity (Sprague et al., 1998) and either join bachelor groups or live in solitary during their adolescent phase (Aimi and Fooden, 2005; Sprague et al., 1998). The older an adolescent male is, the more likely he is to loosen ties with female kin, leave his natal group and join males in the same age category. Therefore, it was hypothesized that the older the adolescent males were, the less time they would spend in central areas of the enclosure since the central areas are more occupied by core members of the group.

H1b) Males make different use of central areas dependent on their stage of adolescence. The youngest age group (4.5 years) has not yet fully dispersed from the main group and makes greater use of central areas than older adolescent males. Males who already reached social maturation or are in the final stage of social maturation (≥ 8.5 years) will regain access to the core group and therefore spend more time in central areas compared to younger age groups (adolescent males).

H2) Studies have shown that males are more likely to be in contact with others of the same age (Nakamichi et al., 1995), as they are more likely to leave their group with males of the same age (Widdig et al., 2002). Therefore, it was expected that age difference negatively correlates with co-presence in adolescent males. Co-presence was defined as the mutual presence of individuals within a radius of one to five meters.

H3) Non-human primates prefer to form affiliative relationships with relatives (Silk, 2002a; Silk et al., 2006). It was hypothesized that adolescent males form stronger relationships with kin than with non-kin adolescent males.

The results of this master's thesis provide important insight into a period in a male Japanese macaque’s life that is difficult to observe in the wild. Analysing social relationships among adolescent male Japanese macaques during dispersal from their natal group will enhance our understanding of male life history in this species. The data furthermore contributes to future long-term studies at the Affenberg Research Station (University of Vienna) investigating how male social relationships are linked to their group integration success and future social rank.

2. Material and methods

2.1 Study site Affenberg Landskron

The founding population of 38 Japanese macaques originally came from the wild Minoo-H group in Japan (GPS: 34.6937° 135.50216°) and was relocated to the “Affenberg Landskron”, Carinthia, in 1996. The following year, the park was opened to visitors for the first time (Pflüger et al., 2021, 2019).

Affenberg Landskron is a 4.5-hectare outdoor forest enclosure surrounded by an electric fence, which is additionally protected by acrylic glass at the top. During the study period, the site included diverse vegetation and offered the macaques a number of different trees and bushes for climbing, foraging and hiding. The site could be divided into peripheral and central areas. While the central areas were more freely accessible, the peripheral areas included densely vegetated zones as well as swampy areas (Figure 2).

A small stream run through peripheral areas of the enclosure. In the center an artificial pool was installed in which the monkeys could swim during the summer months. The semi-natural keeping conditions of the Affenberg population allowed the macaques to establish a largely natural social structure within the group. The vegetation within the enclosure offers various food sources such as bark, leaves, insects and herbs. In addition, the animals were fed once a day (outside visitor season) or twice a day (visitor season) with various types of fruit, vegetables and wheat. The daily provisioning (in total 220kg) was distributed throughout the different areas of the enclosure to give all macaques access to food.

The Affenberg Landskron is open to visitors from the beginning of April to the beginning of November. The enclosure is only accessible to visitors as part of a guided tour, guided along a designated footpath, which covers around one-third of the entire enclosure. During these tours, the macaques receive additional food from the tour guide. The macaques are free to move between all areas of their habitat and can withdraw from visitors any time.

At the start of data collection for this study, the Affenberg population comprised a total of 184 macaques (7 infants (< 1 year), 10 juvenile males (< 4.5 years), 19 juvenile females (< 3.5 years), 23 adolescent males (4.5-8 years), 14 adolescent females (3.5-4.5 years), 46 adult (socio-sexually mature) males (≥ 8.5 years) and 65 adult females (≥ 5 years).

The conditions at Affenberg allow the macaques to interact freely with each other and thus build social relationships with members of their group. The study site at Affenberg Landskron offers researchers the opportunity to observe Japanese macaques in semi-free conditions and to better understand their behaviour through non-invasive behavioural observations. For more details on the study site - the habitat, keeping conditions and management of the population - see (Pflüger et al., 2021).

2.2 Study subjects

In this study, data was collected from a total of 27 adolescent male Japanese macaques *(Macaca fuscata)* aged between 4.5 and 8.5 years (6.5± 1.3 years, mean ± SD) (Table 1). Although Japanese macaque males are considered as adult (sexually and socially mature) by an age of 8.5 years (Aimi and Fooden, 2005), literature suggests that these age boundaries are fluid, with some literature arguing that many factors affect the sexual development and some males reach social maturity one or two years later (Rostal and Eaton, 1983). The main analyses of this study focused on males below 8.5 years to ensure a conservative approach (N=23). Four additional focal males were included who had just reached the age of 8.5 years at the start of data collection. These males (hereinafter "socio-sexually mature males") were included in the analysis regarding center use in different age classes (H1b). These males are furthermore part of a long-term data set on male social development in the Affenberg population. The behavioural data of these animals collected during the present study will therefore enable a comparison with already existing and future data sets.

A two-week training was carried out at the start of the data collection period to ensure reliable behavioural data collection as well as the identification of focal animals. Each macaque could be identified by the face, body structure and unique characteristics. The adolescent males observed in this study are listed in Table 1. The four Japanese macaques who have reached socio-sexual maturity at the beginning of the study period are highlighted in grey.

Table 1: *Overview of the 27 focal males, sorted by age group. Socio-sexually mature males (N=4) are highlighted in grey.*

Name	***Age***	***Name***	***Age***
James	*8.8*	*Johann*	*6.6*
Bud	*8.8*	*Tokio*	*5.9*
Hulk	*8.7*	*Edo*	*5.8*
Wolverine	*8.7*	*Kyoto*	*5.8*
Albert	*7.7*	*Fujimino*	*5.8*
Charles	*7.7*	*Hokkaido*	*5.7*
Nikola	*7.7*	*Nagano*	*5.7*
Mark	*6.8*	*Mito*	*5.7*
Terry	*6.8*	*Arthur*	*4.8*
Tolstoi	*6.8*	*Drosselbart*	*4.8*
Umberto	*6.8*	*Rumpelstilzchen*	*4.7*
Ernest	*6.8*	*Hans*	*4.6*
Edgar	*6.7*	*Frosch*	*4.5*
Erich	*6.7*		

2.3 Relatedness between focal males

Relatedness was assessed for all focal males, including the oldest age group. Data records on the mother and matriline affiliation of each male was provided by the Affenberg Research Station. Maternal relatedness between males was assessed with the coefficient of relatedness (r). This index indicates the probability that two individuals share identical genes due to common ancestry (Widdig, 2022). The closer the relatedness, the greater the coefficient of relatedness (r). Sewall Wright (1922) described the formula for calculating the coefficient of relatedness: $r = \Sigma (0.5)^{L}$.

While L indicates how many generations separate the two individuals, the summation (Σ) describes how many common ancestors they have. This calculation is based on the assumption that a meiotic process occurs in each generation, whereby the probability of passing on a specific allele to offspring is 0.5 in each case (Widdig, 2022).

It could be possible that some of the focal animals had the same father. Due to the lack of paternity records, however, no information on paternal relationships were available. The kinship coefficient was therefore solely based on the maternal data and only maternal brothers could be identified. In this case Σ equals one.

2.4 Research Zones

The enclosure at Affenberg Landskron could be divided into central (C) and peripheral (P) areas (see Figure 2). Compared to the peripheral regions, the central areas were less densely vegetated and more accessible. By distributing the food across the different areas inside the enclosure, all macaques had access to the food provisioning, including those who spent most of the time in peripheral areas. Areas of the enclosure could be further divided into sub-regions. Zone 0C formed the centre of the entire enclosure, surrounded by the visitor path. The visitor path started at the main entrance and run through zones 1C to 5C. Another path run alongside the outer fence, providing access to the outer regions of the enclosure. This path was not accessible to visitors. Zone 4C of the enclosure contained the monkey hospital and the pool.

In 2020 an internal fence was installed separating 6C new enclosure, 6P, 7P and 8P from the rest of the enclosure. Since its installation, the fence comprised several passages, allowing the macaques to move freely through the fence and between the different regions. The separation was built after a temporary group fission in 2020 and kept intact in case of a reoccurring group splits event. It is of note that the group fused back to a coherent group in the same year and remained coherent throughout the data collection period of the present study. On 15 January 2025, the original enclosure was enlarged by adding 0.5 hectares of land to the existing area (zone 8P). This region, located farthest from the centre, offered the monkeys high trees and dense bushes for foraging and hiding.

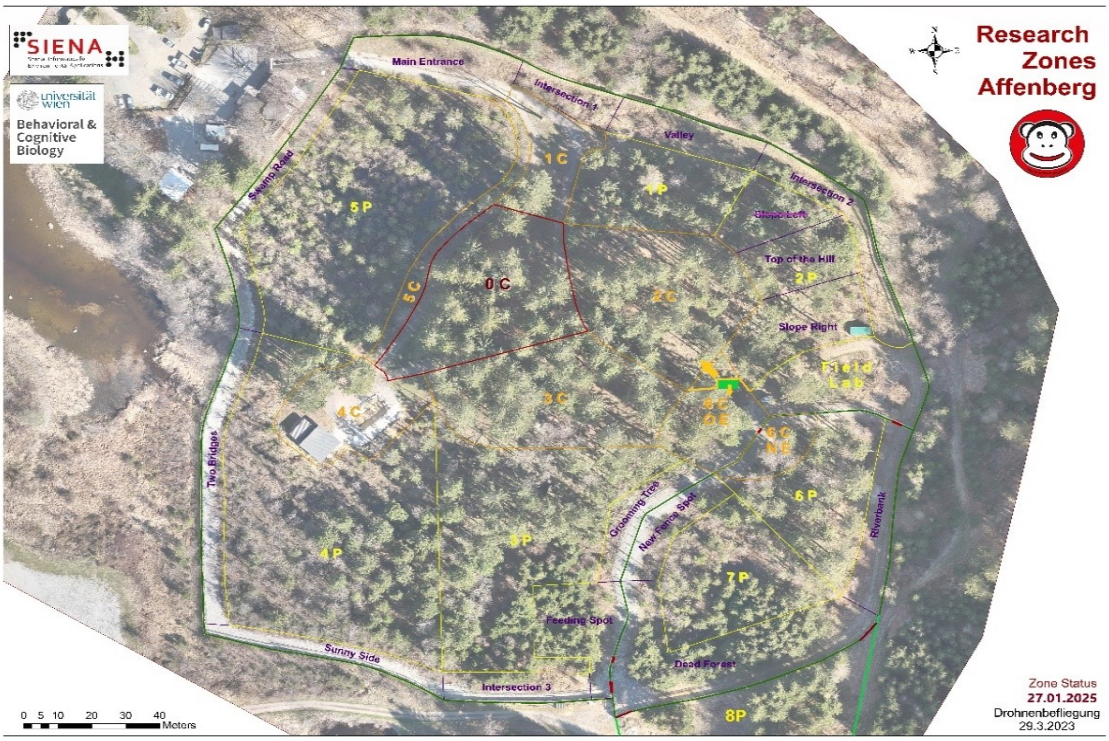

Figure 2: *Research Zones Affenberg, status on 27 January 2025.*

2.5 Data collection

The Affenberg team provided two weeks of training before data collection began. During this time the distinction between different areas inside the enclosure was trained (Figure 2), next to monkey ID and ethogram training. Data collection took place between 3 February and 1 May 2025. Data was collected from Monday to Thursday, between 9:00 a.m. and 4:00 p.m. At the start of data collection, the monkeys were fed once a day (10:00 a.m.). On 29 March, the park opened to visitors and the monkeys were fed twice a day (9:00 a.m and 06:00 p.m.). No data collection was conducted during feeding times.

Behaviours were recorded according to the general ethogram of the Affenberg Research Station (Appendix). Behaviours were classified as durational movement (DM), durational behaviour (DB) or event behaviour (EB). The ten-second rule was applied during data collection: if a DM or DB was interrupted for less than ten seconds, it was classified as the same bout. After a longer interruption of more than ten seconds, a new bout was noted.

Focal animal sampling (Bateson and Martin, 2021) was used as the observation method and the data was recorded continuously for 20 minutes. Scan sampling (Bateson and Martin, 2021) was used at the beginning and end of each focal sampling and at five-minute intervals throughout the 20 min focal sampling. During these instantaneous scans, the number of monkeys within a radius of zero, one, three, or five metres of the focal animal was recorded.

Animals within a radius of zero metres were in body contact with the focus animal. If a focus animal was lost within a 20 min observation phase, the 20-min observation was continued if the animal could be found again within three hours. Otherwise, the observation was closed and a new 20-min observation started if the animal was back in sight.
To determine the areas used by the adolescent males, their location was noted at the start of each observation interval. Any transition between different areas during the observation was noted as well. The observation sheet is given in the appendix (Table A1). Across the entire observation period, each focal animal was observed for a minimum of 295 minutes to a maximum of 336 minutes (mean ± SD = 309 ± 10 minutes).

2.6 Special circumstances during data collection

Three macaques (adult female, adult female, adult male) from the group died during data collection. One of the deceased animals was the alpha female, Jessy. She passed away on 24 February 2025. Her death probably affected the female hierarchy within the group during data collection. Jessy was the mother of three adolescent males who were observed in this study. Since the social relationships between adolescent males and their mothers were not observed and analysed in this study, these three focus animals were not removed from the data analysis.

2.7 Data analysis

The data collected from the observation sheets was entered into an Excel (Version 2507 Build 19029.20184) worksheet. All the recorded data was statistically evaluated using RStudio version 4.5.0 (R Core Team, 2023). The *readxl* package (Wickham and Bryan, 2015) was used to import the data and the *writexl* package (Ooms, 2017) to export it to Excel. The *tidyverse* package (Wickham et al., 2019) was used for data transformation functions and *hms* (Müller, 2016) was used for time specification. The graphical representation of the evaluated data was created in Excel.

Center use and age in adolescent males

To investigate whether adolescent males (N=23) reduce their time spent in central areas by age, the proportion of center use of each of the focal animals was determined. This was accomplished by dividing the sum of minutes, the focus animal spent in central areas, by the total observation minutes of the animal. The exact age of each focal animal (Table 1) was determined using the following formula: (observation start date – birth date) / 365.25. The centre use ratio (proportion of scans in which an individual was in the centre) was converted

into percentage values. To do this, the original proportion was multiplied by 100 so that all values are reported as percentages (% of observation time in the centre).

For the variables “center use” and “age” the Shapiro-Wilk test showed a normal distribution of the residence values. However, due to the small sample size (N=23), Spearmans rank correlation was used for the statistical analysis to obtain more robust, non-parametric estimates.

Center use of different age classes in adolescent and socio-sexually mature males

To assess whether males in different life stages differ in area use and whether the oldest age group (> 8.5 years; socio-sexually mature males) tends to migrate back into the group (central areas of the enclosure) a group-wise comparison was conducted. Therefore, all focus animals (N=27) were divided into three life stages (age categories). Males who just recently reached the adolescent age of 4.5 - 4.8 years were assigned to phase 1 (start of sexually maturity, N=5). The second phase included all adolescent males aged 5.7 – 7.7 years (sexually mature, N=18). The third phase of the adolescent age category included all males above 8.5 years of age (socio-sexually mature, N=4). In order to compare whether these adolescent phases have different proportions of center use, the mean value of all males within an age category was calculated and presented descriptively. Differences in center use across life stages were analysed using a Kruskal-Wallis test due to small and unequal group sizes.

Age difference and co-presence in adolescent males

In order to determine whether males with smaller age differences are more likely to be in close proximity to each other than those with larger age differences, all possible pairing combinations of the adolescent focal animals (N=23) were considered. During the scan sampling it was noted when two individuals were within each other's radius (in body contact or within 1m, 3m or 5m). To determine the co-presence of the respective dyads, the frequencies a dyad was observed in proximity (in body contact, within 1m, 3m or 5m) were summarized. Subsequently, this proximity score was divided by the sum of scans of the two animals, to control for the observation effort per individual involved in a dyad. The exact age difference (days) between the respective adolescent males was also determined for each possible dyad.

A binomial dyadic mixed model (GLMM) was fitted using the R package lme4 for statistical analysis (Bates et al., 2015). The R package DHARMa (Harting, 2022) was used to verify the results, and due to the high number of zero values within the dyads, the inflation zero-inflated model (Brooks et al., 2017).

Relationships within kin and non-kin adolescent males

To determine the affiliative relationships between adolescent males, the Composite Index of Sociality (CIS) (Silk et al., 2006) was used. The behaviours grooming, social play, proximity (1, 3, 5 metres), body contact and co-feeding for every possible dyad were included. Body contact includes 'huddle' as well as 'embrace'.

The Composite index of sociality was computed for each dyad as follows:

$$CIS = \frac{\frac{Pp}{Ap} + \frac{Pg}{Ag} + \frac{Pc}{Ac} + \frac{Pb}{Ab} + \frac{Ppl}{Apl}}{5}$$

P is the duration of the respective behaviour shared between two individuals divided by the sum of the observation time of the two individuals. For example, Pp is the rate of proximity per dyad (g: groom, c: cofeed, b: body contact, pl: play). A is the mean rate of the respective behaviour across all possible dyads. Since five behaviours were included in the calculation for the CSI, the sum was then divided by five. High CIS values represent strong social relationships, while lower values indicate weaker social relationships between individuals. Hence, the higher the index value, the stronger the social relationship between two males (Silk et al., 2006).

To determine whether affiliative relationships (CSI) increased with genetic relatedness between dyad members, a linear mixed-effects model was fitted using lme4 package in R (Bates et al., 2015). As the data set consisted of dyadic observations in which the focus individuals appeared in several dyads, the observations were not statistically independent. To account for repeated measurements, the focus identity (partner.1) was included as a random intersection. Genetic relatedness was entered as a continuous fixed effect predictor: CSI ~ coeff_relat + (1 | Partner.1)

3. Results

3.1 Relatedness between focal males

Some males were maternally related to each other, while others had no maternal-male-relative in the group of focal males. For illustrative purposes the coefficients of relatedness between the focal males are shown in Figure 1 in different colours. The highest coefficient of relatedness was between half-brothers (maternal brothers), at 0.25 (pink), while the lowest coefficient between two males was 0.0039 (yellow). Out of the 27 focal animals, 18 males had at least one half-brother. Seven focal animals had at least one male relative in the focal animal group. One focal animal, Hans, had no male relatives in the investigated group of adolescent males.

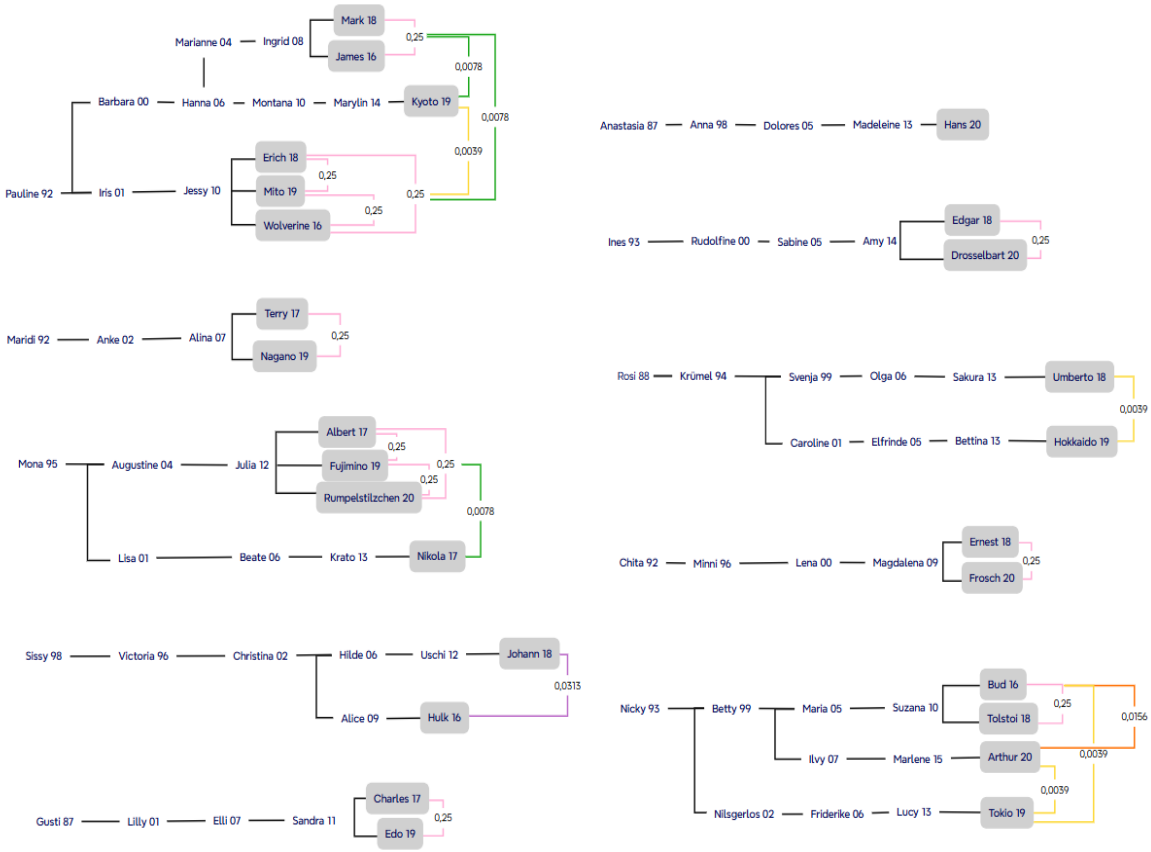

Figure 2: *Coefficients of relatedness between adolescent males. The focal animals (N = 27) are highlighted in grey. The different kinship coefficients (r) are shown in different colours. Pink: r = 0.25; purple: r = 0.0313; orange: r = 0.0156; r = green: 0.0078; r = yellow: 0.0039.*

3.2 Age and center use of adolescent males

The time spent in the center varied across and within all observed age groups of adolescent males (Figure 3). Overall, most males spent between 40 and 75 per cent of the time in the center of the enclosure across all observations. One focus animal aged 6.7 years (Ernest) spent less time in the center than the other adolescent males of the group. He was only found in the center of the enclosure 17% of the time. The longest time spent in the center was observed by the adolescent male Edo. Overall, he spent over 80% of the observed time in the central zones. The youngest male in the observation group, Hans, spent 48% of the time in the center, and the oldest adolescent male, Albert, spent 67% of the time in the central areas. A Spearman rank correlation showed no association between age and center use ($\rho = -0.11$, $p = .60$, $N = 23$).

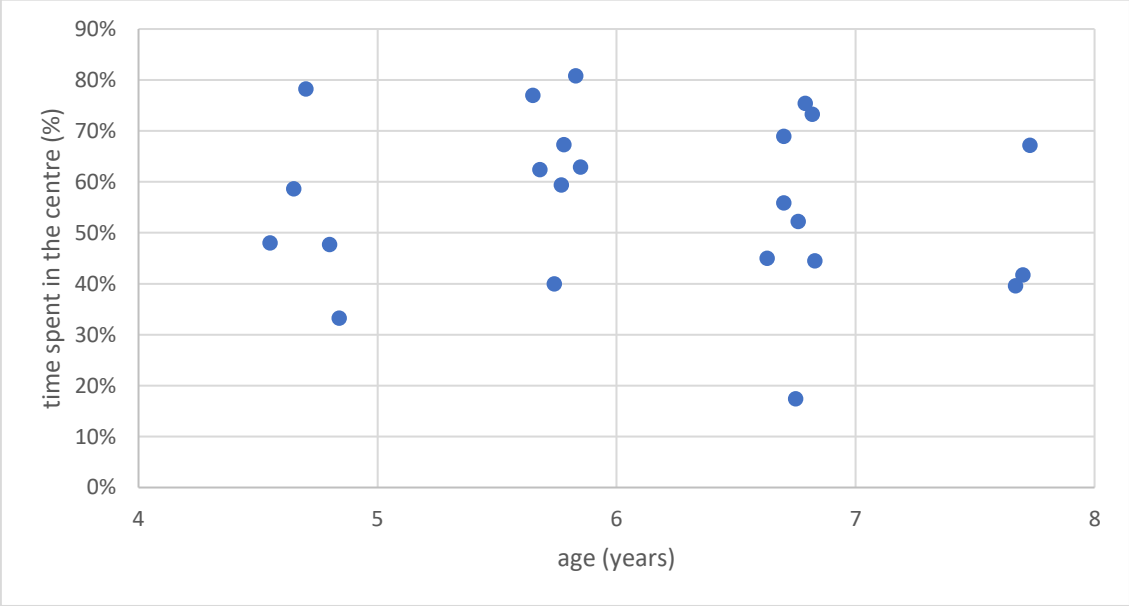

Figure 3: Correlation between age (in decimal years) and time spent at the centre (%) of the 23 adolescent males**.**

3.3 Center use across different life stages in adolescent and socially mature males

Overall, all 27 focal animals spent an average of 57% of the time in the centre of the enclosure. Males that had just reached sexual maturity (4.5 – 4.8 years, N=5) spent an average of 53% (± 15 % SD) of all observations in the centre of the enclosure. Sexually mature males (5.7 - 7.7 years, N=18) spent 57% (± 16 % SD) of the observed time in the centre and the socio-sexually mature males (>8.5 years, N=4) spent an average of 61% (± 6 % SD) of the time in the centre (Figure 4). Sexually mature males show the greatest variation in values, while socio-sexually mature males show the least variation in residence values Figure 4).

Center use did not differ significantly across life stages (Kruskal–Wallis test: $\chi^2 = 0.56$, df = 2, p = 0.755; Figure. 4).

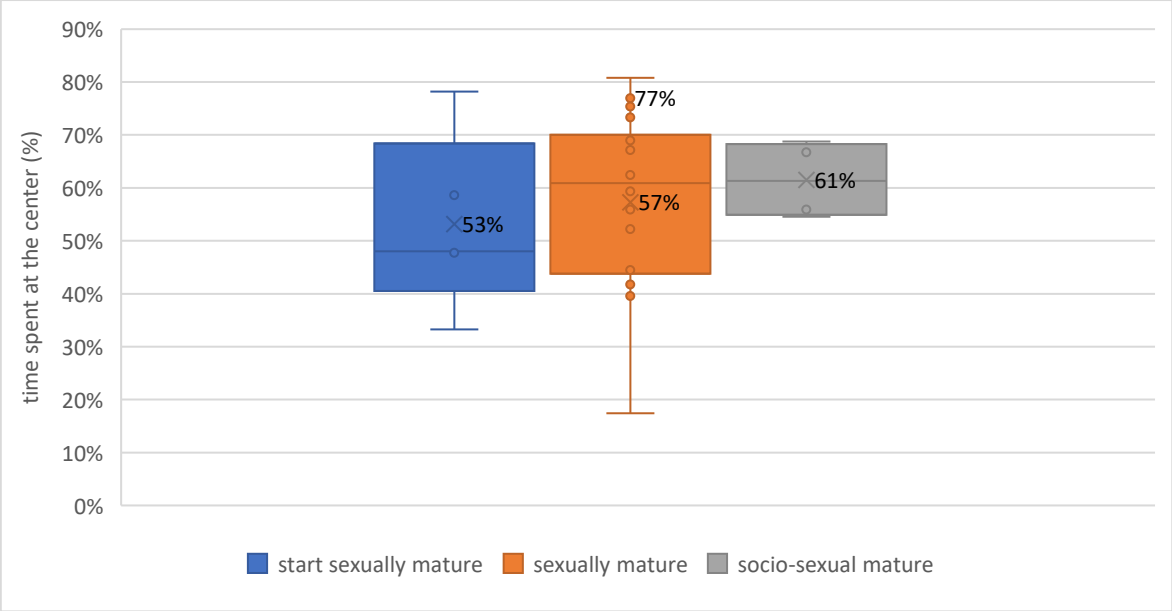

Figure 4: Time spent in central areas (%) per age group. Start sexually mature (N=5); sexually mature (N= 18); socio-sexually mature (N= 4).

3.4 Age difference and co-presence in adolescent males

The relation between age difference and co-presence was assessed in adolescent males (N=23). Within all age difference categories (0-3 years), the median value for copresence was zero and only a slight variation could be observed within the categories. The highest variation was observed for an age difference of one year (SD = ± 0.031) and the lowest variation for an age difference of 3 years (SD = ± 0.006). The influence of the age difference between adolescent males on mutual co-presence within the observed dyads was examined using a binomial dyadic mixed model. The statistical results showed no significant effect between age difference and the probability of co-presence between the individuals (β = 0,16 ± 0,11 SE, z = 1,49, p = 0,136, Figure 5).

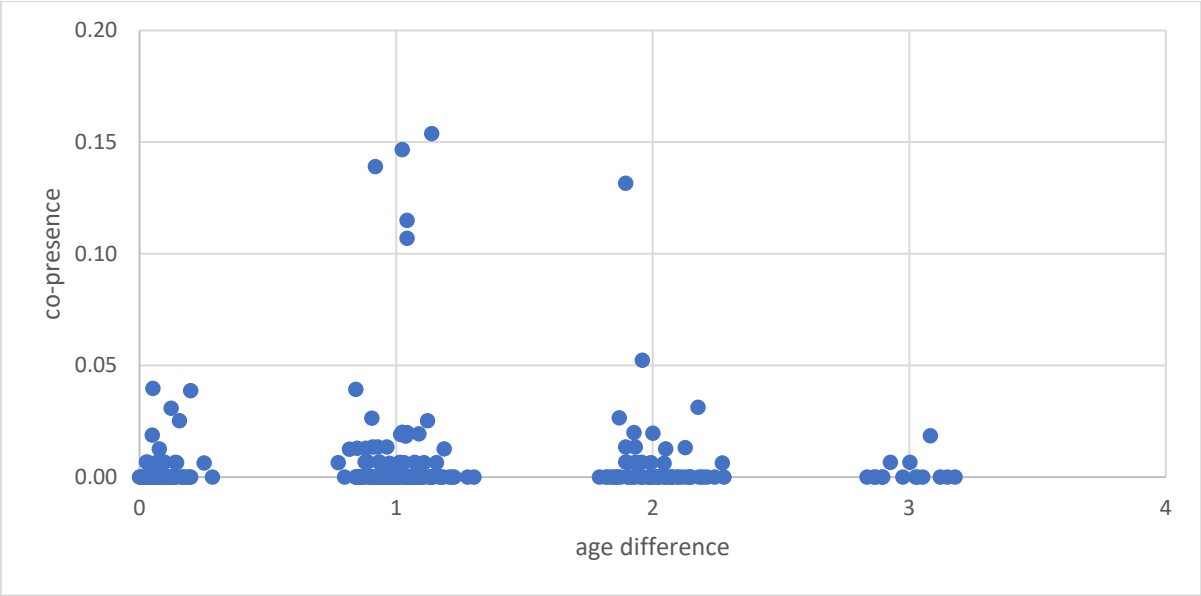

Figure 5: Age difference (in years) and the co-presence of all possible dyads between the 23 adolescent males.

3.5 Kin and non-kin relationships between adolescent males

The strengths of social relationships between related and unrelated adolescent males (N=23) were assessed and compared.

The distribution of CSI values across all dyads of related and unrelated adolescent males was right-skewed, with most dyads showing low or no affiliative interactions. Only 25 out of 248 dyads exceeded a CSI value of 1.51, which represents the top 10% of all CSI values and therefore indicates relatively strong affiliative relationships.

Due to the strong right-skewed distribution of the CSI values of related and unrelated adolescent males, the values were normalized in a logarithmic scale for illustrational purposes (Figure 6).

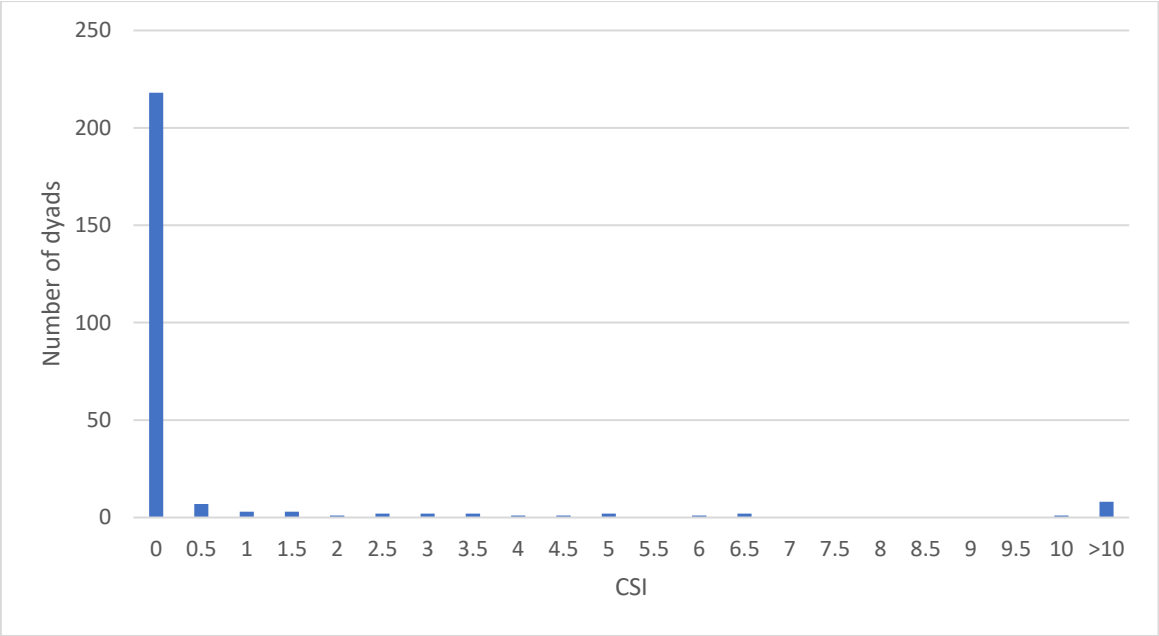

Figure 6: Distribution of Composite Sociality Index (CSI) values of all related and unrelated adolescent males (N=23). CSI values are plotted on x axis and number of dyads (log scale) are plotted on y axis.

Overall, the results show a greater variation in CSI values of related males. A particularly high CSI value (53.77) was found between two half-brothers (r=0.25), Terry (6.82 years) and Nagano (5.68 years). For most brothers (7 out of 8) CSI values were above zero, only one half-brother dyads (Charles-Edo) had CSI values of zero.

A high CSI value of 48.61 was found between Erich (6.70 years) and Kyoto (5.78 years), who shared only a low degree of kinship (r=0.0039).

Some outliers were also found among unrelated dyads. The strongest CSI value (36.02) between unrelated males was observed between the adolescent males Drosselbart (4.80 years) and Rumpelstilzchen (4.65 years). The CSI values of the dyads between Nagano and Rumpelstilzchen (34.88) and Nikola (7.67 years) and Johann (6.63 years) (10.41) were also above the CSI mean value for unrelated males.

Statistical analyses also show that the CSI increases with increasing genetic relatedness. The random intersection for focal identity showed significant variation between individuals (SD = 1.68), while the greatest variability occurred within individuals (residual SD = 5.60), as would be expected for behavioral data.

Overall, the CSI increased significantly with relatedness ($\beta = 47.96$, $t = 5.88$), indicating that more closely related dyads exhibited stronger social relationships.

4. Discussion

The present thesis investigated spatial positioning and social relationships between semi-free ranging adolescent male Japanese macaques in the context of sex-specific dispersal. Since male macaques leave their natal groups upon reaching sexual maturity (Sprague et al., 1998) and join bachelor groups or live solitary in peripheral areas (Aimi and Fooden, 2005; Sprague et al., 1998), we expected age-related differences in spatial positioning within the enclosure. Contrary to this expectation, no association between the age and centre use was detected. The adolescent males could be observed equally in the central and peripheral areas. This shows that their distribution within the enclosure was not dependent on age alone. The conditions of captivity (Hosey, 2005) could be a factor in adolescent males not being able to leave their natal group completely and even if they migrated to peripheral areas, they would remain in their natal group. This could reduce the migration of adolescent males to the peripheral regions of the enclosure compared to adolescent males in the wild, as it has also been observed in other macaque species that the dispersal dynamics between captive and wild groups differ (Beisner et al., 2011; Maestripieri and Hoffman, 2012).

It was also assumed that younger adolescent males (4.5 years), spend more time in the central regions than older adolescent males and socio-sexually mature males (8.5 years) had rejoined the group and could therefore be observed more in the centre than the younger age groups. However, these age-related differences could not be demonstrated. This could be due to the fact that age is not the only factor influencing the spatial behaviour of males.

Rather, it can be assumed that other factors, such as existing social relationships within the group, can influence the spatial behavior of males (Naud et al., 2016). The provision of food for Japanese macaques living in captivity can also influence their spatial distribution, as the regions where food is provided become more attractive to the macaques (Hosey, 2005). Taken together, these results suggest that the spatial integration of male adolescents is more complex than can be predicted based solely on age.

As males increasingly interact with same-age males (Nakamichi et al., 1995) and tend to leave their natal groups together (Widdig et al., 2002), it was hypothesised that age differences between males would be negatively correlated with co-presence. However, this assumption could not be confirmed. Within this study, no significant correlation was found between the age difference of the adolescent males (N=23) and their co-presence within a radius of one to five metres. It should be noted that no direct social interactions were observed in the analysis; only spatial proximity was measured. Spatial proximity is an important indicator of social relationships and in intolerant macaque species such as Japanese macaques, can be an expression of social tolerance and affiliative behaviour (Hinde, 1976; Silk et al., 2006; Cheney and Seyfarth, 2007). However, spatial proximity alone does not necessarily imply that active

social interactions are occurring between individuals. Rather, it is an indicator that the individuals tolerate one another in close proximity and use the same spatial areas of the territory (Hinde, 1976; Cheney and Seyfarth, 2007). For this reason, co-presence can be interpreted as a potential indication of social relationships, which only, in combination with other affiliative behaviours – such as grooming or social play – allows for a more accurate assessment of the social relationships between individuals (Silk et al., 2006). As no age effect could be detected, the results suggest that adolescent males do not primarily choose their spatial proximity to other individuals on the basis of age similarity. One possible explanation could be the semi-free conditions in which the macaques are housed, as environmental conditions can influence the pattern of spatial associations between individuals (Hosey, 2005). In natural populations, adolescent males typically leave their natal group and frequently interact with individuals of the same age during this phase (Widdig et al., 2002). Under semi-free conditions, however, complete dispersal is not possible, so the males remain part of the same social group, even if they temporarily stay in peripheral areas. This distinguishes the social context from that of wild populations, which in turn can influence the patterns of spatial associations between individuals (Beisner et al., 2011; Maestripieri and Hoffman, 2012). It is also possible that close relationships between adolescent males are influenced by factors other than age similarity. For example, individual differences in developmental progress may play a role. The timing of separation from the maternal line can vary greatly during adolescence (Pusey and Packer, 1987), which may result in differences in spatial and social associations that are not strictly age-dependent (Hinde, 1976; Nakamichi, 1996). Furthermore, individual preferences, kinship relationships or pre-existing social bonds could also influence proximity behaviour. Instead of age, individual relationships or social tolerance between specific dyads might thus play a greater role in shaping spatial proximity (Hinde, 1976; Nakamichi, 1996; Ostner and Schülke, 2014; De Moor et al., 2020).

Finally, methodological aspects should also be taken into account. The proximity data in this study are based on five-minute scan samples, which limits the time resolution of spatial associations between individuals. Future studies could therefore benefit from longer observation periods or more detailed social network analyses to gain a more comprehensive understanding of proximity relationships and social interactions among adolescent males.

In addition to these methodological considerations, the structure of the dataset should also be taken into account when interpreting the results.The verification of the dyadic analysis using DHARMa showed no abnormalities in terms of outliers, but a significant zero inflation was detected. Attempts to account for these zero values using a zero-inflated model (glmmTMB) led, however, to convergence problems and unstable model estimates. The binomial dyadic mixed model was therefore retained, as it allowed for a stable and interpretable analysis. The high number of zero values in the data can be attributed to the fact that many dyads could

never be observed in proximity during the observation period. This may indicate different uses of individual space, but could also be due to methodological factors. Within this thesis, a relatively large number of males were observed, which reduced the observation time for each individual. In follow-up studies, increasing the observation time per animal could help to document missing proximal overlaps.

Taken together, the results of this thesis show that age similarities are not the only factor influencing spatial proximity between adolescent male Japanese macaques under semi-free conditions. Rather, the proximity patterns may be shaped by the interaction of various factors, including environmental structure (Hosey, 2005; Beisner et al., 2011) and individual developmental stage (Pusey and Packer, 1987). In addition, kinship may play an important role in shaping social relationships among individuals (Hinde, 1976; De Moor et al., 2020). Regarding the latter previous studied showed that related individuals often maintain stronger social bonds than unrelated group members (Ostner and Schülke, 2014; De Moor et al., 2020). Therefore, the next step was to investigate whether genetic relatedness influences the formation of social relationships among adolescent males.

The results show that the majority of dyads showed low or no affiliative interactions, while only a few dyads had relatively high CSI values. The CSI combines several affiliative behaviours, such as grooming, proximity or social play, to quantify the strength of social relationships between two individuals (Silk et al., 2006). This right-skewed distribution can often be observed in social structures among primates, as there are only a few strong bonds between individuals and the majority of group members interact only weakly with each other (Hinde, 1976; Silk et al., 2006). In line with the hypothesis, the strength of social relationships increased significantly with increasing kinship. On average, more closely related dyads show higher CSI values than less related or unrelated dyads. This is consistent with the theory of kin selection (Hamilton, 1964). Since most half-brother dyads had CSI values above zero, it is clear that even during adolescence, kinship-based relationships are maintained. However, a high variation in CSI values can also be observed among related males. This suggests that kinship alone does not guarantee social relationships. High CSI values were also observed between unrelated males. This shows that social relationships are not exclusively kin-based (De Moor et al., 2020; Ostner and Schülke, 2014) and that other factors, such as the previously investigated age proximity, developmental stages (Nakamichi et al., 1995; Widdig et al., 2002) or individual preferences (Hinde, 1976; Silk et al., 2006) may also contribute to the establishment of social relationships. Individual differences play a key role in the formation of social relationships (Hinde, 1976; Ostner and Schülke, 2014). Such differences can be attributed to personality, social integration or individual developmental trajectories (Snyder-Mackler et al., 2020), among other things and demonstrate the complexity of social relationships.

Overall, the results show that kinship is an important factor in the formation of social affiliative relationships among adolescent male Japanese macaques. However, this thesis also shows that unrelated social relationships cannot be excluded during the adolescent phase of life.

5. Summary of result and outlook

This thesis highlights the complexity of social relationships between adolescent male Japanese macaques and shows that kinship also plays an important role in the formation of social affiliative relationships among the dispersing sex. The central findings of this study are that the strength of social affiliative relationships increased significantly with increasing kinship, but that social relationships could also be observed between unrelated individuals. It was furthermore demonstrated that overlapping area use inside the enclosure and preferences for proximity between two individuals cannot be attributed to age alone.

Contrary to the hypothesis, adolescent males were not observed more frequently in peripheral areas of the enclosure, but were equally distributed across all regions of the enclosure. This refuted the assumption that older adolescent males use peripheral areas more frequently or that males return to central areas at the start of their social maturation. This could be due to the fact that complete migration from the natal group is not possible under semi-free conditions. In addition, the uniform availability of food in all areas of the enclosure could contribute to the males spreading out evenly across the terrain.

Future studies should not only consider the spatial distribution of males, but also incorporate social network analyses. This would make it possible to determine how well adolescent males are integrated into the existing group and what position they occupy within the structure. These analyses would help to see whether males occupy a marginal position during adolescence or already play a central role within the group in semi-free conditions.

Furthermore, no correlation was found between the age of the males and their mutual co-presence. The hypothesis that age differences correlate negatively with co-presence was thus also refuted. The lack of correlation between age and co-presence shows that spatial proximity does not necessarily reflect age-based social preferences. Rather, spatial distribution patterns during adolescence appear to be influenced by an interplay of developmental dynamics, environmental structure, social factors and the preference for kin.

The analysis of social relationships showed that adolescent males were significantly more likely to form stronger social bonds with related adolescent males. The strength of social relationships increased with increasing relatedness. At the same time, however, social relationships between unrelated males were also found, suggesting that social bonds are not based exclusively on kinship.

Several limitations of the study must be taken into account when interpreting the results. The main analyses were based on a comparatively small sample of adolescent males (N = 23), which may limit the statistical power. In addition, the conditions of semi-free keeping at Affenberg Landskron influence the transferability of the results to wild populations, as natural dispersal processes cannot be fully represented. Furthermore, the statistical analysis of dyadic data was limited by a high number of zero values, as many dyads were not observed together during the observation period. Increasing the amount of observation per individual and extending observation periods could help to make more differentiated statements about proximal and dyadic behaviour patterns.

Despite these limitations, the present study provides valuable insights into the social relationships of adolescent male Japanese macaques under semi-free conditions and the results form an important basis for future long-term studies.

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7. Appendix

7.1 Observation table

Table A1: *Observation table. T=timestamp; DM= Durational movement; DB= Durational behaviour; Dur.=Duration; EB= Event behaviour*

Focal: ____________________ Weather: __________________

Date: _____________________ Time: _____________________

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7.2 Ethogram

General application

This is the general ethogram used at the Affenberg Research Station 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 & DB) 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

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).

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.

Face to face (EB): Focal pushes its own face close to another individual's face. 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.

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

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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7.3 Table of main and sub areas

Table A2: *Main and sub areas of the enclosure.*

Main area	***Sub areas***		
Main entrance			
1c			
1p	*Intersection 1*	*Valley*	
2c			
2p	*Intersection 2*	*Top of the hill*	*Slope right*
3c			
3p	*Intersection 3*	*Grooming tree*	*Feeding spot*
4c			
4p	*Sunny side*	*Two bridges*	
5c			
5p	*Swamp road*		
6c	*Old enclosure*	*New enclosure*	
6p	*Riverbank*		
7p	*New fence*	*Dead forest*	
8p			
Field lab			